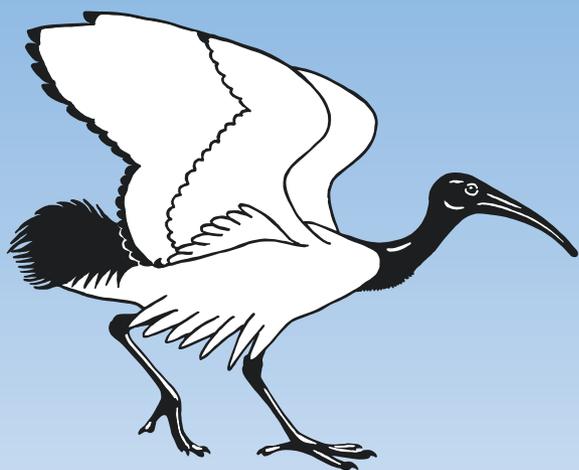


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Bulletin of the BRITISH ORNITHOLOGISTS' CLUB

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CLUB ANNOUNCEMENTS

In November this year the Club will hold its 1,000th evening meeting since its inauguration on 5 October 1892. To celebrate this significant milestone, we are delighted to announce that, in conjunction with the Linnean Society, the Club will be holding two evening talks at the Linnean Society's premises at Burlington House, Piccadilly. On Friday 5 June, Prof. Jared Diamond, Univ. of California at Los Angeles, and a Club member since 2003, will be asking 'What's so special about New Guinea birds?', and on Monday 16 November Dr Jon Fjeldså, Univ. of Copenhagen, will present an overview of the current state of avian systematics and the challenges that remain. As usual, both talks will be free, but advance booking will be required. Full details, including times and booking arrangements, will be posted on the Linnean Society's and the Club's websites, so do check there if interested.

FORTHCOMING MEETINGS

See also BOC website: <http://www.boc-online.org>

BOC MEETINGS are open to **all**, not just BOC members, **and are free**.

Evening meetings are in an **upstairs room at The Barley Mow, 104 Horseferry Road, Westminster, London SW1P 2EE**. The nearest Tube stations are Victoria and St James's Park; and the 507 bus, which runs from Victoria to Waterloo, stops nearby. For maps, see http://www.markettaverns.co.uk/the_barley_mow.html or ask the Chairman for directions.

The cash bar opens at **6.00 pm** and those who wish to eat after the meeting can place an order. **Talks start at 6.30 pm** and, with questions, last c.1 hour.

Monday 23 March 2020—6.30 pm—Beth Okamura—*How birds shape freshwater biodiversity.*

Abstract.—Ever wondered how volcanic islands, garden ponds and gravel pits develop a rich biota? Or why rowan trees grow near pines? The answers in part involve patterns of bird visitations. Darwin appreciated that avian activities might help to explain the widespread distributions of taxa that live in disjunct habitats. This conundrum famously led him to examine the attachment and survival of recently hatched snails on ducks' feet. This talk will consider how our understanding of dispersal of freshwater invertebrates has improved since Darwin's era. I will particularly focus on evidence for waterbird-mediated dispersal of freshwater animals that are poorly known but that have substantial ecological and practical impacts—colonial invertebrates called bryozoans (or 'moss animals') and their myxozoan parasites ('slime animals'). I will illustrate how these unappealingly-named animals serve as 'model systems' that demonstrate the profound effect of waterbird movements on the development and dynamics of freshwater communities, and consequent impacts on water supply and emerging fish diseases.

Biography.—Beth Okamura is a Merit Researcher at the Natural History Museum, London. Prior to this she held positions at the Univ. of Oxford and Bristol, before becoming a Prof. in Aquatic Biology at the Univ. of Reading. Her Ph.D. from the Univ. of California, Berkeley, focused on the ecology and evolution of marine invertebrates, but her move to Oxford led to her long-term interests in how animals that live in isolated lakes and ponds manage to disperse and persist across the landscape. She has particular interests in the role of waterbirds as vectors of dispersal—a question that she is now beginning to address in new ways by analysing DNA contained in faeces of ducks, geese and godwits (*Limosa* spp.).

Friday 5 June—Prof. Jared Diamond—*What's so special about New Guinea birds?* Full details of this special joint evening meeting at the Linnean Society, Burlington House, Piccadilly, London, will be announced shortly.

Abstract.—The tropical island of New Guinea has long played a pre-eminent role in ornithology, which caused it to be chosen as the site for the BOU's Jubilee Expedition in 1909. Part of the reason is New Guinea's

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

Biography.—Jared Diamond is Professor of Geography at the University of California (Los Angeles). He divides his professional life between teaching geography to undergraduate students; field research on the birds of New Guinea and other south-west Pacific islands; writing books about human societies, aimed at the general public; and promoting sustainable environmental policies, as a director of the World Wildlife Fund and Conservation International. He is the author of the Pulitzer prize-winning *Guns, germs and steel*, as well as *Collapse*, and *Upheaval*, among other best-selling books.

Friends of the BOC

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

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

The *Bulletin* and other BOC publications

Since volume 137 (2017), the *Bulletin* of the BOC has been an online journal, published quarterly, that is available to all readers without charge. Furthermore, it does not levy any publication charges (including for colour plates) on authors of papers and has a median publication time from receipt to publication of five to six months. Prospective authors are invited to contact the *Bulletin* editor, Guy Kirwan (GMKirwan@aol.com), to discuss future submissions or look at <http://boc-online.org/bulletin/bulletin-contributions>. Back numbers up to volume 136 (2016) are available via the Biodiversity Heritage Library website: www.biodiversitylibrary.org/bibliography/46639#/summary; vols. 132–139 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).

On the possible vernacular name and origin of the extinct Spotted Green Pigeon *Caloenas maculata*

by Philippe Raust

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<http://zoobank.org/urn:lsid:zoobank.org:pub:AB89DE45-96C1-44EC-9043-13CA9E7137DC>

SUMMARY.—I reviewed data from historical works and a dictionary produced by the first missionaries in French Polynesia, in an endeavour to clarify the geographic provenance and potential date of extinction of the bird known as *tīfī* in Tahiti, and which has been assumed to be the extinct Spotted Green Pigeon *Caloenas maculata*, otherwise known from a single surviving specimen held in Liverpool (UK). The name *tīfī* was used to refer to a columbid, as well as to procellariids, and to other species whose vocalisations are transcribed *ti-ti-ti*. Furthermore, what was presumably the same species was also known as the *tīfīhope'ore*, which according to the Tahitian people resembled a Long-tailed Koel *Urodynamis taitensis* but had a short tail. Spotted Green Pigeon possibly survived until sometime between 1801 and 1831, but by 1848 the species was almost certainly extinct, making the claim that it was seen in Tahiti as late as 1928 appear exceptionally unlikely.

Spotted Green Pigeon *Caloenas maculata* (J. F. Gmelin, 1788) is a very poorly known and extinct member of the Columbidae. The sole extant specimen, held at the Liverpool World Museum (WML), was described in 1783 by naturalist John Latham, and subsequently re-examined by various ornithologists, but remained mysterious until 2014. DNA analysis not only proved its specific recognition as a distinct taxon, but that it was also most closely related to Nicobar Pigeon *Caloenas nicobarica*, and can be grouped in the extended Dodo *Raphus cucullatus* clade of morphologically very diverse pigeons (Heupink *et al.* 2014). The physical characteristics of Spotted Green Pigeon suggest that it was principally arboreal and consumed fruit (Gibbs *et al.* 2001, van Grouw 2014).

The Liverpool specimen is 32 cm long and has very dark brown plumage with a green gloss. The neck feathers are elongated, and most feathers on the upperparts and wings have a yellowish patch on their tips, probably staining as the new feathers have a white tip. It has a black bill with a yellow tip, and the tip of the tail has a pale band. It has relatively short legs and long wings (van Grouw 2014). The specimen belonged to the collection of Major Davies (c.1737–1812), an army officer and topographical painter who was interested in birds. He never visited the Pacific but was in contact with Australian collectors from whom he could have obtained the specimen.

According to Latham, a second specimen of unknown origin was once held in the collection of Sir Joseph Banks, who obtained many birds during the voyages of Captain James Cook in the Pacific, especially on Tahiti. This specimen has since disappeared, but was perhaps the same individual illustrated by Latham, which differs from the WML specimen by the pale grey breast and belly. This suggests that it was an adult, whereas the Davies specimen may have been a juvenile, based on analogy with adult and juvenile Polynesian Imperial Pigeon *Ducula aurorae* (van Grouw 2014).

The species is believed to have originated on an island somewhere in the South Pacific, and del Hoyo & Collar (2014) stated: 'Thought to have come from Tahiti (French Polynesia) ... providence of specimens unknown, but, given the main area of activity of its collectors,

this is most likely to have been a Pacific species. May have been a bird described by Tahiti islanders in 1928, although probably almost extinct before epoch of European exploration of the zone. Causes of extinction unknown.'

Nevertheless, it seems unlikely that this bird could have been seen in 1928, as there were no credible sightings after 1783 (the date of the species' description by Latham), despite that Tahiti was visited by several naturalist expeditions during the 19th and early 20th centuries (Holyoak & Thibault 1982) including the Whitney South Sea Expedition in the 1920s.

Del Hoyo & Collar (2014) based their interpretation on statements by Gibbs *et al.* (2001: 394): 'The provenance of the single surviving specimen ... is unknown'; and 'It is possibly the bird described to Henry (1928) by the people of Tahiti'. However, Gibbs *et al.* (2001) were incorrect to claim that the bird was described to Teuira Henry (1847–1915); rather, the observations were reported to her grandfather, the Revd. John Muggridge Orsmond, as will be explained below.

The only objective element that links this bird to Tahiti is a sentence in the text of *Ancient Tahiti*, written by Teuira Henry, and published (posthumously) in 1928. On p. 386, there is the statement: 'The titi, which cried "titi", now extinct in Tahiti, was speckled green and white and it was the shadow of the mountain gods'. Consequently, it is necessary to examine the history of this book to understand the superficial interpretation made by Gibbs *et al.* (2001) and repeated by del Hoyo & Collar (2014).

In the first half of the 19th century, Revd. John Muggridge Orsmond (1784–1856) collected everything entrusted to him with 'ancient traditions of the Tahitian race, collecting them word for word as they were passed down generations by priests and storytellers'. This invaluable document, prefaced by J. M. Orsmond in 1848, unfortunately disappeared after having been entrusted to the French colonial administration. Teuira Henry (1847–1915), granddaughter of the pastor, devoted much of her life to reconstruct this work based on her memories, and the notes and preparatory documents gathered by her grandfather. The result was published in 1928 in Bulletin 48 of the Bernice Pauahi Bishop Museum, Honolulu, Hawaii; it is recognised as one of the most valuable and reliable sources on the civilisation and history of the Society Islands.

Ancient Tahiti devotes several pages to the birds of Tahiti and the surrounding islands. Some 46 names of landbirds from Tahiti and the Society Islands are listed, whether they are still extant ($n = 32$), extinct ($n = 4$) or unknown to science ($n = 10$). Among other things, this list contains species discovered during Cook's voyages, which were never subsequently encountered, including Raiatea Parakeet *Cyanoramphus ulietanus*, of which only two specimens survive in Tring and Vienna.

J. M. Orsmond was resident on Tahiti between 1817 and 1856, and was thus able to access information from observers alive between 1783 (the date of the species' description by Latham) and 1848 (when his work was finished).

In *Ancient Tahiti*, birds are described within relatively homogeneous groups (parrots, rails, waders, seabirds, etc.) and the minimalist description of the *titi* is included in the paragraph pertaining to the Columbidae, including Grey-green Fruit Dove *Ptilinopus purpuratus* and Polynesian Imperial Pigeon *Ducula aurorae* (both extant), suggesting that for the author and his informants the *titi* was well recognised as a columbid. Moreover, the fact that it was considered by the ancient Polynesians to emanate from the gods of the mountain suggests that it frequented remote altitude forests.

Thus, it is reasonable to speculate that the *titi* was a dark white-spotted columbid that lived in high-altitude forests, thereby approximately corresponding to what little we know of the morphology and the biology of Spotted Green Pigeon. This assumption was rejected on the grounds that the name of *titi* 'is an onomatopoeic name throughout East Polynesia

for procellariids, especially shearwaters' (Steadman 2001). However, the name is not exclusive to procellariids like Black-winged Petrel *Pterodroma nigripennis*, effectively called *titi* on Rapa, or Sooty Shearwater *Puffinus griseus* in New Zealand. Several other birds are or were also known by this vernacular name in Polynesia. For example the dictionary of some Tuamotuan dialects of the Polynesian language (Stimson & Marshall 1964) gave the following definitions for the word *titi*:

A variety of small landbird.	REA [Reao]
A variety of bird, ?the petrel.	VHI [Vahitahi]
A variety of bird, the plover; a stockier bird than the sandpiper, with a shorter beak; it is mottled grey and white.	ANA [Anaa]
A variety of bird; the turnstone.	

Nowadays, the name *titi* also designates a unique landbird found only on a few remote atolls of the Tuamotu Archipelago: the Tuamotu Sandpiper *Prosobonia parvirostris*. In fact, this name applies to many birds whose vocalisation is close to *ti-ti-ti-ti-ti* and Henry (1928) specified that the *titi* emitted the sound 'titi'. One can argue that this kind of vocalisation is not common in columbids, but some birds from this family have strange calls: Marquesan Imperial Pigeon *Ducula galeata* utters a cow-like *waah-waah*, and one given by Barking Imperial Pigeon *D. latrans* sounds like a barking dog (Pratt *et al.* 1987).

The dictionary of the Tahitian Academy (Académie tahitienne 1999) defines the word *titi* as 'Bird now extinct (T.H. 397)'. T.H obviously refers to Teuira Henry. The same dictionary also gives the synonym *titihope'ore* from the compilation of the Revd. John Davies (1772–1855), and edited by the London Missionary Society. The latter dictionary, the result of collective work by the first missionaries in Tahiti, listed no fewer than 9,986 Tahitian words that were recorded by Davies between 1801 and 1831, and was first published in 1851.

Davies defined *titihope'ore* as 'the name of a bird'. He did not mention that the bird was extinct (like T. Henry), although the *titi* possibly survived until 1831. This name can be broken down into *titi-hope-ore*. Davies' dictionary defines *ore* as referring to the negative no, or not, but it might also imply 'less', while *hope* refers to the tail of a bird. Thus *titihope'ore* could be translated as *titi* without (a long) tail.

On Rimatara, in the Austral Islands, Long-tailed Koel *Urodynamis taitensis* is known as the *titi oroveo* (Anon. 2002). Thus the *titihope'ore* might have been a bird similar to *U. taitensis* without its long tail. Long-tailed Koel is dark brown with pale beige to white spots on the tips of the back and wing feathers, and pale underparts, to some extent resembling Latham's illustration. This could explain that due to the morphological similarity (specifically the spotted aspect of the plumage) the name *titi* may have been used for both birds.

It is almost certain that in 1848, when *Ancient Tahiti* was completed, the species concerned was already extinct; Hume (2017) suggests that extirpation occurred in the 1820s.

The history and study of Henry's (1928) text, as well as these other works, reinforce the hypothesis of a Tahitian origin for the Spotted Green Pigeon, whose vernacular name was probably *titi*. But can we definitively prove this? The majority of commentators on Spotted Green Pigeon have doubted that its provenance will ever be firmly established, and none has provided suggestions to solve the mystery of its origin.

Excavations at archaeological sites have discovered many species still extant or extinct prior to or after the arrival of Europeans in French Polynesia: at least 32 undescribed or extinct species are known only from subfossil records in this region (Steadman 2006). In the Leeward Islands and Marquesas, remains of columbids related to the genus *Macropygia*, previously unknown in eastern Polynesia, were excavated (Steadman *et al.* 1992), adding a new genus to the extinct avifauna of French Polynesia. Fossil remains of an extinct species

of *Caloenas*, *C. canacorum* (Balouet & Olson 1989), have been discovered in New Caledonia and Tonga, and this species might also have occurred in Vanuatu and Fiji (Steadman 2006, Hume 2017).

If bones belonging to Spotted Green Pigeon were excavated in Tahiti, their identification would be possible using DNA. Unfortunately, few palaeontological sites on Tahiti have been studied and the examination of fossil bones has yet to reveal any undescribed species (Orliac 1997); moreover, no new site has been searched for avian bones for more than 20 years on the island.

Acknowledgements

The remarks by two referees, Julian P. Hume and Hein van Grouw, who offered suggestions and additional information, seriously improved this manuscript. I am also very grateful to Stuart Butchart and Hannah Wheatley from the Red List team at BirdLife International who helped me to translate the paper in its early stages. My thanks also to Nigel Collar and Josep del Hoyo, who encouraged me to submit this article.

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Are some of the birds endemic to the Tres Marías Islands (Mexico) species?

by Héctor Gómez de Silva, Mónica G. Pérez Villafaña, Javier Cruz-Nieto & Miguel Ángel Cruz-Nieto

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SUMMARY.—The Tres Marías archipelago off western Mexico, rarely visited by ornithologists, is currently considered to have 24 endemic subspecies of landbirds. Using both new and previously overlooked information, we evaluate some of the better-marked taxa by applying recently proposed criteria for determining whether they merit recognition at species level. We propose that six of these be elevated to species (*Cynanthus lawrencei*, *Amazilia graysoni*, *Forpus insularis*, *Pheugopedius lawrencii*, *Icterus graysonii* and *Granatellus francescae*) although for some there is evidence that they occasionally interbreed with close relatives on the adjacent mainland. These taxa are threatened by introduced goats, cats and rats, and we hope that by recognising them as endemic species, greater awareness of their plight might stimulate increased conservation action to preserve them and their ecosystem.

Since taxonomy guides conservation decisions and our perception of ecological/evolutionary patterns (Hosner *et al.* 2018), it must reflect scientific findings as accurately as possible. Recognition of a taxon as a species focuses the attention and resources of conservationists, politicians, media, and the public on taxa that would have been overlooked had they been considered ‘only’ subspecies (Phillips 1981, Meijaard 2014). The Tres Marías archipelago off western Mexico, rarely visited by ornithologists, lies 80 km from the mainland at the closest points and is currently considered to have 24 endemic or near-endemic subspecies of landbirds (herein ‘Tres Marías endemics’; Table 1). Some of these taxa are phenotypically well marked and were originally considered species in the late 19th and early 20th century.

Recently, del Hoyo & Collar (2014, 2016) attempted to apply to all the world’s birds a consistent standard for deciding whether well-marked populations merit species status, namely the Tobias *et al.* (2010) criteria. Del Hoyo & Collar evaluated three of the Tres Marías endemics and decided that two deserve species rank. Apparently, these authors did not evaluate the taxonomic status of the remaining Tres Marías endemics and, perhaps more importantly, they overlooked the important taxonomic work of Grant (1965a). Grant (1965a) provided extensive comparisons between a larger number of specimens from the islands and the adjacent mainland than any other study.

Here, we evaluate some of the better-marked Tres Marías endemic taxa to test whether they deserve species rank under the Tobias *et al.* (2010) criteria, using several sources of information: data assembled by Grant (1965a), our own field observations, the ornithological literature, visual examination of study skins in the collection of the Instituto de Biología de the Universidad Nacional Autónoma de México (IBUNAM), Mexico City, photographs of specimens in the Moore Laboratory of Zoology (MLZ), Occidental College, Los Angeles, and online photographs. We present evidence suggesting that a few Tres Marías endemic

taxa occasionally interbreed with their relatives from the adjacent mainland (this was already known for Tropical Parula *Setophaga pitiayumi* but not for other species).

Study area

The Tres Mariás Islands are a linear chain of continental-shelf islands 80–110 km from the nearest mainland across a shallow sea. From north-west to south-east, the four islands are Isla San Juanito (9 km², highest elevation 60 m), Isla María Madre (145 km², 620 m), Isla María Magdalena (70 km², 540 m) and Isla María Cleofas (20 km², 380 m) (elevations taken from INEGI 1999a,b, 2003a–c). Two of the islands are practically equidistant from the mainland. Additionally, volcanic Isla Isabel (2 km², 190 m) potentially forms a ‘stepping stone’ for movement of individuals between some of these islands and the mainland, though it is much closer to the mainland (Fig. 1).

This area appears to have been united to the southern tip of the Baja California Peninsula and the Nayarit coast in the Miocene (Helenes & Carreño 2014) and was still united with the Nayarit mainland until three million years ago in the Late Pliocene (Fig. 99 and p. 206 *in* Pompa-Mera 2014). The islands were submerged until the Late Pliocene; they must have emerged above sea level well before the Late Pleistocene (*contra* Zweifel 1960, Smith *et al.* 2011, Arbeláez-Cortés *et al.* 2014, Montañón-Rendón *et al.* 2015) as there are Late Pleistocene terrace deposits in the lower-lying areas of both Isla María Madre (McCloy *et al.* 1988, Pompa-Mera *et al.* 2013, Pompa-Mera 2014) and Isla María Cleofas (Foose 1962), and hundreds of metres of uplift must have occurred for that to be the case.

Throughout the Pleistocene sea level rose and fell cyclically, repeatedly reaching 120 m below current sea level during glacial maxima (Waelbroeck *et al.* 2002, Bintanja *et al.* 2005, Rohling *et al.* 2009). Low sea levels exposed parts of the islands and the adjacent mainland that are currently under water, and reduced the isolation of the Tres Mariás to just c.20–25 km (Ortiz-Ramírez *et al.* 2018). These changes (tectonic rifting, uplift and sea-level fluctuations) must have had a strong impact on the population dynamics of the islands’ biota.

The principal vegetation on the islands is seasonally dry, medium-stature tropical forest (González-Medrano & Hernández-Mejía 2007), and is very similar to undisturbed vegetation on

TABLE 1
Bird taxa endemic or nearly endemic to the Tres Mariás islands. Taxa considered herein to be species are in boldface.

Scientific name	English name
<i>Patagioenas flavirostris madrensis</i>	Red-billed Pigeon
<i>Leptotila verreauxi capitalis</i>	White-tipped Dove
<i>Nyctidromus albigollis insularis</i>	Common Pauraque
<i>Cyananthus latirostris lawrencii</i>	Broad-billed Hummingbird
<i>Amazilia rutila graysoni</i>	Cinnamon Hummingbird
<i>Buteo jamaicensis fumosus</i>	Red-tailed Hawk
<i>Picoides scalaris graysoni</i>	Ladder-backed Woodpecker
<i>Caracara cheriway pallidus</i>	Crested Caracara
<i>Forpus cyanopygius insularis</i>	Mexican Parrotlet
<i>Amazona oratrix tresmariae</i>	Yellow-headed Parrot
<i>Myiopagis viridicata minima</i>	Greenish Elaenia
<i>Pachyrhamphus aglaiae insularis</i>	Rose-throated Becard
<i>Vireo hypochryseus sordidus</i>	Golden Vireo
<i>Vireo flavoviridis forreri</i>	Yellow-green Vireo
<i>Pheugopedius felix lawrencii</i>	Happy Wren
<i>Myadestes occidentalis insularis</i>	Brown-backed Solitaire
<i>Turdus rufopalliatu graysoni</i>	Rufous-backed Robin
<i>Melanotis caerulescens longirostris</i>	Blue Mockingbird
<i>Spinus psaltria witti</i>	Lesser Goldfinch
<i>Setophaga pitiayumi insularis</i>	Tropical Parula
<i>Piranga bidentata flammea</i>	Flame-coloured Tanager
<i>Cardinalis cardinalis mariae</i>	Northern Cardinal
<i>Granatellus venustus francescae</i>	Red-breasted Chat
<i>Icterus pustulatus graysonii</i>	Streak-backed Oriole

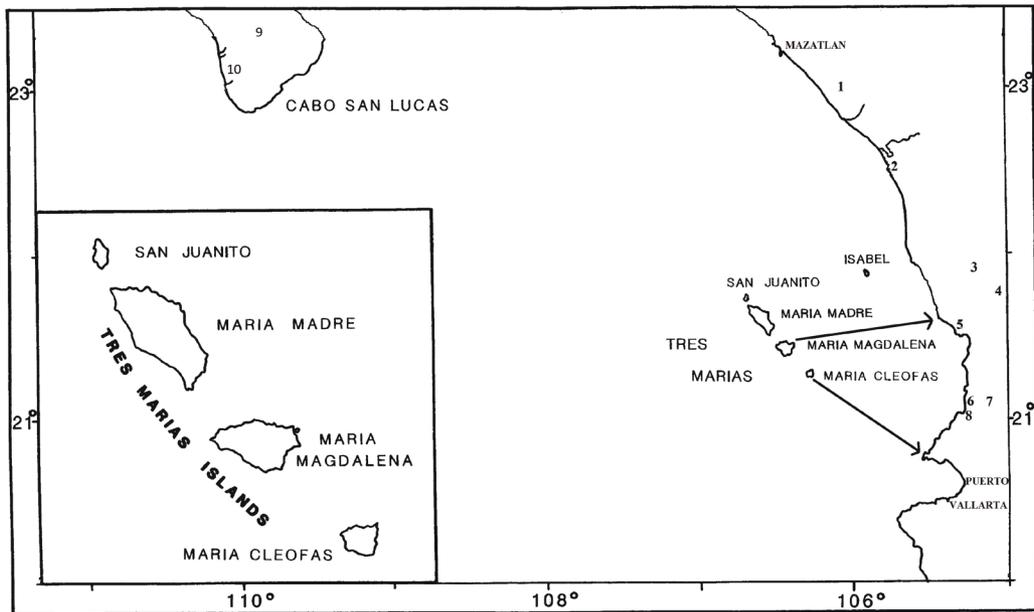


Figure 1. Map showing the location of the Tres Marias Islands with respect to the adjacent mainland (modified from Wilson 1991). The arrows show the two closest routes between the islands and the mainland. The approximate locations of the cities Mazatlán and Puerto Vallarta are indicated. Numbers indicate mainland localities mentioned in the text where Tres Marias taxa or hybrids have been recorded: 1. 'Labrados' (based on Fig. 1 in McLellan 1927), 2. 'Novilleros, west of Acaponeta' = Playa Novillero, 3. Santiago Ixcuintla, 4. Sauta, 5. San Blas and 1 3/4 km north of Singaíta, 6. Chacala, 7. Las Varas, 8. La Peña de Jaltemba, 9. El Oro, and 10. Todos Santos.

the adjacent mainland (Grant 1965a). Rainfall patterns, mean annual rainfall and actual evapotranspiration are similar to those on the adjacent mainland (García *et al.* 1990, Maderey-Rascón 1990, Vidal-Zepeda 1990), but mean annual temperature and total annual rainfall are slightly and distinctly lower, respectively (Cuervo-Robayo *et al.* 2014, García & CONABIO 1998). Thirty-eight species of native landbirds are known or suspected to breed on the Tres Marias, of which 24 are considered endemic subspecies (Howell & Webb 1995 Appendix C, Gómez de Silva *et al.* 2017). Other endemic vertebrates include a single race of reptile (Casas-Andreu 1992) and five species and four subspecies of endemic mammals (Wilson 1991); one of the endemic mammal species is already extinct and another is on the brink (J. Cruzado Cortés pers. comm.).

Methods and taxonomic philosophy

Species are defined by their distinct evolutionary trajectory and substantial, although not necessarily complete, reproductive isolation from other species (Johnson *et al.* 1999, Coyne & Orr 2004: 30). Whereas subspecies generally differ in minor ways in one or a few characters, species usually differ more notably in a larger number of characters. These greater differences are a consequence and sometimes also a cause of reproductive isolation; the number and magnitude of phenotypic differences between two taxa therefore represent evidence of reproductive isolation. Differences between species are usually abrupt, whereas differences between subspecies often tend to be gradual. Tobias *et al.* (2010) established operational criteria to recognise whether taxa merit status as species, based largely on phenotypic and vocal differences.

In extremely summary fashion, according to the criteria of Tobias *et al.* (2010), a taxon is treated as a species if the sum of character scores between it and the most similar taxon is 7 or more. Phenotypic differences between taxa are scored on a scale from 1 to 4, where 1 signifies a 'minor' difference and 4 an 'exceptional' difference; when characters to be scored are quantitative, the score is based on the statistical 'effect size'. Characters are selected on a case-by-case basis, concentrating on those judged to vary most significantly. For the scoring to be conservative, a max. of just three plumage, two morphometric, two acoustic and one ecological / behavioural character can be scored. In addition, when applicable, an extra score of 1 to 3 is applied based on the nature of the biogeographic contact between species, with a score of 1 for frequent hybridisation over a broad contact zone, 2 frequent hybridisation in a narrow contact zone, and 3 parapatry with little or no hybridisation. Furthermore, species status is not triggered by summing minor characters (score 1) alone.

The Tobias *et al.* (2010) criteria and del Hoyo & Collar (2014, 2016) have been praised for their consistency and transparency, and for using effect size rather than statistical significance (e.g. Winker 2010, Brooks & Helgen 2010, Patten 2015), but other aspects have been criticised (Remsen 2015, 2016, Halley *et al.* 2017; although note defence by Collar *et al.* 2015). Perhaps the most significant negative criticism by Remsen (2015, 2016) concerned the treatment of cases with extensive hybridisation along a broad hybrid zone. This criticism is not pertinent here because most of the Tres Mariás endemics are not in parapatry, and there is little or no hybridisation with their mainland counterparts, with the possible exception of *Setophaga* and *Turdus*. The strongest criticism by Halley *et al.* (2017) of using a threshold of divergence to decide if a taxon deserves species status is that it can be unclear which is the relevant taxon for comparison. For the species discussed here, except perhaps Northern Cardinal *Cardinalis cardinalis*, the sister taxon is unquestionably the population on the adjacent mainland, and Grant (1965a) was careful to use that population as a basis for comparison.

There are different routes to speciation, some involving little or no phenotypic change (Winker 2009, Moyle *et al.* 2017: 12). The Tobias *et al.* (2010) criteria are conservative because they are unable to detect such 'cryptic species'. In addition, our taxonomic assessment below is conservative because: (1) for non-quantitative (subjective) characters, we have attempted to assign the lowest possible score, (2) we do not score potential vocal differences because our sample of recordings from the Tres Mariás is small in the context of often large individual variation and large repertoires; and (3) like del Hoyo & Collar (2014, 2016) we have not assessed for possible colour differences in the ultraviolet spectrum. Thus we consider the character scores that we provide to be minima.

Based on the analysis of Grant (1965a), we selected for detailed analysis the species that appeared closest to reaching or exceeding the threshold of species *sensu* Tobias *et al.* (2010), except Red-tailed Hawk *Buteo jamaicensis*, where Grant's sample of adult specimens was based on too small a sample: three vs. two males and five vs. five females.

Concentrating for the most part on measurements of adult specimens, sex by sex, we calculated effect size (Cohen's *d*) of differences between Tres Mariás and nearby mainland specimens by plugging in data from Grant's (1965a) Appendices A and B into an online effect size calculator (<http://www.uccs.edu/~lbecker/>), with standard deviation calculated by multiplying Grant's (1965a) standard error of the mean by the square root of sample size (<https://explorable.com/standard-error-of-the-mean>). We use the phrase 'all external measurements' for wing, tail, tarsus and bill lengths, and sometimes bill width. Grant (1971) demonstrated that tarsus length variation is independent of wing length, and that all external measurements vary independently of each other; nevertheless, we followed Tobias

et al. (2010) and del Hoyo & Collar (2014, 2016) in scoring only up to two morphometric characters.

In the species accounts, English and scientific names follow the American Ornithologists' Union (<http://checklist.aou.org/taxa/>) but subspecies follow del Hoyo & Collar (2014, 2016), except for Mexican Parrotlet *Forpus cyanopygius* where we mention the sometimes recognised *F. c. pallidus*, under Happy Wren *Pheugopedius felix* we consider subspecies *magdalенаe* to be a synonym of *lawrencii* (as did Grant 1965a), and under Streak-backed Oriole *Icterus pustulatus* we mention the sometimes recognised *I. p. yaegeri*. Following the scientific name of the Tres Mariás taxon we name the mainland subspecies used for comparisons after 'vs.' and then we provide the total score we assigned following the criteria of Tobias *et al.* (2010). Thereafter we describe the differences and score assigned, character by character, using 'vs.' between the character description of the island taxon (mentioned first) and the mainland taxon. For quantitative characters, we provide the effect size and the number of island and mainland specimens in Table 2. Phenotypic differences follow Grant (1965a) unless otherwise noted and therefore the number of specimens used by that author in his comparisons is indicated.

Except the three Tres Mariás endemics scored by del Hoyo & Collar (2014, 2016), we break down the character descriptions into categories: colour, morphometrics, evidence of hybridisation and / or additional information. Under the latter we briefly mention the results of relevant molecular studies with regard particularly to reciprocal monophyly, a criterion often considered important in deciding species limits (e.g., Hosner *et al.* 2018). We have separated species into three groups: those scored by del Hoyo & Collar (2014, 2016), those not scored by those authors but confidently scored by us, and those for which we believe there is reason to be still uncertain regarding their taxonomic status (and we do not provide a total score).

Results

Species scored by del Hoyo & Collar (2014, 2016)

BROAD-BILLED HUMMINGBIRD *Cyananthus latirostris lawrencii* (vs. *C. l. magicus* total score 8).

Scored 9 by del Hoyo & Collar (2014) based on colours of throat ('glittering turquoise-green' vs. 'sapphire-blue'), breast ('greeny-bronze' vs. 'turquoise-blue') and undertail-coverts ('whitish-edged darkish-grey' vs. 'pale grey-white'), and slightly shorter bill (most of these characters are visible in Figs. 2–4). However, the throat and breast characters, which del Hoyo & Collar (2014) scored separately, could be viewed as a single character (less blue on iridescence of throat and breast), and we could not clearly discern the difference in breast colour in IBUNAM specimens. Therefore we ignore the breast colour character (thereby 'losing' two points), but this enables a further colour character to be scored. Grant (1965a, based on 23 male and 22 female *lawrencii* vs. 41 male and 25 female *magicus*) mentioned additional colour differences, including darker grey underparts in females (score 1), and that 75% of his *lawrencii* samples of both sexes had darker green upperparts compared to 75% of his *magicus* samples (not scored). Grant (1965a) also mentioned an additional morphometric difference (slightly but significantly smaller grey tips to the rectrices, at least in females; not scored). According to Grant's (1965a) data, shorter bill length in *lawrencii* scores only 1, not 2 as in del Hoyo & Collar (2014), but wings and tail are longer (score 1).

We found that the undertail-coverts character does not distinguish 100% of one taxon from 100% of the other, as implied in the literature (Ridgway 1911, Grant 1965a, del Hoyo &

TABLE 2

Mean (in mm), standard error, *n* (sample size), Cohen's *d* and Tobias *et al.* (2010) scores for the taxa evaluated in this paper (the first three taken from Grant 1965a). 'Island' refers to the taxon from the Tres Marias Islands and 'Mainland' to the taxon from the adjacent mainland. The symbol '—' refers to data not provided by Grant (1965a) due to small sample size or that cannot be calculated due to incomplete information.

Species	Body part	Sex	Mainland mean / standard error (n of individuals)	Island mean / standard error (n of individuals)	Cohen's <i>d</i>	Tobias <i>et al.</i> score
<i>Cyananthus latirostris</i>	Wing	Male	52.64 / 0.39 (38)	53.23 / 0.43 (20)	0.27	low 1
	Tail	Male	31.4 / 0.3 (38)	32.64 / 0.35 (19)	0.73	1
	Bill length	Male	19.58 / 0.13 (37)	18.61 / 0.15 (20)	1.32	1
	length of tip of rectrix 1	Male	3 / 0.1 (34)	1.8 / 0.14 (16)	2.10	low 2
	Wing	Female	51.96 / 0.47 (25)	52.37 / 0.22 (22)	0.23	low 1
	Tail	Female	29.72 / 0.29 (25)	30.28 / 0.21 (22)	0.45	1
	Bill length	Female	20.48 / 0.22 (24)	19.56 / 0.11 (20)	1.10	1
<i>Amazilia rutila</i>	Wing	Male	58.74 / 0.29 (46)	70.58 / 0.44 (27)	5.55	3
	Tail	Male	36.89 / 0.24 (41)	44.54 / 0.36 (26)	4.52	high 2
	Bill length	Male	21.44 / 0.12 (44)	23.84 / 0.14 (27)	3.15	2
	Bill width	Male	3.18 / 0.04 (41)	3.63 / 0.08 (22)	1.40	high 1
	Wing	Female	55.98 / 0.55 (13)	69.04 / 0.46 (18)	6.64	3
	Tail	Female	35.58 / 0.35 (13)	44.36 / 0.34 (16)	6.69	3
	Bill length	Female	21.51 / 0.18 (13)	24.63 / 0.17 (15)	4.77	high 2
	Bill width	Female	3.07 / 0.08 (13)	3.51 / 0.04 (16)	1.89	high 1
<i>Granatellus venustus</i>	Wing	Male	61.52 / (0.28) / 18	65.85 / 0.28 (21)	3.50	2
	Tail	Male	69.74 / 0.65 (16)	76.49 / 0.47 (20)	2.86	2
	Tarsus	Male	19.72 / 0.14 (18)	21.14 / 0.15 (20)	2.24	2
	Bill length	Male	8.76 / 0.09 (17)	8.96 / 0.04 (19)	0.69	1
	width of rectrix 6	male	6.19 / 0.27 (8)	7.22 / 0.17 (9)	1.59	1
	white on rectrix 6	male	28.1 / 1.08 (10)	38.38 / 0.71 (14)	3.36	2
	rectrix 6 length for same individuals as previous row	male	69.19 / 0.73 (8)	76.25 / 0.62 (14)	3.21	2
	length of white/ length of rectrix 6	male	0.405 / 0.01 (8)	0.51 / 0.01 (14)	3.17	2
	Wing	Female	59.48 / 0.33 (11)	63.35 / 0.23 (13)	3.99	2
	Tail	Female	67.83 / 0.61 (11)	74.28 / 0.37 (17)	3.60	2
	Tarsus	Female	19.52 / 0.12 (12)	21.24 / 0.08 (14)	4.75	high 2
	Bill length	Female	8.88 / 0.14 (12)	8.79 / 0.07 (13)	0.23	low 1
	white on rectrix 6	female	25 / 0.32 (5)	34.21 / 0.97 (7)	4.89	high 2
	rectrix 6 length for same individuals as previous row	female	66.6 / 1.37 (5)	73.86 / 0.57 (7)	3.01	2
length of white/ length of rectrix 6	female	0.378 / 0.01 (5)	0.463 / 0.01 (7)	3.47	2	

Species	Body part	Sex	Mainland mean / standard error (n of individuals)	Island mean / standard error (n of individuals)	Cohen's <i>d</i>	Tobias <i>et al.</i> score
<i>Forpus cyanopygius</i>	Wing	Male	88.36 / 0.44 (20)	90.84 / 0.35 (21)	1.38	1
	Tail	Male	40.81 / 0.39 (20)	42.57 / 0.26 (21)	1.18	1
	Tarsus	Male	10.86 / 0.05 (20)	11.92 / 0.11 (21)	2.72	2
	Bill length	Male	13.55 / 0.1 (19)	14.05 / 0.08 (21)	1.24	1
	Wing	Female	86.98 / 0.37 (31)	90.93 / 0.57 (15)	1.85	high 1
	Tail	Female	40.9 / 0.33 (31)	43.29 / 0.33 (15)	1.51	1
	Tarsus	Female	11.06 / 0.08 (31)	12.06 / 0.14 (15)	0.82	1
	Bill length	Female	13.17 / 0.07 (30)	13.98 / 0.09 (14)	2.24	2
<i>Vireo hypochryseus</i>	Wing	Male	63.87 / 0.3 (40)	67.83 / 0.33 (30)	2.14	low 2
	Tail	Male	55.74 / 0.3 (41)	60.45 / 0.23 (24)	2.99	2
	Tarsus	Male	18.71 / 0.1 (43)	19.98 / 0.09 (28)	2.22	2
	Bill length	Male	8.8 / 0.08 (42)	9.1 / 0.08 (29)	0.63	1
	Coracoid	Male	13.74 / 0.09 (12)	12.5 / 0.06 (6)	5.09	low 3
	Femur	Male	14.75 / 0.08 (14)	14.76 / 0.1 (7)	0.04	0
	Wing	Female	61.58 / 0.37 (20)	65.93 / 0.23 (23)	3.09	2
	Tail	Female	53.74 / 0.43 (19)	58.85 / 0.22 (21)	3.40	2
	Tarsus	Female	18.84 / 0.14 (20)	20.06 / 0.15 (23)	1.81	high 1
	Bill length	Female	8.7 / 0.09 (20)	9.13 / 0.04 (19)	1.39	1
	Coracoid	Female	13.47 / 0.04 (9)	12.57 / – (4)	–	–
	Femur	Female	14.71 / 0.08 (10)	14.96 / 0.06 (5)	1.23	1
<i>Pheugopedius felix</i>	Wing	Male	56.89 / 0.25 (37)	59.41 / 0.37 (42)	1.26	1
	Tail	Male	52.49 / 0.29 (31)	56.06 / 0.33 (37)	1.96	1–2
	Tarsus	Male	21.56 / 0.13 (35)	21.93 / 0.1 (43)	0.52	1
	Bill length	Male	10.91 / 0.09 (36)	12.4 / 0.12 (41)	2.24	2
	Wing	Female	53.54 / 0.43 (18)	57.68 / 0.45 (28)	1.95	high 1
	Tail	Female	49.25 / 0.64 (17)	55.06 / 0.54 (27)	2.13	low 2
	Tarsus	Female	21.28 / 0.16 (17)	21.37 / 0.12 (29)	0.14	0
	Bill length	Female	10.54 / 0.14 (18)	12.2 / 0.09 (28)	3.08	2
<i>Melanotis caerulescens</i>	Wing	Male	114.17 / 0.73 (25)	109.82 / 0.57 (49)	1.14	1
	Tail	Male	123.47 / 0.92 (28)	109.46 / 0.75 (44)	2.85	2
	Tarsus	Male	29.18 / 0.18 (29)	28.46 / 0.14 (52)	0.28	low 1
	Bill length	Male	17.42 / 0.18 (28)	20.06 / 0.15 (46)	2.68	2
	Wing	Female	110.26 / 0.7 (25)	106.82 / 0.49 (24)	1.15	1
	Tail	Female	116.38 / 1.07 (25)	104.92 / 0.92 (22)	2.36	2
	Tarsus	Female	29.3 / 0.18 (31)	28.3 / 0.16 (24)	1.11	1
	Bill length	Female	17.13 / 0.21 (28)	19.72 / 0.14 (23)	2.82	2
<i>Icterus pustulatus</i>	Wing	Male	96.22 / 0.3 (66)	104.56 / 0.35 (42)	3.54	2
	Tail	Male	84.61 / 0.37 (61)	91.52 / 0.32 (39)	2.78	2
	Tarsus	Male	24.96 / 0.08 (66)	25.17 / 0.17 (28)	0.27	low 1

Species	Body part	Sex	Mainland mean / standard error (n of individuals)	Island mean / standard error (n of individuals)	Cohen's d	Tobias et al. score
<i>Leptotila verreauxi</i>	Bill length	Male	14.78 / 0.78 (66)	17.35 / 0.12 (37)	0.57	1
	Bill width	Male	5.03 / 0.03 (54)	5.47 / 0.05 (23)	1.91	high 1
	Coracoid	Male	19.88 / 0.1 (42)	18.87 / 0.13 (9)	1.89	high 1
	Femur	Male	21.92 / 0.1 (43)	21.83 / 0.34 (9)	0.10	0
	Dorsal streaks	Male	30.4 / 0.69 (51)	5.4 / 0.75 (30)	5.51	3
	Wing	Female	90.82 / 0.52 (27)	97.8 / 0.42 (15)	3.13	2
	Tail	Female	81.33 / 0.68 (19)	85.67 / 0.8 (15)	1.43	1
	Tarsus	Female	24.81 / 0.13 (27)	25.87 / 0.13 (14)	1.80	high 1
	Bill length	Female	14.88 / 0.15 (26)	16.68 / 0.2 (13)	2.42	2
	Bill width	Female	4.98 / 0.04 (24)	5.44 / 0.04 (11)	2.75	2
	Coracoid	Female	19.28 / 0.11 (25)	18.23 / 0.09 (7)	2.48	2
	Femur	Female	21.92 / 0.1 (43)	21.83 / 0.34 (9)	0.10	0
	Dorsal streaks	female	28.2 / 1.35 (17)	4.4 / 1.35 (12)	4.63	2
	Wing	Male	143 / 0.63 (32)	152.5 / 0.6 (25)	2.73	2
	Tail	Male	109.2 / 0.69 (31)	109.5 / 0.57 (25)	0.09	0
	Tarsus	Male	29.04 / 0.25 (31)	31.58 / 0.24 (25)	1.95	high 1
	Bill length	Male	9.73 / 0.08 (31)	10.86 / 0.09 (22)	0.24	1
	Tail tip length	Male	9.8 / 0.25 (27)	8.3 / 0.3 (20)	1.14	1
	<i>Turdus rufopalliatius</i>	Wing	Female	140.6 / 0.77 (12)	149.8 / 0.54 (21)	3.58
Tail		Female	108.8 / 1.35 (12)	106.5 / 0.43 (21)	0.64	1
Tarsus		Female	27.69 / 0.41 (12)	30.4 / 0.24 (21)	2.13	2
Bill length		Female	9.36 / 0.08 (11)	10.97 / 0.12 (18)	3.97	2
Tail tip length		Female	9.1 / 0.22 (12)	7.6 / 0.33 (17)	1.36	1
Wing		Male	123.19 / 0.59 (32)	127.17 / 0.58 (22)	1.31	1
Tail		Male	99.29 / 0.69 (32)	102.49 / 0.73 (22)	0.87	1
Tarsus		Male	31.48 / 0.21 (32)	34.8 / 0.23 (20)	2.99	2
Bill length		Male	13.26 / 0.08 (30)	15.18 / 0.17 (22)	2.98	2
Wing		Female	120.42 / 0.5 (20)	124.97 / 0.52 (37)	1.66	1
<i>Setophaga pitiayumi</i>	Tail	Female	95.85 / 0.68 (21)	99.6 / 0.52 (39)	1.18	1
	Tarsus	Female	31.19 / 0.17 (22)	34.67 / 0.21 (34)	3.37	2
	Bill length	Female	13.8 / 0.14 (20)	15.42 / 0.11 (35)	2.54	2
	Wing	Male (excluding mainland <i>insularis</i>)	55.42 / 0.33 (21)	58.28 / 0.34 (42)	1.51	1
	Tail	Male (excluding mainland <i>insularis</i>)	42.83 / 0.48 (21)	49.14 / 0.33 (37)	3.00	2
	Tarsus	Male (excluding mainland <i>insularis</i>)	16.14 / 0.09 (22)	19.11 / 0.08 (40)	6.37	3
	Bill length	Male (excluding mainland <i>insularis</i>)	7.68 / 0.07 (22)	7.76 / 0.06 (40)	0.23	low 1
	Wing	Female (excluding mainland <i>insularis</i>)	52.22 / 0.33 (12)	56.38 / 0.28 (20)	3.47	2
	Tail	Female (excluding mainland <i>insularis</i>)	40.34 / 0.37 (11)	48.11 / 0.25 (19)	6.70	3

Species	Body part	Sex	Mainland mean / standard error (n of individuals)	Island mean / standard error (n of individuals)	Cohen's <i>d</i>	Tobias <i>et al.</i> score
	Tarsus	Female (excluding mainland <i>insularis</i>)	16.34 / 0.19 (11)	18.84 / 0.14 (20)	5.16	low 3
	Bill length	Female (excluding mainland <i>insularis</i>)	7.78 / 0.1 (10)	7.62 / 0.06 (20)	0.55	1
<i>Cardinalis cardinalis</i>	Wing	Male	91.04 / 0.78 (9)	95.17 / 0.33 (38)	1.88	high 1
	Tail	Male	101.9 / – (4)	96.96 / 0.61 (28)	–	–
	Tarsus	Male	25.1 / 0.14 (8)	28.06 / 0.12 (44)	5.42	3
	Bill length	Male	13.22 / 0.29 (8)	14.17 / 0.1 (44)	1.27	1
	Bill width	Male	8.52 / 0.04 (8)	9.28 / 0.05 (27)	3.79	2
	Wing	Female	89.93 / 0.64 (6)	91.71 / 0.37 (34)	0.94	1
	Tail	Female	100.5 / 0.9 (6)	93.29 / 0.46 (21)	3.34	2
	Tarsus	Female	25.43 / 0.24 (6)	27.37 / 0.19 (32)	0.95	1
	Bill length	Female	13.47 / 0.32 (6)	13.85 / 0.08 (35)	0.59	1
	Bill width	Female	8.35 / 0.06 (6)	9.01 / 0.07 (26)	2.42	2

Collar 2014). Of 11 male specimens of *lawrencei* at IBUNAM in which it is possible to see the undertail-coverts, typical colours are present in nine specimens but P019534 has a two-toned pattern in which the anterior feathers are typical of *lawrencei* but the largest, posterior feathers are predominantly white with very pale grey central portions, very similar to *magicus* P001630 from Sinaloa (Fig. 5). Also, the usually whitish undertail-coverts of *magicus* reach their greyest extreme in P001631 and P020047 (Fig. 6), albeit a pearly grey rather than the brownish grey of *lawrencei*. We do not believe that any of these specimens are hybrids because no other character suggests this, and their geographic location is too far removed from the Tres Marías (e.g., P020047 is from too far north and inland for *lawrencei* to be a plausible parent).

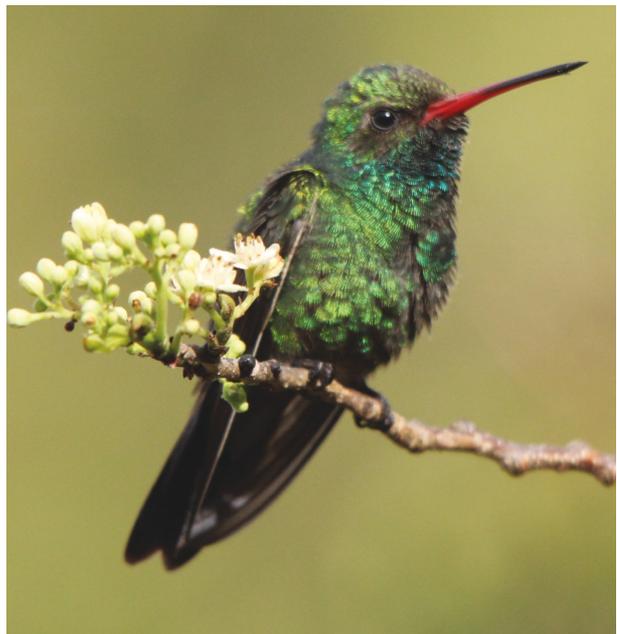


Figure 2. Male Broad-billed Hummingbird *Cyanthus latirostris lawrencei*, Isla María Cleofas, May 2016 (Javier Cruz Nieto)

Occasional *Cyanthus* wander between the Tres Marías and the mainland, and apparently sometimes interbreed. A. J. Grayson (*in* Lawrence 1872: 29) reported seeing one at sea '30 miles north' of the Tres Marías Islands in May 1867, which visited his boat and flew from there toward the islands. Nelson (1899: 46) saw a male *latirostris* fly past his boat in a straight line toward the islands 'about midway' between the Tres Marías and San Blas, Nayarit. An adult male *latirostris* or *lawrencei* was observed '1 mile east' of Isla María



Figure 3. Throat colours of Broad-billed Hummingbird *Cyananthus latirostris* specimens in the Instituto de Biología, Universidad Nacional Autónoma de México collection, on left: two *C. l. magicus*, right: two *C. l. lawrencei*; the apparently larger size and bills of the *lawrencei* specimens are an artefact of the photograph (Héctor Gómez de Silva)



Fig. 4. Typical undertail-coverts colour of male Broad-billed Hummingbird *Cyananthus latirostris magicus* (two specimens at left) and *C. l. lawrencei* (two specimens at right), from specimens in the Instituto de Biología, Universidad Nacional Autónoma de México collection (Héctor Gómez de Silva)



Figure 5. Two specimens of male Broad-billed Hummingbirds *Cynanthus latirostris* with similarly grey anterior undertail-coverts and white or whitish posterior undertail-coverts; above *C. l. magicus*, below, *C. l. lawrencei* (Héctor Gómez de Silva)



Figure 6. Mainland specimens of male Broad-billed Hummingbird *Cynanthus latirostris magicus* with grey undertail-coverts (usually white or whitish) (Héctor Gómez de Silva)



Magdalena by Grant (1965a: 51) on 25 April 1963 flying towards the latter island; and two male *lawrencei* were collected on the mainland at Sauta, Nayarit, by C. Lamb (MLZ 28073 on 5 May 1940, and MLZ 41912 on 23 April 1946, with two male *magicus* collected there around the same date as the 1940 specimen; J. Maley pers. comm.). MLZ 28073 has the



Figure 7. Presumed hybrid Broad-billed Hummingbird *Cyananthus lawrencei* × *magicus* specimen in the Instituto de Biología, Universidad Nacional Autónoma de México collection; note *magicus*-like blue throat and *lawrencei*-like white-edged grey undertail-coverts (Héctor Gómez de Silva)



Figure 8. Presumed hybrid Broad-billed Hummingbird *Cyananthus lawrencei* × *magicus* specimen, Isla María Cleofas, April 2016 (Héctor Gómez de Silva)

only remaining undertail-covert feather typical of *lawrencei* while, *contra* Grant (1965a), MLZ 41912 has the anterior feathers grey-brown and the posterior undertail-coverts very pale whitish grey (like the IBUNAM material in Fig. 5; MLZ specimen photos, courtesy of J. Maley).

Among mainland specimens at IBUNAM, one male (P001633 from just north-west of Las Varas, Nayarit, along the Zacualpan road) appears to be a hybrid. It has a *lawrencei*-like shorter bill and undertail-coverts colour, but a *magicus*-like blue throat (Fig. 7). This is consistent with the observation that hybrids between hummingbirds of the ‘emerald’ group (*sensu* McGuire *et al.* 2014) do not show mixed colours but rather a combination of characteristics of the parental species (Graves 2003a,b).

A male Broad-billed Hummingbird we photographed on Isla María Cleofas on 26 April 2016 appears to combine the plumage characters of *magicus* and *lawrencei*, namely the deep blue throat and blue-green breast / belly of the former with the undertail-coverts of the latter (Fig. 8), thus apparently representing another hybrid.

Del Hoyo & Collar (2014) used the English name Tres Mariás Hummingbird, but we prefer to avoid potential confusion given that there are two species of hummingbird on the islands; consequently, we prefer the name Lawrence’s Hummingbird.

CINNAMON HUMMINGBIRD *Amazilia rutila graysoni* (vs. *A. r. rutila* total score 7)

Scored 4 by del Hoyo & Collar (2014) based on larger size in all external measurements (to which they assign a score of 3) and slightly ‘darker and duskier’ plumage (which they score 1). Regarding colour differences, Grant (1965a, based on 27 male and 18 female *graysoni* vs. 46 male and 14 female *rutila*) stated that the underparts are uniformly dark cinnamon vs. paler cinnamon, particularly on the chin and throat. The belly of some mainland *rutila* at IBUNAM is as dark as the underparts of *graysoni*, but the chin and throat, and often asymmetrical patches on the breast, are always paler (Fig. 9). Grant (1965a) also mentioned that the upperparts are ‘dark green or even red-bronze’ vs. ‘paler green, and in those which have a bronze colour it is always yellow-green, never red’, and that the ‘tips’ (*sic*, actually, subterminal portions) of most, particularly the outer, rectrices are dark greenish bronze to



Figure 9. Two specimens of Cinnamon Hummingbird *Amazilia rutila graysoni* (below) compared with two specimens of *A. r. rutila* (above); note the considerable difference in size. The second specimen from the top is the darkest-throated *A. r. rutila* at Instituto de Biología, Universidad Nacional Autónoma de México; the right side of its throat is paler than the left, and thus more like the typical colour of the subspecies (Héctor Gómez de Silva)

dull violet in 90% of *graysoni* vs. paler, bright greenish bronze in 90% of *rutila* specimens (score at least 1). The underpart colours in these taxa are based on the intensity of cinnamon pigmentation whereas the upperpart colours (as in iridescent colours of hummingbirds generally) are based on a combination of melanin and feather nanostructure; therefore we score 1 for underparts colour and 1 for upperparts colour.

Grant's (1965a) measurements reveal that the bill in *graysoni* is both relatively shorter (effect size for bill length 2 vs. effect size for most external measurements 3 [score 1]) and, especially in males, relatively narrower (effect size for bill width 1 but for bill length 2 [not scored]).

The notably larger overall size of insular *graysoni* is paralleled by Rufous-tailed Hummingbird *Amazilia tzacatl handleyi* of Isla Escudo de Veraguas, Panama (Wetmore 1959, Miller *et al.* 2011) but in the latter case, there is reportedly a narrow 'zone of morphometric intergradation' (Weller 1999), although the data on which the statement was based have not been published to date. There is no zone of intergradation between *graysoni* and mainland *rutila*.

Of the 12 specimens of *graysoni* at IBUNAM, the smallest (P019069 from Isla María Madre) has atypical upperparts, with much-reduced iridescence on the wing-coverts and back compared to either *graysoni* or *rutila*. We consider that this specimen could be a hybrid *graysoni* × *rutila*, the colour of its upperparts being heterotic (a trait of a hybrid outside the range of variation for that trait in either parental species; McCarthy 2006: 17).

RED-BREASTED CHAT *Granatellus venustus francescae* (vs. *G. v. venustus* total score 8)

Scored 7 by del Hoyo & Collar (2016) based on the lack of black breast-band of *francescae*, presence of a white hindcollar, grey of crown extending over nape, tail much longer, and a few additional characters that they did not score. Grant (1965a, based on 29 male and 18 female *francescae* vs. 24 male and 14 female *venustus*) found that the lack of breast-band differentiated 79% of his sample of *francescae* from 94% of *venustus* (Grant 1965a also observed in both taxa that, rarely, a breast-band is present but masked by overlying white feathers). Therefore, this character does not differentiate the taxa completely, and we did not score it, although we believe that it is an important character.

Del Hoyo and Collar (2016) included scores for 'white hindcollar formed by continuing white postocular stripe (at least 1), grey of crown extending over nape (1)'. We think they assigned two scores for what is essentially a single character (Fig. 10), to which we apply a score of 2.

Whereas del Hoyo & Collar (2016) mention, but did not score, 'pink of underparts generally slightly paler and less extensive', Grant (1965a) stated that 'the majority of both mainland and island samples of adult males had approximately the same amount of red ventrally. A few island specimens were observed to have less, and a few mainland specimens more, than this.' It is unclear whether this character should be scored. However, we would score the colour of the underparts of immature males; Grant (1965a), based on a sample of perhaps $n = 8$ vs. $n = 6$, reported that immature males differ in having almost no red on the underparts in *francescae* (and in his sample no trace of a black breast-band) vs. much red on the underparts and a complete breast-band (score 2). Based on Grant's (1965a) data the relative amount of white on the outermost rectrix (measured as the length of the white patch on r6 / length of r6) merits a score of 2, but we conservatively score it 1. Whereas del Hoyo & Collar (2016) afforded a score of 2 for 'tail much longer', measurements in Grant (1965a) indicate that the score of 2 applies equally to wing, tarsus and tail lengths, but bill length is shorter (score 1).



Figure 10. Comparison of the nape and presence / absence of the white hindcollar in male Red-breasted Chat *Granatellus venustus*: above, Instituto de Biología, Universidad Nacional Autónoma de México specimen of *G. v. venustus* (Héctor Gómez de Silva); below, *G. v. francescae*, Isla María Cleofas, May 2016 (Mónica G. Pérez Villafaña)

Endemics not scored by del Hoyo & Collar (2014, 2016) but confidently scored by us

MEXICAN PARROTLET *Forpus cyanopygius insularis* (vs. *F. c. cyanopygius* / *pallidus* total score 7)

Coloration.—Males have breast, belly, neck-sides and postocular region pale malachite-green, somewhat glaucous, contrasting strongly with the yellowish-green or apple-green cheeks, throat, forehead and forecrown vs. apple-green underparts in slight contrast (if any) with the face colour (Figs. 11–12; Ridgway 1911, Grant 1965a, based on 21 male and 15 female *insularis* vs. 20 male and 31 female *cyanopygius*, www.inaturalist.org/observations/5258308, www.inaturalist.org/observations/5258315 [score 2]). This coloration is similar to male Pacific Parrotlet *F. coelestis* of western Ecuador and north-west Peru (e.g., www.hbw.com/ibc/photo/pacific-parrotlet-forpus-coelestis/close-pacific-parrotlet and www.hbw.com/ibc/photo/pacific-parrotlet-forpus-coelestis/male; the illustration of the latter species in del Hoyo & Collar 2014 is inaccurate). Rump, lower back and greater coverts of males bright cerulean blue vs. bright turquoise-blue (Ridgway 1911, Grant 1965a [score 1]). Secondaries



Figure 11. Pair of Mexican Parrotlets *Forpus cyanopygius insularis* copulating, Isla María Cleofas, May 2016; note the male's pale malachite-green underparts, neck-sides and postocular region contrasting with the yellower green cheeks, throat, forehead and forecrown, and that the male's undertail-coverts are not concolorous with the breast and belly (*contra* Grant 1965a) (Javier Cruz Nieto)



Figure 12. Instituto de Biología, Universidad Nacional Autónoma de México specimens of Mexican Parrotlet *Forpus cyanopygius* from Nayarit; the two specimens on the right are adult male *insularis*, their malachite-green breast and belly contrasts strongly with the throat, unlike in *cyanopygius* specimens (Héctor Gómez de Silva)

and proximal primaries darker and duller blue, edged cerulean blue vs. greenish blue (nearly cerulean blue) edged distally with pale yellowish green (Ridgway 1911 [score 2]). A. J. Grayson (*in* Lawrence 1872), Lawrence (1872), Ridgway (1888, 1911) and Grant (1965a) described the upperparts of both sexes of *insularis* as darker and more glaucous green (not scored, we are unable to discern this difference in the three *insularis* vs. six *cyanopygius* / *pallidus* specimens at IBUNAM). Grant (1965a) added that the flanks and undertail-coverts are the same colour as the breast / belly in all *insularis* males in his sample, but the detailed description of *insularis* by Ridgway (1911), the two IBUNAM specimens of adult male *insularis*, and our field photographs (e.g., Fig. 11) contradict that.

Morphometrics.—Larger in all external measurements (score 2).

Additional information.—Smith *et al.*'s (2012) molecular study found that *insularis* has diverged more from a common ancestor than *cyanopygius* / *pallidus*, consistent with a faster rate of divergence in small, isolated populations (Woolfit 2009), and the Bayesian modelling programme BP&B assigned the probability of *insularis* being a separate species as higher than 95%.

GOLDEN VIREO *Vireo hypochryseus sordidus* (vs. *V. h. hypochryseus* total score 5–6)

Coloration.—Throat, breast, flanks and upperparts duller and greener in *sordidus*, especially in fresh plumage and when specimens collected in the same season are compared (score 1 or possibly 2, Grant 1965a, based on 30 male and 23 female *sordidus* vs. 44 male and 20 female *hypochryseus*). Grant (1965a) reported that Nelson's (1898) claimed difference in bill colour is incorrect.

Morphometrics.—Larger in all external measurements, especially tail length of both sexes and wing length of females (score 2), with a significantly shorter coracoid both absolutely and relatively (effect size almost reaches the threshold for score of 3, but we assign a score of 2) and a relatively shorter femur (not significantly different between taxa, whereas all external measurements are larger [not scored]). Arbeláez-Cortés *et al.* (2014) analysed the morphometrics of ten *sordidus* and 37 specimens from the rest of the range, and confirmed the larger size of *sordidus*.

Additional information.—Arbeláez-Cortés *et al.* (2014) and Ortiz-Ramírez *et al.* (2018) reported reciprocal monophyly but shallow genetic divergence between these taxa.

HAPPY WREN *Pheugopedius felix lawrencii* (vs. *P. f. pallidus* total score 8)

Coloration.—White mid-breast and mid-belly vs. rufous breast and belly in *pallidus* (Fig. 13; Grant 1965a, based on 43 male and 30 female *lawrencii* vs. 37 male and 18 female *pallidus* [not scored]). Among 18 *lawrencii* at IBUNAM, a few are washed warm on the breast, but are still usually paler than the palest *pallidus*. Even if there is warm colour across part of the breast, there is much white on the mid-breast and mid-belly. Examination of the 'warmest' specimens of *lawrencii* (P016585) revealed a diagnostic character not previously mentioned in the literature (e.g. Nelson 1898, Ridgway 1904, Grant 1965a): the colour of the underwing-coverts. In *lawrencii*, these are white or whitish, contrasting with the warm breast-sides, whereas *pallidus* has cinnamon / rufous underwing-coverts concolorous with the breast (score 3) (Fig. 14). Ear-coverts have significantly more white than black feathers vs. black and white feathers approximately equally prominent (score 2) (Fig. 13). One or other of these differences between *lawrencii* and *pallidus* is of somewhat similar magnitude to those between certain subspecies of, e.g., Coraya *Pheugopedius coraya*, Rufous-and-white *Thryophilus rufalbus*, Buff-breasted *Cantorchilus leucotis*, Carolina *Thryothorus ludovicianus* and White-browed Wrens *T. albinucha*, but in those cases there are zones of intergradation and smooth clines, whereas between *lawrencii* and *pallidus* the differences are abrupt and



Figure 13. Left: typical underparts colour and cheek pattern in Happy Wren *Pheugopedius felix pallidus*, Laguna El Chumbeño, Francisco Villa, Nayarit, Mexico, May 2016 (Amy McAndrews); right: *P. f. lawrencii*, Isla María Cleofas, April 2016 (Mónica G. Pérez Villafaña)

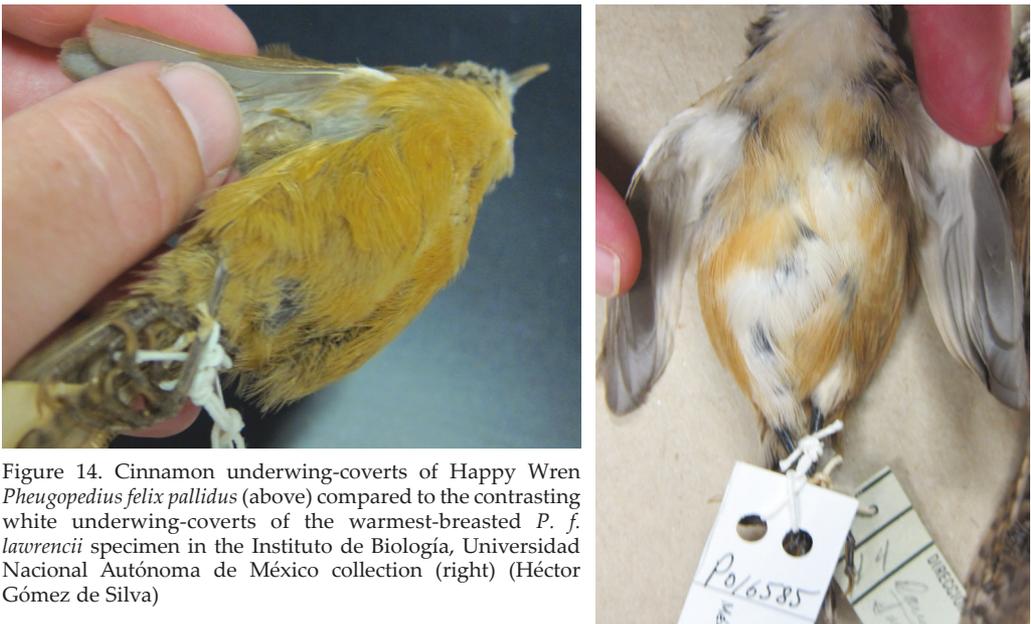


Figure 14. Cinnamon underwing-coverts of Happy Wren *Pheugopedius felix pallidus* (above) compared to the contrasting white underwing-coverts of the warmest-breasted *P. f. lawrencii* specimen in the Instituto de Biología, Universidad Nacional Autónoma de México collection (right) (Héctor Gómez de Silva)

occur in both characters simultaneously. Grant (1965a) noted that in both plumage features, juveniles from the mainland approach those of Tres Mariás birds.

Morphometrics.—Longer wing, tail and, especially in females, bill (score 2) but tarsus relatively shorter (not significantly different in female and only slightly bigger in male [score 1]).

BLUE MOCKINGBIRD *Melanotis caerulescens longirostris* (vs. *M. c. caerulescens* total score 4)

Coloration.—Based on 52 male and 24 female *longirostris* vs. 29 male and 32 female *caerulescens*, Grant (1965a) found that ‘less than half’ of *longirostris* were paler in the throat and crown feathers than ‘most’ of his *caerulescens* sample but the palest specimens of each were indistinguishable. Therefore there is large overlap (no score).

Morphometrics.—Slightly larger but has proportionately much longer bill in both sexes (score 2) whereas the tail is shorter, especially in males (score 2). Additionally, Grant (1965a) found that coracoid length may be shorter in island birds but did not provide sufficient information to calculate effect size because he considered his sample to be inadequate (three male and six female *longirostris* vs. five male and two female *caerulescens*). However, the measurement ranges have slight to no overlap, which suggest the difference is not minor (not scored).

STREAK-BACKED ORIOLE *Icterus pustulatus graysonii* (vs. *I. p. microstictus* and *I. p. yaegeri* total score 7).

Coloration.—Very few short and narrow streaks on back, usually in scapular region vs. more prominent and numerous streaks throughout back (Fig. 15; Grant 1965a, based on 39 adult male and 13 adult female *graysonii* vs. 69 adult male and 29 adult female *microstictus* / *yaegeri* [score 2]). Median coverts ‘pale yellow to yellowish-white’ vs. ‘usually (orangey) yellow’ in *yaegeri*, the geographically closest mainland taxon, and white in *microstictus*, which occurs further inland than *yaegeri* (Phillips 1995 [score 1]). Grant (1965a) mentioned but did not quantify a tendency to differ in yellow vs. orange plumage. Generally, *graysonii* is less orange overall (consistent with the median coverts character, above, and with Ridgway 1902, Jaramillo & Burke 1999) and we support this based on our field work, although one adult *graysonii* among the dozens seen was intensely orange (Fig. 16).

Morphometrics.—Larger in external measurements (score 2), but with a significantly shorter coracoid both absolutely and relatively (score 2) and a relatively shorter femur (not significantly different whereas all external measurements are significantly different [not scored]). The bill is also differently shaped (‘longer in relation to width’, Grant 1965a [not scored]).

Evidence of hybridisation.—Phillips (1995) collected a mainland specimen that he presumed to be a rare variant of *yaegeri* and had ‘plain yellowish interscapulars, with hardly perceptible black streaking (on the back). But the middle wing-coverts are richer, and bill shorter, than *graysonii*’. This specimen is now in the IBUNAM collection (P022269). Its precise locality, according to the label, is ‘1¼ km N of Singaita’, whereon it is also mentioned ‘Apparently alone in brush, near normal-backed pair’. The bird not only resembles *graysonii* in its back pattern but also in size (Fig. 15). Therefore it combines phenotypic characters and is almost surely a hybrid. We found a second mainland specimen (P015891 from Santiago Ixcuintla) that resembles *graysonii* in its fewer and narrower back streaks, but streaks are present even on the central back (Fig. 15). In overall length this specimen is comparable to other mainland specimens, and we believe it is also a hybrid.



Figure 15. Back pattern, size and intensity of orange in Streak-backed Oriole *Icterus pustulatus* specimens from Nayarit, from left to right: two typical *microstictus* / *yaegeri*, two presumed hybrids (with Phillips' specimen at right) and a typical *graysoni*; note the similar overall size of *graysoni* and Phillips' specimen, which is, however, more orange overall (especially the head), while the other presumed hybrid (which appears almost as long due to specimen preparation) has back streaks intermediate between *graysoni* and typical mainland Nayarit orioles (Héctor Gómez de Silva)



Figure 16. An intensely orange individual of Streak-backed Oriole *Icterus pustulatus graysoni*, Isla María Cleofas, March 2016 (Javier Cruz Nieto)

Additional information.—Cortés-Rodríguez *et al.* (2008) and Ortiz-Ramírez *et al.* (2018) found reciprocal monophyly but shallow genetic divergence between *graysonii* and mainland specimens. Shallow genetic divergence is also seen in other sister species of orioles even when they possess distinctly different plumage features (e.g. Kondo *et al.* 2004).

Tres Marías endemics that require further study

WHITE-TIPPED DOVE *Leptotila verreauxi capitalis* (vs. *L. v. angelica*)

Coloration.—Breast colour 'paler and less red' in all specimens (Grant 1965a, 25 male and 21 female *capitalis* vs. 32 male and 12 female *angelica*), although the single darkest *capitalis* was almost indistinguishable from the single palest *angelica*. Also, 50% of island specimens had more extensive white throats than in all mainland birds, 75% of island birds had fewer and paler brown feathers on the thighs and flanks than 100% of mainland birds, and in c.75%



Figure 17. Above: White-tipped Dove *Leptotila verreauxi angelica*, Cruz de Huanacastle, Nayarit, Mexico, April 2019 (Marie O'Neill), below: *L. v. capitalis*, Isla María Cleofas, May 2016; note the contrasting white forecrown and cheeks, extensively whitish underparts, and darker brown back, wings and tail (Mónica G. Pérez Villafaña)

of island birds the vinous breast colour extended less far onto the belly than approximately 75% of mainland birds; 'hence island birds appear to have a larger, white abdomen' (Grant 1965a). The face is whiter due to the ear-coverts being white or whitish vs. usually pale pinkish grey, and because the white forehead reaches further posteriorly and contrasts

sharply with the hindcrown / nape / postocular area (Fig. 17; Nelson 1898). The whiter face recalls Grenada Dove *L. wellsi* and both that and the more extensive white underparts resemble Caribbean Dove *L. jamaicensis*. However, unlike those species, the ear-coverts and forehead / forecrown contrast with a pink rather than blue-grey hindcrown / nape / postocular area. Half of Grant's (1965a) *capitalis* sample was darker dorsally than 100% of his *angelica* sample, consistent with Ridgway's (1916) diagnosis and Fig. 17.

Morphometrics.—Wing, tarsus and bill longer (Grant 1965a; largest effect size is for bill length of females, score 2) whereas the tail of females is shorter, and in both sexes the white on the tail tip is slightly shorter (score 1). The presence vs. absence of sexual dimorphism in tail length is a further difference between *capitalis* and *angelica*.

Reasons for uncertainty.—The whiter underparts and face of *capitalis* resemble *L. verreauxi decolor*, *L. v. decipiens* and some *L. v. verreauxi* (e.g. hbw.com/ibc/1016351 and hbw.com/ibc/996812 from Costa Rica, hbw.com/ibc/980837 from Colombia and hbw.com/ibc/1086049, hbw.com/ibc/1002421 but not darker hbw.com/ibc/1002417 from the Lesser Antilles). Occasional White-tipped Doves from scattered localities in mainland Mexico resemble *capitalis* (e.g. <https://macaulaylibrary.org/asset/55312471>, <https://macaulaylibrary.org/asset/57930541>, <https://macaulaylibrary.org/asset/57744481>, and <https://macaulaylibrary.org/asset/39082171>) at least in some features (e.g., <https://macaulaylibrary.org/asset/25545561> with whitish ear-coverts but forehead / forecrown showing little contrast; or <https://macaulaylibrary.org/asset/43367021> with forecrown less extensive and pinker breast, or <https://macaulaylibrary.org/asset/32166601> with very whitish flanks but strongly pinkish breast, malar region and ear-coverts). We hypothesise that the mutation(s) responsible for a whitish face and underparts contrasting with the mid-crown / nape / postocular area have arisen independently several times in *Leptotila*, becoming fixed in *capitalis*, *decolor*, *decipiens*, Caribbean and Grenada Doves, but not in *L. v. verreauxi* or other races, similar to other known cases of 'parallel speciation' (e.g. Cooper & Uy 2017 and references therein). Clearly more research is needed to understand colour variation in *L. verreauxi* and relatives.

RUFOUS-BACKED ROBIN *Turdus rufopalliatu*s *graysoni* (vs. *T. r. rufopalliatu*s)

Coloration.—Underwing-coverts tawny-ochraceous contrasting with dull cinnamon sides and flanks vs. underwing-coverts concolorous or nearly so with the breast, sides and flanks (Ridgway 1907). Grey breast-band vs. grey only in the streaked feathers at the lower edge of the throat; in extreme cases this causes grey, rather than rufous, to be the dominant colour of the underparts (Grant 1965a, based on 24 male and 42 female *graysoni* vs. 32 male and 22 female *rufopalliatu*s; Howell & Webb 1995 Plate 51.3b, our Fig. 18). However, a grey breast-band sometimes shows up in mainland *rufopalliatu*s even well away from the Tres Mariás (e.g., see Fig. 19) and while some *graysoni* have the breast-band 'faintly... tinged with dull salmon-color', in mainland *rufopalliatu*s most of the breast-band is 'salmon color to almost cinnamon-rufous' (Phillips 1991). Assuming that all individuals we saw and photographed in the Tres Mariás were *graysoni*, our photographs confirm the blurred distinction (e.g., Fig. 20).

'Back grayish, usually more or less tinged with brownish but hardly, if at all, contrasted to nape' vs. 'scapulars, and usually back, strongly washed with cinnamon-rufous to russet...', in strong contrast to the grayer crown and nape (if not badly worn and faded)' (Phillips 1991). Howell & Webb (1995) described the back of *graysoni* as 'greyish-rufous to olive-brown'. Our photographs from the Tres Mariás show a range, from brown close to the upperparts of White-throated Thrush *T. assimilis* and showing little contrast with the nape and crown, to more rufous contrasting with the nape and crown (e.g., Figs. 18, 20 and 22). Upperwing-coverts 'dull cinnamon or duller' vs. 'salmon color to almost cinnamon-



Figure 18. Typical Rufous-backed Robin *Turdus rufopalliatus graysoni* with broad grey breast-band concolorous with head and nape, pale salmon flanks, brown back and wing-coverts with very little back / nape contrast, and rather narrow throat streaks, Isla María Cleofas, May 2016 (Héctor Gómez de Silva)



Figure 19. Mainland Rufous-backed Robin *Turdus rufopalliatus* far from the Tres Mariás, with an anomalous grey breast-band resembling *T. r. graysoni* and note the prominent throat streaks and warm-coloured back, wing-coverts and flanks, Cuernavaca, Morelos, Mexico, June 2017 (Juan Manuel Ramos Merino)

rufous' and sides and flanks dull orange-brown vs. rufous (Phillips 1991), which seem like subtle distinctions. All or most individuals we photographed on the Tres Mariás had sides and flanks similar to some mainland *rufopalliatus* (e.g., Fig. 21, http://2.bp.blogspot.com/-G0D2EpXGckI/VHza0MTHSjI/AAAAAAAAACSQ/sMP9Yby2Yic/s1600/_DSC0103.JPG). Grant (1965a) mentioned that *graysoni* 'show a tendency to possess paler and narrower chin and throat streaks than mainland birds, easily recognizable only when the extreme forms of the two samples are compared' (consistent with, e.g., Figs. 18 and 20). Phillips (1991) mentioned 'feet apparently darker' in *graysoni* but did not evidence this, and it is not supported by our field observations. In conclusion, individuals of *graysoni* representing the



Figure 20. Presumed Rufous-backed Robin *Turdus rufopalliat* *graysoni* with mainly narrow throat streaks, a strong salmon wash on the breast, and wing-coverts and back colours close to those of non-*graysoni* *T. rufopalliat*, Isla María Cleofas, November 2015 (Javier Cruz Nieto)



Figure 21. Mainland Rufous-backed Robin *Turdus rufopalliat* far from the range of *T. r. graysoni* with a salmon wash on the breast resembling some *graysoni*, Parque María Enriqueta, Mexico City, June 2017 (Héctor Gómez de Silva & Mónica G. Pérez Villafaña).



Figure 22. Rufous-backed Robin *Turdus rufopalliat* *graysoni* with brown back and wing-coverts resembling the upperparts colours of White-throated Thrush *T. assimilis*, Isla María Cleofas, May 2016 (Héctor Gómez de Silva)

extremes of plumage (e.g., with narrowly striped throats, predominantly grey underparts and / or brown backs) are easily identified, but there appears to be sufficient variance and overlap that colour differences cannot be adequately scored. The literature suggests that the main differences are duller plumage and no sexual dimorphism vs. much brighter, richer plumaged males (e.g., Grant 1965a, Phillips 1991, Howell & Webb 1995). Individuals of unknown sex and / or in faded plumage would not be identifiable.

Morphometrics.—Larger in all external measurements, especially tarsus length and bill length (score 2). Montaña-Rendón *et al.* (2015), based on 268 adult specimens from throughout the range of *T. rufopalliatius* (*sensu lato*), confirmed the existence of marked morphometric differences.

Additional information.—Montaña-Rendón *et al.* (2015) and Ortiz-Ramírez *et al.* (2018) found reciprocal monophyly and deep genetic divergence between *graysoni* and *rufopalliatius*.

Reasons for uncertainty.—Apparently, *graysoni* occurs sympatrically with *rufopalliatius* in coastal Nayarit (Grant 1965a, Phillips 1981, Howell & Webb 1995), with specimens of *graysoni* from Playa Novillero (west of Acaponeta), Santiago Ixcuintla, Sauta, San Blas, Chacala and Las Varas (most from February–April, but singles from 12 May and, especially, 20 June suggest residency and opportunities for interbreeding; Phillips 1981: 306; Table 2). The absence of clear distinctions in plumage between some *graysoni* and other races (see above) makes it particularly difficult to identify potential hybrids based on plumage, and there is slight overlap in morphometrics, especially bill length of females (Grant 1965a). Montaña-Rendón *et al.* (2015) and Ortiz-Ramírez *et al.* (2018) apparently did not include DNA of *graysoni* from the mainland, nor indeed of any *rufopalliatius* from the Nayarit coastal plain, where hybrids, if any, would be expected (all of their Nayarit *rufopalliatius* were from a single locality in the foothills). Because the extent of hybridisation, if any, is presently unknown, we recommend further studies before concluding whether *graysoni* represents a species.

TROPICAL PARULA *Setophaga pitiayumi insularis* (vs. *S. p. pulchra*)

Coloration.—Reddish-tinged vs. pale buff flanks (score at least 1), much less white on outer rectrix (score 1), no or scattered black feathers at base of culmen vs. entirely black ‘culmen bridge’ feathers (score 2). Additionally, only the outer pair or two of tail feathers have white in 100% of *insularis* (both sexes) vs. three outer tail feathers in 82% of male and 73% of female *pulchra* (not scored) (from Grant 1965a, based on 42 male and 20 female *insularis* from the Tres Mariás, and 11 male and eight female *insularis* from the mainland vs. 23 male and 12 female *pulchra*).

Morphometrics.—Larger in all external measurements, especially the longer tarsus in males and longer tail in females (both score 3, although this seems suspiciously high because these differences are not immediately evident to the eye) but bill in females shorter (score 1).

Reasons for uncertainty.—Race *insularis* also occurs in mangroves in mainland Nayarit (Grant 1965a), and there is a specimen from Labrados, Sinaloa (McLellan 1927) and records from Todos Santos and El Oro, Baja California Sur (Ilf *et al.* 2008). Hybrid *insularis* × *pulchra* have been documented at Peña de Jaltemba (Grant 1965a, two specimens that combine the flanks colour of *insularis* with the wing length of *pulchra* and are intermediate in tail and / or tarsus length) and San Blas (Ilf *et al.* 2008, four specimens with intermediate measurements). Also, Grant (1965a: 52) noted that his sample of mainland *insularis* somewhat approached *pulchra* in frequency of different tail patterns, and possibly also in some mensural characters, suggesting introgression. Hybridisation may be extensive where they are parapatric. Furthermore, it is also unclear if phenotypic characters differentiating



Figure 23. Tropical Parula *Setophaga pitiayumi insularis*, Isla María Cleofas, May 2016; note the reddish-tinged flanks and lack of black feathers above the base of bill (Mónica G. Pérez Villafaña)

insularis may partially bridge the gap between *S. p. pulchra* and race *graysoni* from Socorro Island. Tail length of *insularis* is much closer to *graysoni* than *pulchra* (Ridgway 1902; under Socorro Parula, del Hoyo & Collar 2016 cite mean tail lengths for male *insularis* and *pulchra* that are too short, cf. Ridgway 1902).

In plumage, adult *graysoni* generally resembles juveniles of other races of *S. pitiayumi*. However, there may be a stepped cline in the percentage of adults with juvenile-like plumage; *insularis* is intermediate in proportions and especially the extent of black in the lores and orbital area (Grant 1965a: 38). Also, while black is usually thought to be completely absent in the face of *graysoni*, Baptista & Martínez-Gómez (2002: 38) found that a small percentage of individuals do show some black. There may also be a cline in the extent of white in the rectrices between *pulchra*, *insularis* and *graysoni* (Regelski & Moldenhauer 2012).

All of the above indicates that *graysoni* is perhaps not as phenotypically distinct from *pitiayumi* as scored by del Hoyo & Collar (2016) who considered *graysoni* to be a separate species, while simultaneously overlooking one important character of *graysoni* that sets it apart from the rest of *S. pitiayumi*, namely the grey of the face extends to include the malar in *graysoni* (as in Northern Parula *S. americana*) vs. the yellow of the throat extends up to include the malar in *pitiayumi* including *insularis* (Dunn & Garrett 1997, Iliff *et al.* 2008). Also, del Hoyo & Collar (2016) tentatively added a score of 2 to the diagnosis of *graysoni* based on a 'more complex voice, involving several songs, resembling those of *S. ruticilla*, *S. pensylvanica* and *S. americana*' while *insularis* apparently has a similar varied repertoire (HGdS pers. obs.). Furthermore, *S. pitiayumi* (with or without *graysoni*) may be paraphyletic with respect to *S. americana* (Lovette & Bermingham 2001, Evans *et al.* 2015). The situation is clearly very complex and requires further study, including testing the extent of introgression / hybridisation of *insularis* and *pulchra* on the Nayarit (and Sinaloa?) mainland, and a phylogeographic study of *S. pitiayumi* (*sensu lato*) with samples from throughout the species' range.

NORTHERN CARDINAL *Cardinalis cardinalis mariae* (vs. *C. c. affinis*)

Coloration.—Based on 44 male and 35 female *mariae* vs. ten male and six female *affinis*, Grant (1965a) reported that 92% of males had a purple tinge to the plumage vs. 100% without any purple tinge (score 1), 100% of *mariae* females had cream-white abdomens vs. pale buff in 83% (score 1); and the grey chin and throat of females covered a larger area vs. more restricted white or rarely grey chin (score 2, grey is caused by ‘the black basal half of the feather showing through the overlying white feather-tips, and in island specimens the extent of white in the feather tip is reduced’).

Morphometrics.—Longer wing, tarsus and bill (especially bill length in males) (score 2) but shorter tail (score 2). Bill more bulging (consistent with Ridgway 1901 [not scored]).

Additional information.—Smith *et al.* (2011), Smith & Klicka (2013) and Ortiz-Ramírez *et al.* (2018) found reciprocal monophyly and deep genetic divergence between *mariae* and mainland specimens. Smith & Klicka (2013) and Ortiz-Ramírez *et al.* (2018) reported that small population size has accelerated molecular evolution in *mariae*.

Reasons for uncertainty.—Grant’s (1965a) sample of *affinis* was inadequate (morphometric characters were evaluated in 4–9 males and six females, and plumage characters in ten males and six females), which is especially problematic because female plumage apparently fades considerably in specimens and males display extensive individual variation (Van Rossem 1932). Furthermore, Baja California race *igneus* is as likely to be the sister species of *mariae* as *affinis*, and it was not explicitly compared by Grant (1965a) who stated only that ‘five specimens of *igneus* were available too, and it was noted that [*mariae*] differed from both subspecies (*igneus* and *affinis*) mainly in the same way.’ Nelson (1898) in the original description of *mariae* described it as being closest to *igneus*, and at least in bill shape it is intermediate between *mariae* and *affinis* (Ridgway 1901: 648–649). Ortiz-Ramírez *et al.* (2018: 726) mentioned that when analysing the haplotype network, *mariae* was closer to *igneus* than *affinis*, although this apparently contradicts both their own highest-probability scenario of colonisation (in their Fig. 4) and the phylogenies of Smith *et al.* (2011) and Smith & Klicka (2013). Therefore, this case requires further study.

Discussion

Following the taxonomic ranking criteria of Tobias *et al.* (2010) we propose / endorse elevating to species six Tres Marías endemic birds (Table 1). This number of endemic species represents 16% of the islands’ resident landbirds, which compares closely with the 14% of Mexican mainland species that are endemic (*sensu* Berlanga *et al.* 2015). It would be surprising for an archipelago that is 80+ km from the mainland to have no or very few endemic species. By comparison, Cozumel Island is just 19 km from the mainland and <7% of its breeding landbirds are endemic, Guadalupe Island is 240 km from the mainland and 7–8% are endemic, and the Revillagigedo archipelago is 700+ km from the mainland and 25% are endemic (following Howell & Webb 1995, Appendices C–D).

The relatively recent (Early to Mid-Pleistocene, see Study area above) emergence of the Tres Marías Islands and their proximity to the mainland might suggest that endemism is unlikely to be a strong feature of the fauna, but Cozumel Island, which has 3–4 endemic bird species and a similar number of endemic mammals, emerged even more recently, in the Late Pleistocene, c.120,000 years ago (Spaw 1978).

While hybridisation between a Tres Marías endemic and its mainland relative had been documented for *Setophaga pitiayumi*, we provide evidence suggesting occasional interbreeding between Tres Marías Islands and adjacent mainland taxa in another three cases.

While biodiversity loss is much more than the extinction of species (e.g., Ceballos & Ehrlich 2002, O'Grady *et al.* 2004), we trust that, by drawing attention to the existence of endemic birds that merit recognition as species, the uniqueness and conservation importance of the Tres Mariás has been highlighted. Different species of breeding landbirds on the Tres Mariás show varying degrees of distinctiveness from their nearest mainland counterparts, at both the subspecific (Grant 1965a) and the species levels (herein). Tres Mariás landbirds provide a fascinating case study of speciation in process; their study contributed to the early research and understanding of evolution by the influential ecologist Peter R. Grant (e.g. Grant 1965b, 1965c).

It is well known that insular ecosystems and avian populations are seriously damaged by introduced goats, cats and rats, all of which now occur on at least the three larger Tres Mariás islands (Gómez de Silva *et al.* 2017: 3). These exotic species have been successfully removed from other islands off western Mexico (Aguirre-Muñoz *et al.* 2008), but planned eradication programmes in the Tres Mariás (Grupo de Conservación de Islas 2007a,b, Universidad Autónoma de Baja California 2008) have not been effected. Introduced mammals are currently the most serious threat to Tres Mariás biota, and we hope that their removal can be undertaken soon.

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A review of the status, distribution and ecology of Friedmann's Lark *Mirafrapa pulpa*, including its habitat associations

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SUMMARY.—Friedmann's Lark *Mirafrapa pulpa* is a poorly known species endemic to East African savannas, and classified as Data Deficient by BirdLife International. In light of our limited knowledge, I reviewed the species' ecology, status and distribution, finding no more than 51 dated records (or discrete periods of occurrence) in a search of the literature and internet databases. However, the restriction of these records to two distinctive regions of the Chyulu and Nyambeni foothills suggests that Friedmann's Lark may be closely tied to pockets of ash-based soil associated with geologically recent volcanic formations. These gritty, white-coloured soils are characterised by slower drainage in contrast to the region's otherwise widely occurring red soils, and retain year-round the dense grass cover apparently preferred by *M. pulpa*. It is therefore likely to be the distribution of these ash-based soils and associated dense grassland that determines the distribution of Friedmann's Lark. Based on this hypothesis, and the species' well-known erratic occurrence, its year-round area of occupancy may amount to no more than 20% of its overall extent of occurrence, amounting to c.5,000 km², potentially qualifying Friedmann's Lark as Near Threatened under IUCN criteria.

Following the discovery of Friedmann's Lark in 1912 (Friedmann 1930a), and a gap of five decades before the species was encountered again, basic knowledge of the species began to improve between the 1970s and 1990s, when it was found on several occasions in the Tsavo area of southern Kenya (Lack 1977, Pearson *et al.* 1992, Zimmerman *et al.* 1996). Subsequently, it has been reconfirmed to occur in the Shaba area of central Kenya, close to where specimens were collected in 1912 (Friedmann 1930b, Records Sub-committee 2002), yet numbers appear to be small, and several key questions concerning the species' precise habitat requirements and breeding ecology remain unanswered. Because of these fundamental shortfalls, no threat category has been assigned to the species to date, and it remains in the 'holding category' Data Deficient (Butchart 2007, BirdLife International 2020).

Complicating an assessment of the species' ecology and conservation needs, Friedmann's Lark is a notoriously cryptic species. It tends to sing during only a few wet months of the year, while its occurrence at even better-known sites is frequently erratic. Although its song is very distinctive, the species' morphological similarity to Singing Bushlark *M. cantillans* has commonly posed identification problems in the past (Lack 1977, 1992).

However, following the publication of accurate field guides in the late 1990s and early 2000s, and with now easily accessible audio material, knowledge of the species among field observers has improved significantly in the last two decades. This has resulted in a slowly growing number of records, and permits a closer review of the species' ecology and status than was previously possible. A question of particular importance, on which I seek to shed

some light here, concerns the factors behind the patchy distribution and specific habitat requirements of Friedmann's Lark, and the seasonality of its occurrence.

Status and distribution

Friedmann's Lark is known only from southern Ethiopia, and central Kenya south to northern Tanzania (Lack 1992). Knowledge of the species' ecology was well summarised by Lewis & Pomeroy (1989), who considered it to be an obscure inhabitant of bushed grasslands, seen during sporadic influxes associated with rains, and also, at least locally, a nocturnal migrant (Pearson *et al.* 1992). Areas of repeated occurrence, supported by both historic and / or recent records, include the following.

(1) Archer's Post and the adjacent Buffalo Springs and Shaba National Reserves in north-central Kenya (Friedmann 1930b, Records Sub-committee 2002, Borrow 2010), covering an area of *c.*1,500 km². Reports are almost exclusively in April–May, but also in August and November. Juvenile specimens taken in May 1912 (Lewis & Pomeroy 1989; Appendix 1), are thought by some to perhaps involve same-age Singing Bushlarks *M. cantillans* (P. A. Donald *in litt.* 2019), but otherwise represent the only breeding data for the species.

(2) The Tsavo region of southern Kenya, extending south into northern Tanzania (Lack 1977, Pearson *et al.* 1992, Zimmerman *et al.* 1996; N. Baker *in litt.* 2019, B. Finch *in litt.* 2019), and covering approximately 23,500 km². Within this broader range, the few regularly frequented areas (>3 records) include the plains north-east of Kilaguni Lodge in Tsavo West National Park, the western part of Tsavo East National Park, the Taita Hills lowlands including the Maktau area and Rukinga Ranch, and Mkomazi Game Reserve in northern Tanzania. A small number of records immediately south-west of the Pare Mountains, in northern Tanzania, mark the southern limit of the range. Most reports from these areas are in April–May and November–January, supplemented by scattered dry-season records in February–March and August–September.

Aside from these two regions, wanderers (presumably from the Tsavo population) have been found at several places. The type specimen (Friedmann 1930a), collected at the Sagan River in southern Ethiopia in May 1912, and the sole record from that country (Ash & Atkins 2009), is generally believed to have involved a wanderer. North-east of Tsavo West National Park, wandering birds were found at Kiboko in the 1960s and 1970s (Lewis & Pomeroy 1989; audio recording by M. North), while Zimmerman *et al.* (1996) mentioned a record at nearby Kibwezi, although the date is unknown. Reports of the species from the northern Kenya Rift Valley, at Kapedo and in the Ilemi Triangle in the 1980s, are now thought to be erroneous based on a reappraisal by the original observer (Lack 1992; P. Lack *in litt.* 2019). Consequently, the two areas detailed above encompass the sole regularly known distribution of Friedmann's Lark. Where known, coordinates of records are provided in the Gazetteer.

The two areas inhabited by this lark are characterised by an arid-semiarid, bimodal rainfall regime, with annual rainfall amounting to 250–1,000 mm, falling primarily in March–May and October–December (Brown & Britton 1980, Lewis & Pomeroy 1989). Although records during the dry months are very few (Fig. 1b), and the species is also sometimes unrecorded for several consecutive years (Fig. 1a), Friedmann's Lark may undergo mass breeding and irruptive dispersal events during and following good rains, such as those preceding December–January occurrence in well-grassed areas of Tsavo East National Park (Lack *et al.* 1980). It has been found in good numbers on rare occasions during particularly suitable rainfall conditions (e.g., Pearson *et al.* 1992). However, this

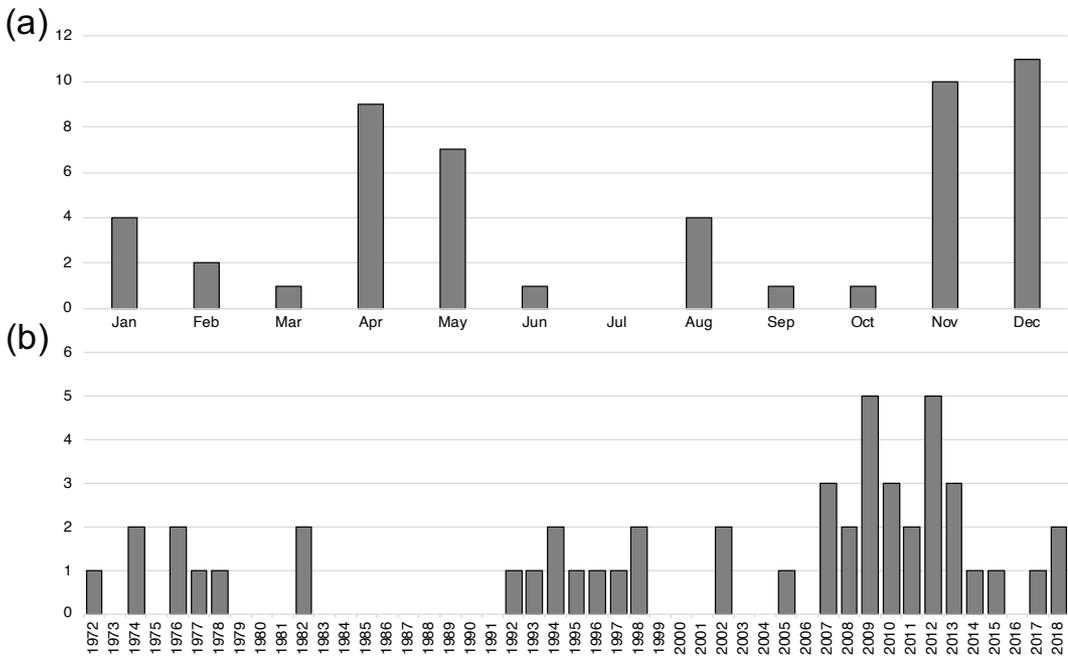


Figure 1(a) Monthly (1912–2018) and (b) annual (since 1972) summaries of Friedmann's Lark *Mirafra pulpa* records.

sporadic abundance has yet to be studied in detail, and its breeding ecology is wholly unknown (Ryan & Sharpe 2019). With no repeat occurrences of the 100+ birds observed in Tsavo East in December 1992 (Pearson *et al.* 1992), and the whereabouts of most individuals when not singing during the rains being largely unknown (Lack 1977, Borrow 2010), it appears that Friedmann's Lark is genuinely rare. The absence of records from the well-watched Buffalo Springs / Shaba areas, between the specimens collected there in 1912 and its rediscovery in May 2002 (Records Sub-committee 2002), which itself could have involved local extirpation followed by re-colonisation, suggests a precarious existence for the species in that area.

While this lark has been described as 'seasonally uncommon' (Lack *et al.* 1980, Lack 1985), it is otherwise known from some 51 dated records or discrete periods of occurrence, as determined by my personal communications with field observers, a search for literature records, and a review of reports in online databases and digital media platforms (e.g., eBird, iNaturalist, The British Library of Sounds, xeno-canto.org, the Macaulay Library, Surfbirds.com, bird tour company trip reports, and YouTube). All but eight records are from Kenya, and there are just seven specimens, and 20 records documented by in-hand examination, video, photographs or audio recordings. Another 26 records regarded here as reliable are based on sight records by experienced observers familiar with the species (Appendix 1). Numbers reported since Pearson *et al.* (1992), primarily during suitably wet conditions, have never exceeded ten singing males and in most cases, involved only 2–4 or 'several' singing birds. Numbers are likely to be considerably lower during years of (presumably) suboptimal conditions when the species is not reported at all (e.g., 1999–2001 and 2003–04; Fig. 1a).

Habitat associations

Vegetation communities typically frequented by Friedmann's Lark include particularly dense grassland up to 1 m tall with some bare ground, and a range of woody shrubs covering 2–8% (Lack 1977, Pearson *et al.* 1992). Areas that have recently burned may also be favoured (Pearson *et al.* 1992) but sites where dense grass cover dies back and thins out during the dry months, such as in parts of Tsavo East National Park, are not thought to be occupied year-round (Lack *et al.* 1980, Lack 1997). A few records in the dry months of February and August–September at Lake Jipe, Mkomazi Game Reserve and Shaba National Reserve, however, suggest probable year-round presence in at least some areas. At these sites, immediately adjacent to major highland areas with relatively high annual rainfall, locally moist conditions may permit suitably dense grass cover to persist throughout the year. The importance of dense grassland is echoed by Lack (1977) who noted a preference for the western side of Tsavo East National Park, which is wetter and more densely grassed than the east. Behaviours noted in the field include a tendency to sing from bushed

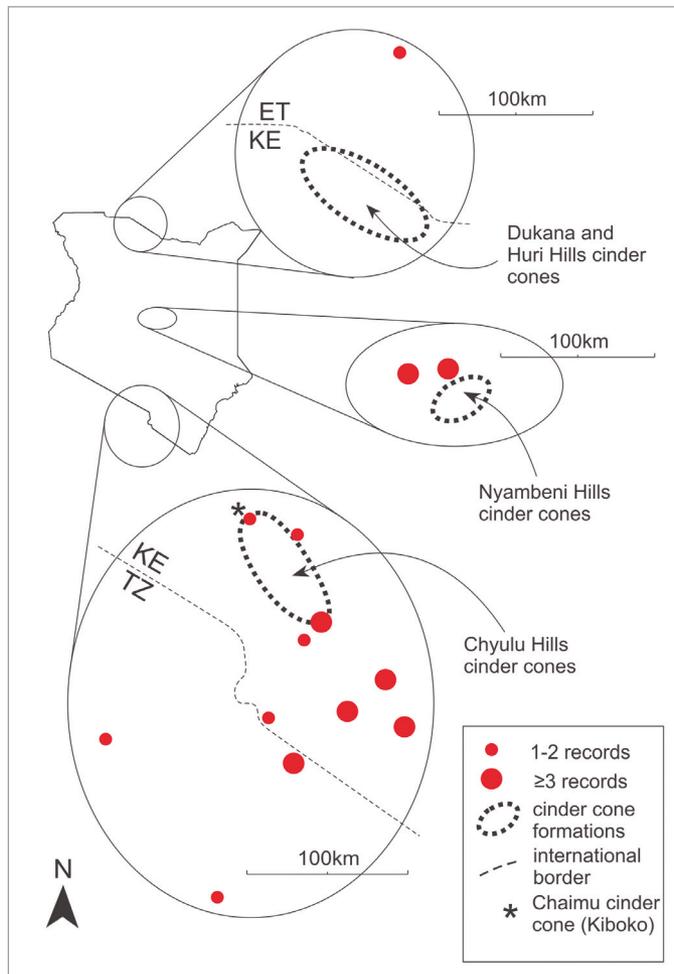


Figure 2. Spatial distribution of records of Friedmann's Lark *Mirafra pulpa* records in relation to the cinder-cone formations of the Dukana / Huri Hills in Kenya (KE) and Ethiopia (ET), and the Nyambeni and Chyulu Hills in Kenya. Records extend to Tanzania (TZ).



Figure 3. Satellite imagery (© Google Earth) showing the denser grassland and poorer drainage (evidenced by abundant water pans) that characterise white ash-based soils (right side) in comparison to red soils (left side) in the Kilaguni Lodge area of Tsavo West National Park (Kenya).

grassland on low ridges (B. Finch *in litt.* 2019), while all sites of regular occurrence are at elevations between 500 and 1,100 m (up to a max. of 1,400 m).

A possibly important observation not yet made with respect to the distribution of some favoured areas, relates to the soils at these sites and their proximity to recent volcanic activity. A review of the wider geography of the two regions regularly frequented by Friedmann's Lark shows these areas to be immediately adjacent to volcanic cinder-cone formations. At both the southern end of the Chyulu Hills and the Nyambeni Hills, basaltic cinder cones date from the late Pleistocene to Holocene, with some eruptions recorded in the Chyulu Hills as recently as the 19th century (Hackman *et al.* 1989, Haug & Strecker 1995). Cinder cones are indicative of light pyroclastic lava that commonly forms ash deposits, which give rise to distinctive soils. The Tsavo region, and areas south to Mkomazi Game Reserve, are within reach of ash falls from the cinder cones of the southern Chyulu Hills, and the Buffalo Springs-Shaba region is only a short distance north of the cinder cone formations of the Nyambeni Hills (Fig. 2).

In both these areas, soils on which the densest grassland habitat forms are commonly gritty and whitish in colour, sometimes found on low ridges, and probably formed from ash ejected by the nearby cinder cones. Such volcanic ash-based soils appear to have unique drainage characteristics, retaining sufficient moisture during dry periods to permit the formation of dense grassland year-round. Satellite imagery showing dense grassy cover on white soils vs. red soils, with the former also characterised by abundant water pans (Fig. 3), supports this theory. In Kenya, such white volcanic ash-based soils and their associated grassland type are apparently restricted to the environs of these two ranges of hills.

Discussion and Conclusions

While Williams's Lark *M. williamsi* is well known to favour weathered lava-based soils in Kenya (Zimmerman *et al.* 1996), an association with volcanic soils has not previously been suggested for Friedmann's Lark. Such a habitat specialisation, related to the distribution

of a particular type of ash deposit (vs. lava), may help to explain this species' puzzling distribution. While there are records of Friedmann's Lark from soil types other than ash-based soils, this appears to be the case only after heavy rains result in a fresh cover of dense grassland on other soils (e.g., December–February in Tsavo East National Park; Lack 1985). As grassland on soils other than those formed from ash thins out during the dry season, these areas apparently become unsuitable for the species, with for example only *M. cantillans* recorded with certainty on the red soils of Tsavo East National Park in May–November (Lack 1985). It seems possible that during these dry periods, birds retreat to areas closer to the cinder-cone formations, where ash-based soils and associated dense grassland are more abundant. In this context, the distribution of this soil-grassland association would comprise the core of the species' range, and while *M. pulpa* may disperse nocturnally into nearby dense grasslands on other soil types following adequate seasonal rains, it is unable to colonise them permanently because they do not offer sufficiently dense habitat year-round. Further supporting the view that grassland on ash-based soils is indeed the preferred habitat, and the source of seasonal dispersal, is the observation of more than 100 singing birds in a small area of white soils in the immediate vicinity of the southern Chyulu Hills, near Kilaguni, in the early 1990s (Pearson *et al.* 1992), as well as the 1965 record from Kiboko (Appendix 1), involving one or more birds singing on the flanks of the Chaimu cinder cone.

In light of my review, the global conservation status of Friedmann's Lark may warrant updating to reflect its small global distribution, intermittent occurrence, highly specialised habitat requirements within broader savanna ecosystems, and its apparently genuine rarity. While there are still no robust data from which to estimate population size, several observations outlined herein permit an assessment of extinction risk for Friedmann's Lark against other threat criteria which are geography-based (IUCN 2012). While the global extent of occurrence of Friedmann's Lark, based on two widely separated subpopulations, is large, the year-round area of occupancy within this range is undoubtedly considerably smaller. Within the regional extent of occurrence of both subpopulations, records are very patchily distributed and large areas appear to be either entirely unoccupied or used on only a seasonal or sporadic basis. Based on this, unoccupied areas may amount to <20% of the 25,000 km² identified as the regional extent of occurrence (see Status and Distribution), resulting in an area of occupancy that is unlikely to exceed 5,000 km². This figure approaches the 2,000 km² threshold for qualification as Vulnerable under criterion B2. As such, and given that regularly occupied sites (three or more records) number scarcely ten in total, Friedmann's Lark may merit the status Near Threatened. That changes in rainfall patterns related to climate change might adversely affect Friedmann's Lark within this small global range is also cause for concern. Coupled with predicted climatic stochasticity, such cyclical population dynamics as shown by the species could render it increasingly vulnerable to risk of extinction.

Targeted surveys and basic ecological knowledge are much needed for Friedmann's Lark, and should focus on: (1) estimates of population size in either or both of the known regions of occurrence, with a focus on documenting its breeding ecology and variation in population size related to rainfall, and (2) searches for Friedmann's Lark in other areas of potentially suitable habitat, especially in proximity to cinder-cone formations and ash-based soils associated with the Gregory Rift System, particularly during dry periods.

The latter include formations on the western slopes of the Huri Hills (03°36'35"N, 37°49'31"E), and the nearby Dukana Hills and Mega Basalt Field (04°00'00"N, 37°20'23"E). Both of these geological features are within 150 km of the type locality in southern Ethiopia, and should be surveyed following seasonal rains, both for the lark and to assess the

grassland habitat. Given that southern Ethiopia is some 500 km from the population in the Buffalo Springs / Shaba area, it is possible that an undiscovered population closer to southern Ethiopia might account for the type specimen, perhaps in the vicinity of the above-mentioned regions of remote northern Kenya.

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Appendix: List of dated records of Friedmann's Lark *Mirafra pulpa* (NMK = National Museum of Kenya, Nairobi, reg. no., USNM = US National Museum, Smithsonian Institution, Washington DC, reg. no., BLS = British Library of Sound recording no., IBC = Internet Bird Collection media no., ML = Macaulay Library media no., XC = Xeno-canto recording no., iNat = iNaturalist media no.). NP = National Park; NR = Nature Reserve.

Date	Observer	Country	Location	Documentation	Source
1 19 May 1912	E. Mearns	Ethiopia	Sagan River, Shoa	Type specimen	Friedmann (1930a); USNM 246241
2 2 Aug 1912	E. Mearns	Kenya	Archer's Post, Buffalo Springs NR	Specimens	Friedmann (1930b); USNM 246219, 246221, 246222

Date	Observer	Country	Location	Documentation	Source
3 2 Apr 1965	M. North	Kenya	Chaimu Hill, Kiboko	Audio recording	ML 8044
4 2 Dec 1972	G. Backhurst	Kenya	Ngulia Lodge, Tsavo West NP	Specimen	Lack (1977); NMK 16142
5 8 Jun 1974	A. R. Gregory	Kenya	Kiboko	Audio recording	BLS 022M-WA03044X0031-0018V0
6 12 Nov 1974	D. Pearson	Kenya	Ngulia Lodge, Tsavo West NP	Specimen	Lack (1977); NMK 16143
7 30 Mar 1976	P. Lack	Kenya	Tsavo East NP	Sight record	Lack (1977)
8 16 Apr 1976	P. Lack	Kenya	Tsavo East NP	Sight record	Lack (1977)
9 4 Jan 1977	P. Lack	Kenya	near Voi Safari Lodge, Tsavo East NP	Specimen	Lack (1977); NMK 16144
10 29 Nov 1978	D. Pearson	Kenya	Ngulia Lodge, Tsavo West NP	Ringed	Turner <i>et al.</i> (1978)
11 15 Aug 1982	D. Turner	Kenya	Lake Jipe, Tsavo West NP	Sight record	Turner & Pearson (1983)
12 2 Dec 1992	D. Pearson	Kenya	12 km NE of Kilaguni Lodge, Tsavo West NP	Audio recording	Pearson & Turner (1998)
13 4 Dec 1993	Ngulia Ringers	Kenya	Ngulia Lodge, Tsavo West NP	Ringed	Pearson & Turner (1998)
14 19 Sep 1994	N. Baker	Tanzania	Mkomazi Game Reserve	Photograph	Turner (1998)
15 1994 (Nov)	N. Baker	Tanzania	Mkomazi Game Reserve	Sight record	Tanzania Bird Atlas unpubl. data
16 1995 (Dec)	P. Lack	Tanzania	Mkomazi Game Reserve	Sight record	Turner (1998)
17 1996 (Jan)	P. Lack	Tanzania	Mkomazi Game Reserve	Sight record	Tanzania Bird Atlas unpubl. data
18 1997 (Dec)	G. Backhurst	Kenya	35 km west of Ngulia Lodge, Tsavo West NP	Sight record	Backhurst (1997)
19 4 Feb 1998	D. Fisher	Kenya	Lake Jipe Lodge area, Tsavo West NP	Audio recording	BLS W1CDR0000788 (available offline only)
20 1998 (Aug)	N. Baker	Tanzania	Terat	Sight record	Tanzania Bird Atlas unpubl. data
21 29 May 2002	C. Jackson	Kenya	Shaba NR	Sight record	Records Sub-committee (2002)
22 2002 (Oct)	B. Finch	Kenya	Rukinga Ranch, 40 km SSW of Voi	Sight record	Records Sub-committee (2002)
23 18 Dec 2005	R. Bishop	Kenya	3.5k m SW of Kilaguni Lodge, Tsavo West NP	Sight record	pers. comm.
24 22 Apr 2007	B. Finch	Kenya	Shaba NR	Sight record	pers. comm.
25 15 Aug 2007	B. Finch	Kenya	Shaba NR	Photograph	pers. comm.
26 7 Nov 2007	B. Finch	Kenya	Buffalo Springs NR	Video	pers. comm.
27 3 Nov 2008	N. Borrow	Kenya	Shaba NR	Photograph	Borrow (2010)
28 1 Dec 2008	B. Finch	Kenya	Salt Lick Lodge, Maktau, Tsavo West NP	Sight record	pers. comm.
29 6 Apr 2009	C. Kariuki	Kenya	Maktau Gate area, Tsavo West NP	Sight record	pers. comm.
30 15 Apr 2009	B. Finch	Kenya	Shaba NR	Sight record	pers. comm.
31 11 May 2009	B. Finch	Kenya	Shaba NR	Sight record	pers. comm.
32 28 Nov 2009	A. Smets	Kenya	Tsavo East NP	Photograph	Borrow (2010)
33 15 Dec 2009	A. Jacot	Kenya	Kilaguni Lodge area, Tsavo West NP	Video	https://www.youtube.com/watch?v=J_rKiWE8ESk
34 2 May 2010	C. Davies	Kenya	Shaba NR	Audio recording	XC 57940

Date	Observer	Country	Location	Documentation	Source
35 20 May 2010	C. Kariuki	Kenya	Shaba NR	Sight record	pers. comm.
36 19 Nov 2010	B. Finch	Kenya	Kilaguni Lodge area, Tsavo West NP	Sight record	pers. comm.
37 2011 (Apr)	B. Finch	Kenya	Maktau Gate area, Tsavo West NP	Sight record	pers. comm.
38 2011 (Nov)	N. Borrow	Kenya	Buffalo Springs NR	Photograph	Surfbirds Gallery
39 2012 (Jan)	H. Matheve	Kenya	Rukinga Ranch, 40 km SSW of Voi	Sight record	pers. comm.
40 7 Apr 2012	B. Finch	Kenya	Kilaguni Lodge area, Tsavo West NP	Sight record	pers. comm.
41 28 Apr 2012	M. Lilje	Kenya	Shaba NR	Photograph	iNat 7131884
42 2012 (Nov)	P. Morris	Kenya	Buffalo Springs NR	Sight record	Birdquest trip report
43 23 Dec 2012	N. Baker	Tanzania	Kitwai Plains	Sight record	Tanzania Bird Atlas unpubl. data
44 1 Jan 2013	C. Kariuki	Kenya	Rukinga Ranch, 40 km SSW of Voi	Sight record	pers. comm.
45 7 Feb 2013	N. Baker	Tanzania	Kitwai Plains	Sight record	Tanzania Bird Atlas unpubl. data
46 2013 (May)	A. Scott Kennedy	Kenya	Kilaguni Lodge area, Tsavo West NP	Photograph	Surfbirds Gallery
47 15 Dec 2014	L. Petersson	Kenya	Tsavo East NP	Photograph	IBC 1311265
48 3 Dec 2015	C. Kariuki	Kenya	Rukinga Ranch, 40 km SSW of Voi	Sight record	pers. comm.
49 24 Nov 2017	M. Cade	Kenya	Kilaguni Lodge area, Tsavo West NP	Video	https://www.youtube.com/watch?v=RoqH_4xBFII
50 17 Apr 2018	M. Grant	Kenya	Buffalo Springs NR	Photograph	ML 108545821
51 18 May 2018	D. Bormann	Kenya	Buffalo Springs NR	Photograph	ML 102482451

Gazetteer

Site	Locality	Coordinates
Ethiopia	Sagan River, Shoa	05°02.827'N, 37°42.042'E
Kenya	12 km NE of Kilaguni Lodge, Tsavo West NP	02°49.778'S, 38°08.000'E
Kenya	3.5 km SW of Kilaguni Lodge, Tsavo West NP	02°56.153'S, 38°02.912'E
Kenya	35 km W of Ngulia Lodge, Tsavo West NP	03°05.520'S, 37°54.477'E
Kenya	Archer's Post, Buffalo Springs NR	00°37.395'N, 37°40.306'E
Kenya	Buffalo Springs NR	00°33.107'N, 37°37.001'E
Kenya	Chaimu Hill, Kiboko	02°15.431'S, 37°43.273'E
Kenya	Kilaguni area, Tsavo West NP	02°55.609'S, 38°03.609'E
Kenya	Lake Jipe Lodge area, Tsavo West NP	03°36.041'S, 37°46.960'E
Kenya	Maktau Gate area, Tsavo West NP	03°24.420'S, 38°07.112'E
Kenya	near Voi Safari Lodge, Tsavo East NP	03°20.619'S, 38°33.520'E
Kenya	Ngulia Lodge, Tsavo West NP	03°00.823'S, 38°12.642'E
Kenya	Rukinga Ranch, 40 km SSW of Voi	03°45.312'S, 38°29.645'E
Kenya	Salt Lick Lodge, Maktau, Tsavo West NP	03°32.804'S, 38°12.936'E
Kenya	Shaba NR	00°38.433'N, 37°55.937'E
Kenya	Tsavo East NP	03°13.356'S, 38°38.254'E
Tanzania	Kitwai Plains	04°54.038'S, 37°34.545'E
Tanzania	Mkomazi Game Reserve	03°58.132'S, 38°00.490'E
Tanzania	Terat	03°55.879'S, 36°34.051'E

Azara's no. 243 'Trepador de pico corto' is a Lesser Woodcreeper *Xiphorhynchus fuscus*

by Paul Smith

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SUMMARY.—The identity of Azara's no. 243 'Trepador pico corto' has never convincingly been elucidated, and the only previously proposed identification is demonstrably incorrect. Azara provided a brief but diagnostic description in which he mentioned clear differences from his no. 242 'Trepador común' (= Narrow-billed Woodcreeper *Lepidocolaptes angustirostris*). It is possible to confirm the identity of his no. 243 as Lesser Woodcreeper *Xiphorhynchus fuscus* (Vieillot, 1818). To my knowledge no scientific names were ever proposed on the basis of this description.

The pioneering natural history studies of the Spanish military engineer Félix de Azara (1742–1821) in Paraguay and the La Plata Basin represented one of the first serious attempts to document the fauna of the southern cone of South America (Beddall 1983). Azara produced a remarkably detailed three-volume descriptive work on the region entitled *Apuntamientos para la historia natural de los pájaros del Paraguay y Río de la Plata* (Azara 1802–05), introducing many of its birds to a European audience for the first time. Azara had no formal biological training, but grouped birds into 'families' based on his own observations of similarities in structure, and his keen eye for detail enabled him to correctly identify taxonomic relationships with surprising success (though not of course without some mistakes). He did not apply scientific names to his descriptions, instead giving his species vernacular names alone. The unpublished Spanish original was translated into French by Charles-Nicolas-Sigisbert Sonnini de Manoncourt (Azara 1809), and subsequently Louis Jean-Pierre Vieillot attached scientific names to many of these descriptions. More than half of the 448 species that Azara described proved to be new to science. A detailed chronology of his travels, life and work was provided by Contreras (2010).

However, to date not all of Azara's descriptions have been conclusively associated with known species, and a series of authors have attempted to re-identify these descriptions and apply them to known taxa (Sonnini in Azara 1809, Hartlaub 1847, Berlepsch 1887, Bertoni 1901, Laubmann 1939, Pereyra 1945, Smith 2017, 2018a,b,c,d, in press, Smith *et al.* 2018). A brief paragraph of text dedicated to no. 243 'Trepador pico corto' is one of the descriptions that has never been satisfactorily associated with any known species. Azara (1805) used his text to distinguish this bird from his no. 242 'Trepador común' which refers to Narrow-billed Woodcreeper *Lepidocolaptes angustirostris* (Fig. 1). The original description is reproduced below with original punctuation and my own translation follows it, including a conversion of measurements into modern units (unit conversion: 1 inch = 25.4 mm; 1 line = 2.21 mm).

'No sé sino que le compré muerto en el Paraguay. Longitud 7 ½ pulgadas: cola 2 7/12: braza 10 5/6. Anteriormente había comprado otro idéntico que era cerca de una pulgada menor. Todas las tintas y su distribución son lo mismo que en el precedente, á quien tuve á la vista para el cotejo; sin mas diferencia que ser las blanquizas no tan claras, y todas las demás mas vivas y fuertes. Las únicas diferencias que encontré en el resto se reducen, á que el pico del anterior es 5 líneas mas largo, aunque del mismo grueso, material y forma. La boca de aquel era blanquizca, y la del presente amarilla. La



Figure 1. Narrow-billed Woodcreeper *Lepidocolaptes angustirostris*, Teniente Enciso National Park, Boquerón department, Paraguay, July 2006 (Paul Smith)



Figure 2. Lesser Woodcreeper *Xiphorhynchus fuscus*, Hotel El Tirol, Itapúa department, Paraguay, June 2005 (Paul Smith)

lengua del precedente poco más angosta y más aguda, y la cola algo menos vigorosa y cóncava. Estas diferencias me han parecido muy suficientes para creerlos de diversa especie; pues en esta familia, como en todas las abundantes en caracteres comunes, tiene mas peso qualquiera diferencia, que muchas identidades; y la que hay en la longitud del pico es aquí muy grande'.

'I know nothing more than I bought it dead in Paraguay. Length $7\frac{1}{2}$ inches: tail $2\frac{7}{12}$: wingspan $10\frac{5}{6}$. Previously I had bought another identical specimen that was almost an inch smaller. All of the colours and their distribution are the same as those of the previous

TABLE 1

Comparative measurements between Azara's nos. 242 and 243, and Paraguayan individuals of Narrow-billed Woodcreeper *Lepidocolaptes angustirostris* (trapped in Parque Nacional Teniente Enciso, dpto. Boquerón) and Lesser Woodcreeper *Xiphorhynchus fuscus* (Hotel El Tirol and Estancia Nueva Gambach, dpto. Itapúa). Comparative measurements of another confusion species, Scalloped Woodcreeper *Lepidocolaptes falcinellus* are based on Brazilian specimens from the literature. Measurements (in mm) were taken from live birds by PS, or are referenced to source. Bill length was measured along the culmen from the bill tip to the feathers by both PS and Azara, with Silva & Straube (1996) measuring bill from the tip to the anterior edge of the nares (resulting in a slightly shorter comparative measurement). Bill depth was measured at the anterior edge of the nares by PS, and at the bare area adjacent to the feathers of the bill base by Azara. Tail length was measured along the underside of the tail from the base to the tip of the longest feathers by all sources (described by Azara as 'from the coccyx to the tip of the tail').

	No. 242	No. 243	<i>Lepidocolaptes angustirostris</i> (n = 12)	<i>Xiphorhynchus fuscus</i> (n = 6)	<i>Lepidocolaptes falcinellus</i> (Silva & Straube 1996)
Body length	209.5 ('others are somewhat smaller')	165.1–190.5	180–220 (Marantz <i>et al.</i> 2019c)	150–185 (Marantz <i>et al.</i> 2019b)	170–200 (Marantz <i>et al.</i> 2019d)
Tail length	76.2	65.6	76.0 (69–83)	71.2 (68–75)	81.8 (78.9–85.5, n = 114)
Bill length	33.2	22.1	31.5 (29–34)	23.6 (23–25)	31.3 (28.6–33.9, n = 129)
Bill depth	5.5	5.5	5.0 (4.5–5.5)	4.8 (4.5–5.0)	NA

species, which I had available for comparison; with no other differences than the whitish areas were not so clean, and the rest of the plumage was brighter and more strongly coloured. The only other differences I found can be summarised as the bill of the previous species being 5 lines longer, although of the same width, material and shape. The mouth lining of that individual was whitish; that of the present specimen yellow. The tongue of the previous a little narrower and sharper, the tail somewhat less vigorous and concave. These differences seem to me sufficient to consider it a distinct species, you see in this family, like all of those with many characters in common, any difference is of greater importance than many similarities; and the difference in the length of the bill is very great.'

Ever since Lichtenstein (1818) tentatively associated the 'Trepador pico corto' with Straight-billed Woodcreeper *Dendroplex picus* (J. F. Gmelin, 1788), a species distributed well north of Paraguay, from Panama south to Amazonian Bolivia and the northern Pantanal of Brazil (Marantz *et al.* 2019a), there has been little effort to improve on that identification. In fact, it was repeated by Hartlaub (1847), Sclater (1890), Laubmann (1939) and Pereyra (1945) despite there being no records of *D. picus* from Paraguay. The only doubting voice had been Sonnini's (Azara 1809) premature dismissal of the validity of the description with the following statement:

'Je ne sais si les légères différences que M. d'Azara a fait remarquer entre cet oiseau et le précédent, suffisent pour constituer deux espèces distinctes ; et mon doute est d'autant plus fondé, que des deux seuls pics - grimpereaux à bec court, observés par ce voyageur, l'un avait un pouce de longueur totale de moins que l'autre ; d'où l'on peut conclure que les dimensions de ces oiseaux sont sujettes à varier. Il ne serait donc pas étonnant que leurs becs ne fussent pas de la même grandeur. Quant aux teintes plus ou moins fortes des couleurs qui, du reste, ont la même distribution, l'on sait qu'un caractère aussi faible n'a jamais indiqué une distinction d'espèces. (S.)'

'I do not know whether the slight differences which Monsieur d'Azara has remarked upon between this bird and the preceding, suffice to constitute two distinct species; and my doubt is all the more founded on the fact that of the only two Trepador pico cortos observed by this traveller, one had a total length of an inch less than the other, from which it can be concluded that the dimensions of these birds are subject to variation. It would not be

surprising that their beaks were not of the same size. As for the more or less strong hues of colours which, moreover, have the same distribution, we know that such a feeble character has never indicated a distinction of species.'

Sonnini's misplaced certainty was repeated by Vieillot (1818), who took the unusual step of electing not to give the description a formal scientific name. However Sonnini erred, and Azara was correct that his description does indeed represent a distinct species. No. 243 can be conclusively identified as Lesser Woodcreeper *Xiphorhynchus fuscus* (Fig. 2), based on the diagnostic characters highlighted by Azara (1805) and the comparative measurements he provided (Table 1).

Lesser Woodcreeper is a common species in the Paraguayan Atlantic Forest region. It is distinguished from Narrow-billed Woodcreeper *Lepidocolaptes angustirostris* by its shorter bill, buffy tinge to those parts of the plumage that are white in *L. angustirostris*, and the richer coloration of the upperparts. One other potential confusion species also occurs in Paraguay's forests, Scalloped Woodcreeper *Lepidocolaptes falcinellus*. However, that species is characterised by the pure white throat and base colour to the underparts, and possesses body and bill measurements that closely resemble the congeneric *L. angustirostris* (Table 1).

Acknowledgements

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The nest, nestlings and morphometrics of Sapphire-spangled Emerald *Amazilia lactea bartletti*

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SUMMARY.—The Sapphire-spangled Emerald *Amazilia lactea* complex is currently represented by three subspecies with disjunct geographical ranges. *A. l. bartletti* occurs over a limited portion of south-western Amazonia in Brazil, south-east Peru and northern Bolivia, and is a very little-known taxon in nature. We present data on the breeding and biometrics of this race based on six nests found between 1999 and 2019, and 58 adult individuals captured between 2010 and 2018 in eastern Acre state, Brazil. The nest of *A. l. bartletti* is a low cup / base type, constructed primarily of kapok wool and decorated with lichens on the outer walls. The nestling period was estimated at 18–20 days. Our data indicate that *A. l. bartletti* breeds from at least December until March.

Sapphire-spangled Emerald *Amazilia lactea* comprises three subspecies with markedly disjunct geographical distributions: *A. l. lactea* in south-east Brazil, from Santa Catarina north to Bahia; *A. l. zimmeri* in south-east Venezuela; and *A. l. bartletti* in south-west Amazonian Brazil, adjacent south-east Peru and northern Bolivia (Zimmer 1950, Weller *et al.* 2020). Based on plumage and morphometrics, the *Handbook of the birds of the world* currently treats *bartletti* at species rank, Spot-vented Emerald *A. bartletti* (del Hoyo & Collar 2014). However, for the purposes of this study we follow the taxonomy and nomenclature of Piacentini *et al.* (2015), who considered this taxon as a subspecies of *A. lactea*.

Sapphire-spangled Emerald inhabits the edges of primary forest, as well as secondary forest, plantations, and urban environments. Almost all of the available breeding data for this species pertain to *A. l. lactea* (Oniki *et al.* 2000, Weller *et al.* 2020). To augment our knowledge of reproduction and biometrics of the race *A. l. bartletti*, we present data on the nest, nestlings, morphometry, and mass of this race from observations made in eastern Acre state, in south-west Brazilian Amazonia.

Methods

Study area.—Nests reported here were found during non-systematic observations made between 1999 and 2019 at the Campus and Zoobotanical Park of the Universidade Federal do Acre (UFAC) (09°57'03.22"S, 67°52'30.65"W), Rio Branco, while adults were captured, measured and banded annually there in 2010–18. A description of the habitats and avifauna of the study area can be found in Guilherme (2001).

Nests.—Inactive *A. l. bartletti* nests were collected and deposited in the nest collection of the ornithology laboratory at UFAC (Table 1). Measurements of these nests were taken using digital callipers.

Capture, marking and biometrics.—During 2010 to 2018, 58 adults were trapped using mist-nets, 12 m long and 2.5 m high with a 36-mm mesh. Capture effort was c.4,000 net / hours / year. Birds were marked using numbered metal rings supplied by CEMAVE (Centro Nacional de Pesquisa e Conservação de Aves Silvestres), under the scope of project 1099, coordinated by EG (senior bird bander, reg. no. 324654). We weighed adults and nestlings

TABLE 1
Measurements (mm) of Sapphire-spangled Emerald *Amazilia lactea bartletti* nests held in the ornithology laboratory of the Universidade Federal do Acre (UFAC), Rio Branco, Brazil.

Nest	Total height	External Diameter	Internal diameter of cup	Depth of cup	Wall thickness
AC-054	36	36.87 × 47.43	26.53 × 30.62	21	5.39
AC-056	30	32.6 × 39.17	18.28 × 24.75	23	8.68
AC-080	38	33.26 × 39.26	18.31 × 22.50	22	11.94
Mean ± SD	34.6 ± 4.2	34.24 ± 2.3 × 41.9 ± 4.7	21.04 ± 4.8 × 25.9 ± 4.2	22 ± 1	8.67 ± 3.3

using a Pesola® balance with 100 g capacity and 1 g precision in 2010–14, and a digital scale (0.05 g precision) in 2015–18. We collected standard morphometric data (wing length flattened, bill length from the tip to the feathers, and total length) following the protocol outlined by Proctor & Lynch (1993). To measure wing and total length we used a ruler with a millimeter scale, while to measure bill length we used analogue callipers (0.05 mm precision) in 2010–14, and digital callipers (0.01 mm precision) in 2015–18.

Results

Nests and nestlings.—Six nests of *A. l. bartletti* were found between 1999 and 2019 (Table 2; Figs. 1A, 1F, 2A). Of these, four were active when discovered and two inactive (Table 2). Four of the six had the support plant identified to genus or species (Table 2). Measurements, means and standard deviation of the parameters for three of the six nests are presented in Table 1.

The nests, of the low cup / base type (*sensu* Simon & Pacheco 2005), were sited on horizontal branches and comprised cotton-like fluff (kapok) obtained from seeds of *Ceiba* sp. or *Ochroma* sp. The outer walls of the nests were lichen-decorated (Figs. 1A, B, F, 2A, B, E).

Nestlings hatch virtually featherless (Fig. 2C–D), with two lines of down on the dorsal spinal tract (*sensu* Lucas & Stettenheim 1972; Fig. 2C). They have dark skin on the dorsal and lateral surfaces, closed eyes and an orange bill (Fig. 2C–D).

Nest 2.—When it was found on 21 February 2013, this nest contained two recently hatched nestlings (Fig. 1 A–B). It was constructed on the branch of a mango tree c.2 m above ground (Table 2). The nest was monitored for 18 days until the nestlings fledged. During this period, they were fed by just one adult, presumably the female, which collected nectar

TABLE 2
Nests of Sapphire-spangled Emerald *Amazilia lactea bartletti* found in the Campus and Zoobotanical Park of the Universidade Federal do Acre, Rio Branco, Brazil, between 1999 and 2019.

Nest	Date found	Supporting plant	Situation
1	5 February 1999	Not identified	active
2	21 February 2013	<i>Mangifera indica</i>	active
3	8 December 2015	Not identified	active
4	23 March 2017	<i>Tectona grandis</i>	active
5	14 June 2017	<i>Manihot esculenta</i>	inactive
6	30 July 2019	<i>Spondias</i> sp.	inactive



Figure 1. Nests of Sapphire-spangled Emerald *Amazilia lactea bartletti* and floral resources at the Campus and Zoobotanical Park of the Universidade Federal do Acre, Rio Branco, Brazil: (A) nest constructed on a mango *Mangifera indica* tree, with two nestlings, 3 March 2013; (B) the same nest from above, 5 March 2013; (C) adult female collecting *Monotagma* sp. nectar for the nestlings depicted in A and B; (D–E) flowers of *Costus* sp. and *Hibiscus rosa-sinensis*, respectively, where the adult female collected nectar to feed the nestlings depicted in photos A and B; (F) nest found on 8 December 2015 with an adult female incubating eggs (A–E: Jônatas Lima; F: Edson Guilherme)

from flowers of native and exotic species near the laboratory blocks and campus classrooms (Fig. 1C–E) including *Costus* sp., *Hibiscus rosa-sinensis* and *Monotagma* sp. (Fig. 1C–E). On 9 March 2013, the nestlings, already feathered and mass 5 g, were banded (code A07384 and A07400). On 10 March 2013 the young were seen perched on branches near the nest, but still being fed by the female. The minimum nestling period was therefore 17 days.

Nest 4.—This nest was found on 23 March 2017, also with two recently hatched nestlings. The nest was constructed on a branch of an exotic *Tectona grandis* plant, c.1.8 m above ground (Table 2; Fig. 2A, B, E). On the day of discovery, the nestlings weighed 2.2 g and 1.6 g, respectively. On 4 April 2019, 12 days later, we banded and measured the nestlings. As we approached, one of the nestlings flew to the edge of the forest and was not seen again. The other was banded (code A 62933) and weighed 4.69 g. Morphometrics taken from this nestling were: bill 11 mm; wing 33 mm and total length 65 mm. Next day, this nestling was also not present near the nest.

Morphometrics.—Fifty-eight adult *A. l. bartletti* were trapped and measured between 2010 and 2018. The mean and standard deviation of the measured parameters were: bill 20.7 ± 1.5 (range 17–25 mm, $n = 51$); wing 53.2 ± 3 (41–61 mm, $n = 58$); tail 29.7 ± 2.5 (25–35 mm, $n = 58$); total length 92.5 ± 5.8 (86–106 mm, $n = 49$) and mass 4.7 ± 0.6 (3–6 g, $n = 58$).



Figure 2. Nest of Sapphire-spangled Emerald *Amazilia lactea bartletti* with two nestlings on a horizontal branch of *Tectona grandis*: (A) outer nest wall showing lichen ornamentation; (B) dorsal view of nest with recently hatched nestlings (2–3 days old); (C–D) dorsal and ventral views of a nestling on the day it was found (23 March 2017); (E) feathered nestlings on 30 March 2017; (F) nestling on the day it was banded (4 April 2017) (Edson Guilherme)

Discussion

The first record of *A. l. bartletti* in Brazil involved a female collected in 1951 in the vicinity of Rio Branco, the capital of Acre (Pinto & Camargo 1954; Museu de Zoologia da Universidade de São Paulo, MZUSP 35630). In Acre, *A. l. bartletti* is one of the commonest hummingbirds, being present in forest fragments (mainly at their edges), farms, and squares and gardens in cities (Guilherme 2016).

There is just one reference to an *A. l. bartletti* nest found in Bolivia (del Hoyo *et al.* 2019), whereas all other known breeding information for *Amazilia lactea* refers to the south-eastern South American race *A. l. lactea* (Ihering 1900, Ruschi 1986, Oniki *et al.* 2000, Weller *et al.* 2020). Thus the nests reported here represent the first detailed information for *A. l. bartletti* (del Hoyo *et al.* 2019).

The shallow cup-shaped nest constructed of kapok fibres is similar to that described for *A. l. lactea* (Ihering 1900, Oniki *et al.* 2000). The kapok used (Fig. 2B) probably came from the fruits of *Ceiba lupuna* or *Ochroma pyramidale*, which are common tree species in the UFAC Campus and Zoobotanical Park. As noted by Oniki *et al.* (2000), the presence of bark strips or thin twigs in the outer wall is low and, in some nests, practically non-existent. Mean measurements of the nests of *A. l. bartletti* are consistent with those of *A. l. lactea* reported by Ihering (1900) and Oniki *et al.* (2000).

Nests of *A. l. bartletti* are decorated with lichens like those of *A. l. lactea* (Oniki *et al.* 2000), Copper-rumped Hummingbird *A. tobaci* (Muir & Butler 1925), Rufous-tailed Hummingbird

A. zacatl (Skutch 1931), Glittering-throated Emerald *A. fimbriata* (Haverschmidt 1952) and Azure-crowned Hummingbird *A. cyanocephala* (Ornelas 2010). Decorating the outer walls of the nests with lichens is primarily a camouflage strategy (McCormac & Showman 2010).

We estimate the nestling period as between 18 and 20 days, based on nest 2 which contained two recently hatched nestlings and was followed until they fledged 17 days later. We believe that the nestlings hatched at least two or three days prior to the nest's discovery. According to Oniki *et al.* (2000), the nestling period of *A. lactea* may be no longer than 20 days, i.e. slightly shorter than the 22 days reported by Ruschi (1986) and Weller *et al.* (2020) for *A. l. lactea*. The literature indicates that in other species of *Amazilia* the nestling period varies from 18 to 23 days (Fierro-Calderón & Martin 2007). Skutch (1931) reported that young Rufous-tailed Hummingbirds left the nest when 21 days old, Glittering-throated Emerald at 20 days (Haverschmidt 1952) and young Copper-rumped Hummingbirds when 19–23 days old (Muir & Butler 1925, Baird 2017).

Nestlings of *A. l. bartletti* are black-skinned dorsally, and pink on the belly, while the bill and mouth-lining are yellow / orange, just as described for Glittering-throated Emerald (Haverschmidt 1952) and similar to Azure-crowned Hummingbird (Ornelas 2010). The mass at fledging is presented here for the first time, and is close to mean adult weight, indicating that young only leave the nest when they achieve adult mass. Glittering-throated Emerald young also leave the nest when they reach c.5 g (Haverschmidt 1952). However, nestlings fledge when their bill is slightly smaller than that of the adult, as also observed in Glittering-throated Emerald (Haverschmidt 1952).

Foraging data for *A. l. bartletti* is virtually non-existent (del Hoyo *et al.* 2019). Our observations indicate that like *A. l. lactea* (Oniki *et al.* 2000), *A. l. bartletti* feeds its nestlings with nectar from native and exotic plants growing in open areas and gardens near the nest. From the dates of the active nests we found (Table 1) it appears that *A. l. bartletti* breeds in south-western Amazonia from at least December until March.

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Birds of Humaitá Forest Reserve, Acre, Brazil: an important forest fragment in south-west Amazonia

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SUMMARY.—Humaitá Forest Reserve (HFR) is a forest fragment in the state of Acre, Brazil. Between 2009 and 2019, this fragment has been inventoried by multiple ornithologists and birdwatchers. To provide a comprehensive list of the avifauna of HFR, we compiled all of the available data, including published reports and recent, unpublished surveys. The list includes 356 bird species belonging to 60 families and 23 orders. This species richness is the greatest recorded in those forest fragments that have been inventoried in eastern Acre. We found that HFR is an important site for the conservation of many threatened species, and migrants, as well as poorly known species with a restricted geographic distribution, such as Semi-collared Puffbird *Malacoptila semicineta*, Goeldi's Antbird *Akletos goeldii*, Rufous Twistwing *Cnipodectes superrufus* and Acre Tody-Tyrant *Hemitriccus cohnhafti*.

South-west Amazonia is one of the world's biologically richest regions in terms of birds, with more than 500 species at some localities (e.g. Terborgh *et al.* 1984, Parker *et al.* 1994, Brown & Freitas 2002, Whittaker *et al.* 2002). The avifauna of the Brazilian state of Acre, which borders Peru, Bolivia and the Brazilian states of Rondônia and Amazonas, is well known, with more than 700 species documented (Guilherme 2016). In addition to species richness, the region is also characterised by high endemism, with many species unique to the Inambari centre of endemism between the Solimões and Madeira Rivers (Haffer 1978, Cracraft 1985, Silva *et al.* 2019). In Acre, at least 23 species are confined to the Inambari centre, and 12 of these occur in Brazil only in Acre and adjacent parts of Amazonas (Guilherme 2012, 2016). Furthermore, some species are restricted to eastern Acre, including many bamboo specialists (Guilherme & Santos 2009, Guilherme 2012, 2016).

Eastern Acre is also the region most affected by anthropogenic impacts in south-west Amazonia, at the western extreme of the 'Arc of Deforestation' in southern Amazonia, where cattle-ranching and cash-cropping are expanding relentlessly (Fearnside 2017). Acre's capital, Rio Branco, is also in this region, which is characterised by a mosaic of many urban and rural forest fragments within an anthropogenic matrix dominated by cattle pasture (Guilherme 2016).

Fragmentation of forest not only impacts avian communities, in particular by eliminating certain ecological guilds (Stouffer & Bierregaard 1995, Bierregaard & Stouffer 1997, Stratford & Stouffer 1999), but may also affect the physiological integrity of individual birds (Hernández-Palma & Stouffer 2018). Long-term studies of bird communities in forest fragments may provide potentially valuable insights into the impacts of fragmentation on community structure vis-à-vis pristine habitats (Rutt *et al.* 2017).

Although the number of bird surveys has progressively increased in Amazonia, systematic long-term surveys of a given area are still rare (Rutt *et al.* 2017). We compiled a list of the avifauna of Humaitá Forest Reserve (HFR), a forest fragment owned by the Instituto Nacional de Colonização e Reforma Agrária (INCRA), but which has been ceded

to the Universidade Federal do Acre (UFAC) for research purposes. Other inventories available for HFR include medium-sized and large mammals (Botelho *et al.* 2012) and palms (Pinheiro *et al.* 2015). In 2009, the ornithological database of the HFR was consolidated during doctoral research by EG (Guilherme 2009). Since then, further work has been conducted in HFR, including by TLS and colleagues (Silva *et al.* 2015), TNM & EG (Melo & Guilherme 2016), DP & EG (Pedroza & Guilherme 2019) and JL and colleagues (Lima *et al.* 2019). While ongoing research in HFR over the past ten years has produced an increasingly solid database on its avifauna, no comprehensive list of birds was available for the reserve, until the present study.

Methods

Study area.—Humaitá Forest Reserve (HFR) is in the municipality of Porto Acre (09°45′52″S, 67°38′02″W), Acre, Brazil (Fig. 1), and covers *c.*2,000 ha (Botelho *et al.* 2012). The fragment is surrounded by the Humaitá Settlement Project and farms, with the Acre River forming its eastern limit. Climate is tropical humid, with mean annual temperatures of 24–26°C (Alvares *et al.* 2013) and mean annual rainfall of 1,900 mm (Alvares *et al.* 2013). Vegetation is a mosaic of open forest with bamboo, and open forest with palms on *terra firme* and seasonally flooded (*várzea*) soils (Barroso *et al.* 2011).

Data collection.—The preliminary bird species list for HFR was based on three published inventories (Guilherme 2009, 2016, Silva *et al.* 2015). We added unpublished records by other observers, together with those on digital platforms such as Wikiaves and Xeno-canto. Registration numbers of records on Wikiaves (WA) and Xeno-canto are indicated in the species accounts and Appendix. Species were identified via captures in mist-nets, visual observations or their vocalisations. Specimens collected in HFR and deposited in the ornithology laboratory at UFAC, Rio Branco, and the Museu Paraense Emílio Goeldi (MPEG), Belém, were also examined. Voucher specimens and media identification numbers published online were considered as physical evidence of the species' occurrence in HFR.

Species classification.—The list was reviewed to identify migratory, endemic species, habitat specialists, cynegetic and threatened species. Migratory species were classified

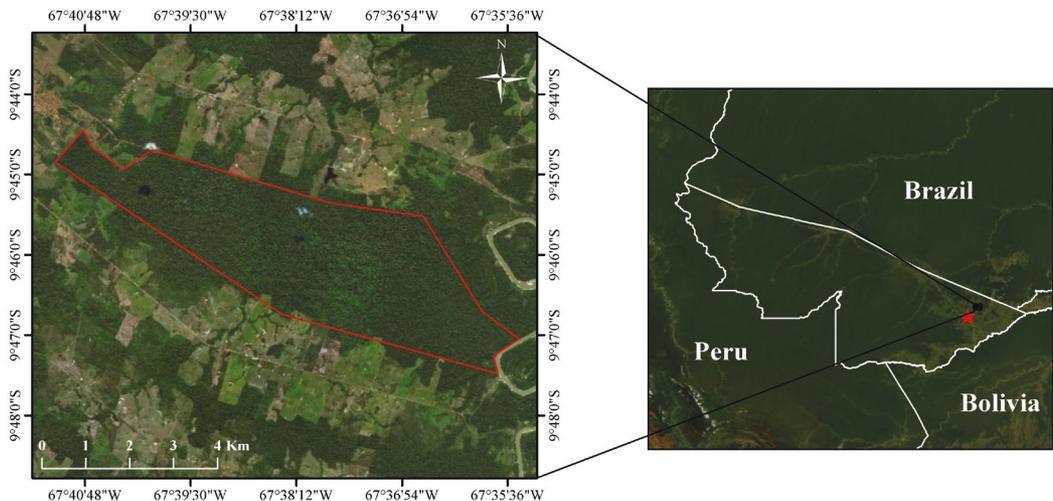


Figure 1. Location of the Humaitá Forest Reserve (HFR) in the state of Acre, Brazil, near the city of Rio Branco (red star). The area that corresponds to the HFR, administered by the Federal University of Acre, is outlined by the red polygon.

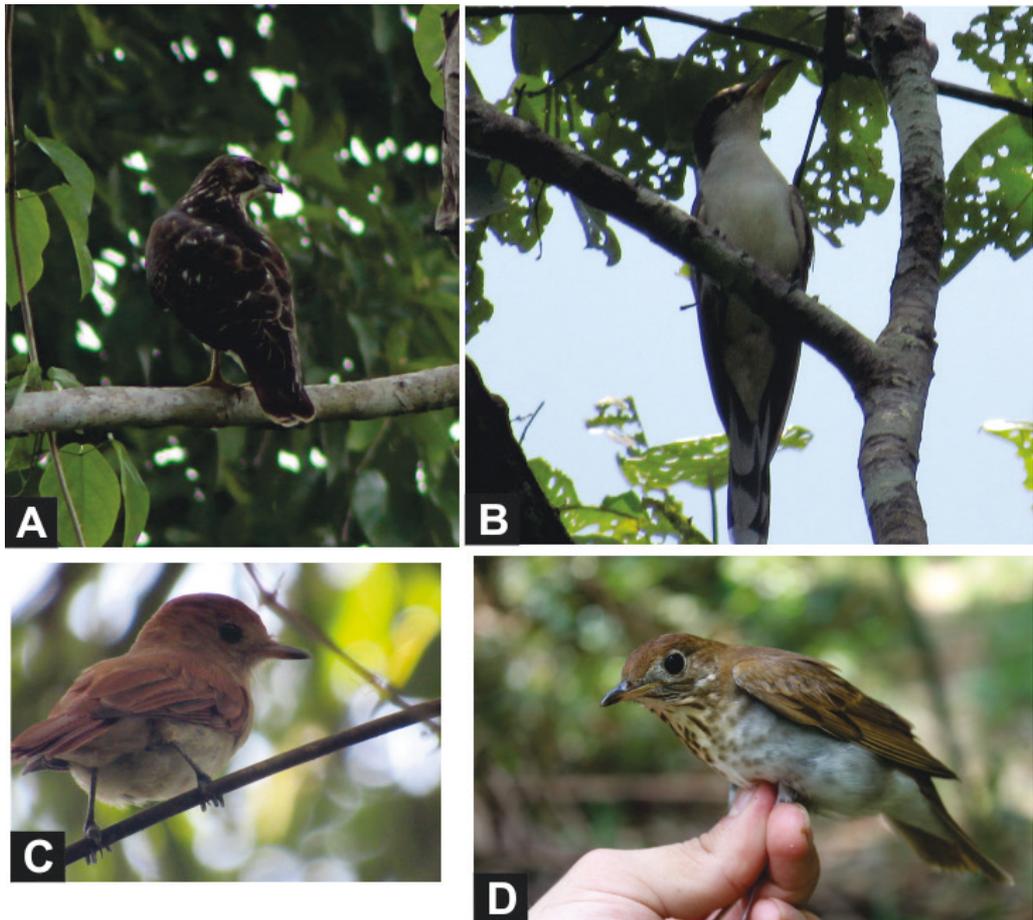


Figure 2. Examples of migratory species recorded in the Humaitá Forest Reserve, Acre, Brazil. (A) Broad-winged Hawk *Buteo platypterus* (Diego Pedroza); (B) Yellow-billed Cuckoo *Coccyzus americanus* (David P. Guimarães); (C) Rufous Casiornis *Casiornis rufus* (David P. Guimarães). (D) Swainson's Thrush *Catharus swainsoni* (Diego Pedroza).



Figure 3. Three endemic species from the Inambari center associated with patches of *Guadua* bamboo recorded in the Humaitá Forest Reserve, Acre, Brazil. (A) Rufous-headed Woodpecker *Celeus spectabilis* (David P. Guimarães). (B) Rufous Twistwing *Cnipodectes superrufus* (Tomaz N. de Melo). (C) Acre Tody-Tyrant *Hemitriccus cohnhafti* (Ricardo Plácido).

using Somenzari *et al.* (2018), while bamboo forest specialists and species associated with patches of *Guadua* bamboo were identified based on Kratter (1997), Guilherme & Santos (2009), Lebbin (2013) and Guilherme (2012, 2016). Species endemic to the Inambari centre of endemism (*sensu* Silva *et al.* 2005, 2019) were identified using Haffer (1978), Cracraft (1985) and Guilherme (2012, 2016). Game (cynegetic) species targeted by subsistence hunters were classified following Ojasti (1993), Sick (1993) and Sigrist (2014). Conservation status follows IUCN (2019).

Feeding guild and foraging stratum of each species was also determined, based on Wilman *et al.* (2014). Scientific nomenclature follows that of the Comitê Brasileiro de Registros Ornitológicos (Piacentini *et al.* 2015). In some cases, voucher specimens were collected under ICMBio / SISBio authorisation no. 23269-1, and deposited either at UFAC, Rio Branco, or MPEG, Belém. Some birds were banded using numbered metal rings supplied by CEMAVE (Centro Nacional de Pesquisa e Conservação de Aves Silvestres), under the scope of project 1099, coordinated by EG (senior bird bander, reg. no. 324654).

Results

Compilation of records made in HFR between 2009 and October 2019 revealed the presence of 356 bird species in 60 families and 23 orders (Appendix). Families represented by the largest numbers of species were Thamnophilidae ($n = 37$ species, 10.3% of the total), Thraupidae ($n = 28$ species, 7.9%), Tyrannidae ($n = 26$ species, 7.3%), Rhynchocyclidae ($n = 17$ species, 4.8%) and Psittacidae ($n = 14$ species, 3.9%). Overall, 195 species (54.8%) are passerines and 161 (45.2%) non-passerines.

The most species-diverse foraging guilds (Appendix) were the insectivores (196 species), frugivores (56 species) and omnivores (42 species). Most birds forage in the midstorey (84 species), canopy (50 species) or alternate between the understorey and midstorey (40 species).

Thirteen bird species visit HFR on migration (Fig. 2). Slightly more than half of these (53.8%, $n = 7$) are austral migrants, with the remainder 23.1% ($n = 3$) being intra-tropical migrants and 23.1% ($n = 3$) Nearctic migrants. Eleven species (3.1%) are endemic to the Inambari centre of endemism. Eighteen species (5.04%) are either bamboo forest specialists or possess some degree of association with tracts of *Guadua* bamboo in south-west Amazonia (Fig. 3). Twenty-nine species (8.1%) are considered to be cynegetic (Appendix), including Tinamidae ($n = 9$ species, 2.5% of the total), Anatidae ($n = 1$ species, 0.3%) and Cracidae ($n = 3$ species, 0.8%). Sixteen (4.5%) species are included in higher categories of threat by the IUCN (2019), including nine Near Threatened (2.5%) and seven Vulnerable (2%) (Appendix). Below, we comment on aspects of the biology and distribution of selected species.

Species accounts

BROAD-WINGED HAWK *Buteo platypterus*

Nearctic migrant. Observed by DP at the edge of HFR on 9 November 2017 (WA2792378; Fig. 2A). Only the second record in Acre (Guilherme 2016). Stotz *et al.* (1992) reported the species' occurrence in neighbouring Rondônia between October and March. This indicates that the record at HFR was within its overwintering period in south-west Amazonia.

ASH-COLOURED CUCKOO *Micrococcyx cinereus*

Austral migrant. Guilherme (2009) first reported the species in HFR. A female, collected on 20 July 2007, is deposited in Belém (MPEG 63485). The date of this record corresponds to the coldest part of the austral winter in southern Brazil, where the species breeds (Payne 2019a).

YELLOW-BILLED CUCKOO *Coccyzus americanus*

Nearctic migrant. One observed by DPG foraging for insects in the canopy on 30 October 2017 (WA3515980; Fig. 2B). Breeds in North and Middle America, and migrates to South America in the boreal winter (Payne 2019b). The date of this record indicates that *C. americanus* arrives in the region shortly before the start of the boreal winter. Only the third record in Acre (GBIF 2019, Wikiaves 2019).

RUFOUS-HEADED WOODPECKER *Celeus spectabilis*

Bamboo forest specialist. Common in HFR, where invariably observed in bamboo. The territorial song and drumming is audible over long distances, and evidence of its feeding behaviour is often observed on bamboo stalks. A pair with two juveniles observed by TNM on 12 August 2014, in bamboo near the reserve headquarters (Fig. 3A).

BLUISH-SLATE ANTSHRIKE *Thamnomanes schistogynus*

Endemic. Guilherme (2009) presented the first records in HFR. Specimens have been deposited in Belém (MPEG 59967, 59968). Subsequently, in 2018, DPG monitored the species. He found that *T. schistogynus* is a mixed-species flock leader in HFR, and occurs in bamboo forest and *terra firme* forest with palms.

YELLOW-BREASTED WARBLING ANTBIRD *Hypocnemis subflava*

Endemic; bamboo forest specialist. Silva *et al.* (2015) made the first record in HFR, and DP monitored the species in 2017. In HFR, the species occurs exclusively in bamboo forest, foraging for prey in bamboo culms and leaves. Population density was estimated in 16-ha grids, with some individuals being banded, at 0.55–0.66 pairs per ha in bamboo patches (Pedroza & Guilherme 2019). In DPG's 2018 study of mixed-species flocks, *H. subflava* was a constant presence in flocks led by *Thamnomanes schistogynus* and the flock's home range coincided with bamboo patches.

RUFOUS TWISTWING *Cnipodectes superrufus*

Endemic; bamboo forest specialist; Vulnerable. In August–September 2014, TNM observed one in bamboo patches near the reserve headquarters; see Melo *et al.* (2015) (Fig. 3B). On 5 June 2018, DPG trapped and ringed (CEMAVE F55386) one in a bamboo patch, and on 1 August 2018, JML trapped and ringed a second individual (CEMAVE F63509) in a part of the forest apparently without any major concentration of *Guadua* bamboo, whereas the species typically occurs in patches of dense bamboo (Tobias *et al.* 2008). HFR is the northernmost locality at which *C. superrufus* has been recorded (Melo *et al.* 2015, Guilherme 2016).

ACRE TODY-TYRANT *Hemitriccus cohnhafti*

Endemic; bamboo forest specialist; Near Threatened. Recently described species for which few natural history data are available (Zimmer *et al.* 2013, Melo *et al.* 2015). One was recorded in a bamboo patch at HFR on 19 November 2018, by R. Plácido (WA2376966) (Fig. 3C). The record extends the species' known range 95 km north of the nearest previously known locality, on the Transacrea highway in Acre (Melo *et al.* 2015).

LARGE-HEADED FLATBILL *Ramphotrigon megacephalum*

Bamboo forest specialist. Silva *et al.* (2015) first recorded this species in HFR, and TNM subsequently studied its foraging behaviour, which is focused exclusively on bamboo leaves and branches (Melo & Guilherme 2016). Density of *R. megacephalum* along a 10-km transect in the study area was estimated 1.5 individuals/km², with the species being exclusively

recorded in areas of bamboo. In the 2018 study of mixed-species flocks, DPG considered *R. megalcephalum* to be a constant in flocks led by *Thamnomanes schistogynus*.

DUSKY-TAILED FLATBILL *Ramphotrigon fuscicauda*

Species associated with bamboos. Guilherme (2009) was the first observer to record *R. fuscicauda* in HFR. Ecologically more flexible than *R. megalcephalum*, it occurs in both bamboo-dominated habitats and areas without bamboo, although it is commonly found on bamboo, and is observed foraging close to *R. megalcephalum* (Melo & Guilherme 2016). Density of *R. fuscicauda* along a 10-km transect in HFR was estimated at 0.8 individuals/km². DPG considered this species to be another constant participant in mixed-species flocks led by *Thamnomanes schistogynus*.

Discussion

Bird species richness recorded in HFR (356 species) corresponds to 50.4% of the 708 species currently documented in the state of Acre (Guilherme 2016). This is an impressive number of species, considering that the fragment covers just 2,000 ha. The number of bird species recorded in HFR has progressively increased since 2009, when just 120 species had been recorded in the area based solely on specimens in museums (Guilherme 2009). The increase is due to constant ornithological field work in this forest, together with sporadic visits by amateur birdwatchers in the last ten years. Surveys in HFR prior to 2019 indicate that the site has a similar bird species richness to that in areas of continuous forest inventoried in Acre during shorter term studies, including Rio Acre Ecological Station (Guilherme & Aleixo 2010) and Chico Mendes Extractive Reserve (Mestre *et al.* 2010). Bird species richness in HFR is also considerably greater than that recorded in isolated fragments inventoried over the long term, e.g., Catuaba Experimental Farm (Rasmussen *et al.* 2005) (c.36 km from HFR) and the UFAC Zoobotanical Park (Guilherme 2001, 2016) (c.31 km from HFR).

Both of these sites are in eastern Acre and administered by UFAC. Prior to 2001, 150 bird species had been recorded in the Zoobotanical Park (Guilherme 2001), an area of c.100 ha (Meneses-Filho 1995), although this total increased to 196 species over the next 15 years (Guilherme 2016). In the Catuaba Experimental Farm fragment of 1,200 ha (Medeiros *et al.* 2013), 257 bird species were recorded by Rasmussen *et al.* (2005), and this number rose to 275 over the next 11 years (Guilherme 2016). Despite the increasing inventory, total richness at both sites is still lower than at HFR. The Zoobotanical Park is a small fragment within an urban matrix and has virtually no connectivity to other forested areas (Guilherme 2001), whereas Catuaba Experimental Farm is much larger, located within a rural matrix, and surrounded by properties with private reserves of forest (as mandated under current Brazilian environmental legislation). In contrast to these sites, HFR is a much larger area of forest, relatively distant from populated areas, and lies within a matrix of pasture and numerous private forest reserves that together with HFR form a single fragment. Although these areas are not directly comparable due to differences in the size and configuration of the fragments, their history of isolation and characteristics of the matrix (Ferraz *et al.* 2007), the progressive increase in number of species recorded at each site over time indicates that additional species will be recorded in HFR by further surveys.

Approximately 5% of bird species in HFR are associated with bamboo forests of south-west Amazonia (Kratler 1997, Guilherme & Santos 2009, Guilherme 2012, 2016). These species include two of the rarest birds at HFR, Rufous Twistwing and Acre Tody-Tyrant (Tobias *et al.* 2008, Zimmer *et al.* 2013, Harvey *et al.* 2014, Melo *et al.* 2015). The presence of ecological guilds most sensitive to fragmentation, such as mixed-species flocks

of understory insectivores, terrestrial insectivores and army ant followers, reflects the conservation potential of HFR for birds. The presence of several gamebirds, especially Razor-billed Curassow *Pauxi tuberosa*, Spix's Guan *Penelope jacquacu* and large tinamids such as Grey Tinamus *Tao* and Great Tinamous *T. major*, indicates the viability of their local populations, despite hunting (DP & TNM pers. obs.). These findings are similar to those of Botelho *et al.* (2012) for medium and large mammals in HFR. Although they tend to become rarer, large cracids appear to be able to persist in areas with moderate hunting pressure (Barrio 2011, Kattan *et al.* 2016). The presence of Crested *Morphnus guianensis* and Harpy Eagles *Harpia harpyja*, which are also targeted by hunters (Trinca *et al.* 2007, Muñiz-López 2017) is a further indication of the favourable conditions. HFR is almost completely surrounded by cattle pastures, which environment lacks resources for the majority of migratory birds (Saab & Petit 1992), making HFR an important site for migratory species from different regions of the Americas during the year.

HFR is a potentially important area for bird conservation in eastern Acre, given that it has the highest bird species richness recorded anywhere in the state. In addition, it harbours important endemics and habitat specialists, and serves as a strategic stopover for migratory species. Birdwatching, which was initiated in 2013 at HFR by TNM, has attracted people from elsewhere in Brazil and other countries. This type of sustainable tourism has the potential to yield important economic benefits for the region. The proximity to the capital, Rio Branco, and the presence of rare birds such as Ash-throated Gnatcatcher *Conopophaga peruviana*, *Cnipodectes superrufus* and *Hemitriccus cohnhaffti*, should attract growing numbers of birders, who in turn can continue to monitor bird populations and add new species to the site list. Some rare species, such as *Morphnus guianensis*, were already found at HFR by hobby birders. Supervision by competent authorities (e.g., Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis - IBAMA) of this important reserve and continued monitoring of its avifauna should guarantee its role as a safe haven for the biodiversity of a region under increasing anthropogenic pressure.

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Appendix

Bird species recorded in the Humaitá Forest Reserve between 2009 and 2019, in Acre, Brazil. Guilds: FR = frugivore; INS = insectivore; INV = invertebrates; NEC = nectarivore; O = omnivore; PS = granivore; VS = vertebrate scavenger. Strata: AE = aerial; W = water; C = canopy; G = ground; G/C = ground/canopy; G/UND/MID = ground/understorey/mid-high; G/UND = ground/understorey; MID = mid-high; MID/C = mid-high/canopy; MID/C/AE = mid-high/canopy/aerial; UND = understorey; UND/AE = understorey/aerial; UND/MID = understorey/mid-high; UND/MID/C = understorey/mid-high/canopy. Conservation status: * = Near Threatened, ** = Vulnerable. Ecological characteristics (see first column): B = Bamboo forest specialist or associated with bamboo, NM = Nearctic migrant; AM = austral migrant; IM = intra-tropical migrant; E = endemic; C = cynegetic (gamebird). Voucher: MPEG = Museu Paraense Emílio Goeldi, Belém; AC = ornithology laboratory at Universidade Federal do Acre; WA = Wikiaves; XC = Xeno-canto; CEMAVE = ringed.

Family/Species/ Conservation status	English name	Guild	Stratum	Source	Voucher
TINAMIDAE					
<i>Tinamus tao</i> **,C	Grey Tinamou	FR	G	Present study	
<i>Tinamus major</i> *,C	Great Tinamou	FR	G	Guilherme (2009)	MPEG 63461
<i>Tinamus guttatus</i> *,C	White-throated Tinamou	FR	G	Present study	
<i>Crypturellus cinereus</i> C	Cinereous Tinamou	FR	G	Present study	
<i>Crypturellus soui</i> C	Little Tinamou	O	G	Present study	
<i>Crypturellus obsoletus</i> C	Brown Tinamou	FR	G	Present study	
<i>Crypturellus undulatus</i> C	Undulated Tinamou	FR	G	Guilherme (2009)	MPEG 63460, WA3325303
<i>Crypturellus strigulosus</i> C	Brazilian Tinamou	FR	G	Present study	
<i>Crypturellus atrocapillus</i> *,C,E	Black-capped Tinamou	O	G	Present study	
ANATIDAE					
<i>Amazonetta brasiliensis</i> C	Brazilian Teal	O	G	Present study	
CRACIDAE					
<i>Penelope jacquacu</i> C	Spix's Guan	FR	MID	Present study	
<i>Ortalis guttata</i> C	Speckled Chachalaca	FR	MID/C	Guilherme (2009)	MPEG 63462, WA3334008
<i>Pauxi tuberosa</i> C	Razor-billed Curassow	FR	G	Present study	
ODONTOPHORIDAE					
<i>Odontophorus stellatus</i>	Starred Wood Quail	O	G	Present study	
CICONIIDAE					
<i>Mycteria americana</i> MI	Wood Stork	VS	G	Present study	
ARDEIDAE					
<i>Tigrisoma lineatum</i>	Rufescent Tiger Heron	INV	W	Guilherme (2009)	MPEG 63463
<i>Cochlearius cochlearius</i>	Boat-billed Heron	INV	G	Guilherme (2009)	MPEG 63464
<i>Bubulcus ibis</i>	Cattle Egret	INV	G	Present study	
<i>Ardea alba</i>	Great Egret	VS	W	Present study	

Family/Species/ Conservation status	English name	Guild	Stratum	Source	Voucher
THRESKIORNITHIDAE					
<i>Mesembrinibis cayennensis</i>	Green Ibis	INV	G	Guilherme (2009)	MPEG 63611
CATHARTIDAE					
<i>Cathartes aura</i>	Turkey Vulture	VS	G	Present study	
<i>Cathartes melambrotus</i>	Greater Yellow-headed Vulture	VS	G	Present study	WA1371809
<i>Coragyps atratus</i>	Black Vulture	VS	G	Present study	WA1371808
<i>Sarcoramphus papa</i>	King Vulture	VS	G	Present study	WA1371810
ACCIPITRIDAE					
<i>Leptodon cayanensis</i>	Grey-headed Kite	O	UND/MID	Present study	
<i>Elanoides forficatus</i> ^{MN}	Swallow-tailed Kite	INV	MID	Present study	
<i>Harpagus bidentatus</i>	Double-toothed Kite	INV	C	Present study	
<i>Ictinia plumbea</i>	Plumbeous Kite	INV	AE	Present study	
<i>Buteogallus schistaceus</i>	Slate-coloured Hawk	VS	G	Present study	
<i>Urubitinga urubitinga</i>	Great Black Hawk	VS	C	Present study	WA3324073
<i>Rupornis magnirostris</i>	Roadside Hawk	VS	G/UND/MID	Guilherme (2009)	MPEG 63471, WA3334003
<i>Pseudastur albicollis</i>	White Hawk	VS	C	Present study	
<i>Buteo nitidus</i>	Grey-lined Hawk	VS	UND/MID/C	Present study	
<i>Buteo albonotatus</i>	Zone-tailed Hawk	VS	G	Present study	
<i>Buteo platypterus</i> ^{MN}	Broad-winged Hawk	VS	G	Present study	WA2792378
<i>Morphnus guianensis</i> *	Crested Eagle	VS	MID/C/AE	Present study	WA959961
<i>Harpia harpyja</i> *	Harpy Eagle	VS	MID/C	Present study	WA3158637, WA5138635
<i>Spizaetus tyrannus</i>	Black Hawk-Eagle	VS	MID	Present study	
<i>Spizaetus ornatus</i> *	Ornate Hawk-Eagle	VS	MID	Present study	
EURYPYGIDAE					
<i>Eurypyga helias</i>	Sunbittern	VS	W	Present study	XC468211
RALLIDAE					
<i>Aramides cajaneus</i>	Grey-necked Wood Rail	O	W	Present study	WA3325007, 1460974
<i>Laterallus viridis</i>	Russet-crowned Crake	INV	G	Present study	
<i>Laterallus exilis</i>	Grey-breasted Crake	INV	G	Guilherme (2009)	MPEG 63612
<i>Porphyrio martinicus</i>	Purple Gallinule	PS	G/UND	Guilherme (2009)	MPEG 59901
CHARADRIIDAE					
<i>Vanellus cayanus</i>	Pied Lapwing	INV	G	Guilherme (2009)	MPEG 63613
<i>Vanellus chilensis</i>	Southern Lapwing	INV	G	Present study	
JACANIDAE					
<i>Jacana jacana</i>	Wattled Jacana	INV	W	Guilherme (2009)	MPEG 63621
STERNIDAE					
<i>Phaetusa simplex</i>	Large-billed Tern	VS	W	Present study	
COLUMBIDAE					
<i>Columbina talpacoti</i> ^C	Ruddy Ground Dove	PS	G	Present study	

Family/Species/ Conservation status	English name	Guild	Stratum	Source	Voucher
<i>Patagioenas plumbea</i> ^C	Plumbeous Pigeon	O	C	Guilherme (2009)	MPEG 63473, WA969204, 969193
<i>Patagioenas subvinnacea</i> ^{C,**}	Ruddy Pigeon	FR	MID/C	Guilherme (2016)	WA3324169
<i>Leptotila verreauxi</i>	Grey-fronted Dove	PS	G	Present study	
<i>Leptotila rufaxilla</i> ^C	White-tipped Dove	PS	G	Guilherme (2009)	MPEG 63622, 63623
<i>Geotrygon montana</i>	Ruddy Quail-Dove	O	G	Guilherme (2009)	MPEG 59906, 59907, 59908, 59909, WA3333994
CUCULIDAE					
<i>Coccyzua minuta</i>	Little Cuckoo	INV	UND/MID	Present study	AC 186, MPEG 63484, 64562, WA1461971
<i>Micrococcyx cinereus</i> ^{MA}	Ash-coloured Cuckoo	INV	MID	Guilherme (2009)	MPEG 63485
<i>Piaya cayana</i>	Squirrel Cuckoo	INV	C	Guilherme (2009)	
<i>Piaya melanogaster</i>	Black-bellied Cuckoo	INV	C	Present study	
<i>Coccyzus melacoryphus</i>	Dark-billed Cuckoo	INV	G	Present study	
<i>Coccyzus americanus</i> ^{MN}	Yellow-billed Cuckoo	INV	MID/C	Present study	WA3515980
<i>Coccyzus euleri</i>	Pearly-breasted Cuckoo	INV	G	Present study	
<i>Crotophaga major</i>	Greater Ani	O	G/C	Present study	
<i>Crotophaga ani</i>	Smooth-billed Ani	O	G	Present study	
<i>Dromococcyx pavoninus</i> ^B	Pavonine Cuckoo	INV	G/UND	Present study	WA3325305
TYTONIDAE					
<i>Tyto furcata</i>	American Barn Owl	VS	G	Present study	
STRIGIDAE					
<i>Megascops choliba</i>	Tropical Screech Owl	INV	UND	Present study	
<i>Megascops usta</i>	Austral Screech Owl	INV	UND	Guilherme (2009)	MPEG 63692, WA1832511
<i>Lophotrix cristata</i>	Crested Owl	INV	UND/MID	Present study	WA951066
<i>Pulsatrix perspicillata</i>	Spectacled Owl	VS	G	Present study	WA3324168
<i>Strix huhula</i>	Black-banded Owl	INV	C	Present study	WA960060, WA988215
<i>Glaucidium hardyi</i>	Amazonian Pygmy Owl	INV	G	Silva <i>et al.</i> (2015)	
<i>Glaucidium brasilianum</i>	Ferruginous Pygmy Owl	INV	G	Present study	WA2798994, WA2798993
<i>Athene cucularia</i>	Burrowing Owl	VS	G	Present study	
NYCTIBIIDAE					
<i>Nyctibius grandis</i>	Great Potoo	INV	MID	Present study	WA1462134
<i>Nyctibius aethereus</i>	Long-tailed Potoo	INV	MID	Present study	
<i>Nyctibius griseus</i>	Common Potoo	INV	MID	Present study	
CAPRIMULGIDAE					
<i>Nyctiphrynus ocellatus</i>	Ocellated Poorwill	INV	AE	Present study	WA1435565, WA1456885, WA1456880
<i>Antrostomus sericeicaudatus</i>	Silky-tailed Nightjar	INV	MID	Present study	XC430737, WA2301402

Family/Species/ Conservation status	English name	Guild	Stratum	Source	Voucher
<i>Lurocalis semitorquatus</i>	Short-tailed Nighthawk	INV	MID	Present study	
<i>Nyctidromus albicollis</i>	Pauraque	INV	G	Present study	WA3325281
<i>Hydropsalis parvula</i>	Little Nightjar	INV	MID	Guilherme (2009)	MPEG 63493
<i>Hydropsalis climacocerca</i>	Ladder-tailed Nightjar	INV	G/UND/MID	Guilherme (2009)	MPEG 63614
APODIDAE					
<i>Chaetura cinereiventris</i>	Grey-rumped Swift	INV	AE	Present study	
<i>Chaetura brachyura</i>	Short-tailed Swift	INV	AE	Present study	
<i>Tachornis squamata</i>	Fork-tailed Palm Swift	INV	MID	Present study	
TROCHILIDAE					
<i>Glaucis hirsutus</i>	Rufous-breasted Hermit	NEC	UND	Guilherme (2016)	AC 591
<i>Threnetes leucurus</i>	Pale-tailed Barbthroat	NEC	UND	Silva <i>et al.</i> (2015)	AC 581
<i>Phaethornis ruber</i>	Reddish Hermit	NEC	UND	Guilherme (2009)	MPEG 64565, AC 585
<i>Phaethornis hispidus</i>	White-bearded Hermit	NEC	UND	Silva <i>et al.</i> (2015)	AC 584, WA1460980
<i>Phaethornis philippii</i>	Needle-billed Hermit	NEC	UND	Present study	
<i>Phaethornis bourcierii</i>	Straight-billed Hermit	NEC	UND	Guilherme (2009)	MPEG 59922, 59923
<i>Phaethornis malaris</i>	Great-billed Hermit	NEC	UND	Silva <i>et al.</i> (2015)	AC 582
<i>Campylopterus largipennis</i>	Grey-breasted Sabrewing	NEC	MID	Guilherme (2009)	MPEG 59924, 64563
<i>Anthracothorax nigricollis</i>	Black-throated Mango	NEC	C	Present study	
<i>Chlorostilbon mellisugus</i>	Blue-tailed Emerald	NEC	MID	Present study	
<i>Thalurania furcata</i>	Fork-tailed Woodnymph	NEC	UND/MID/C	Silva <i>et al.</i> (2015)	WA1371286
<i>Hylocharis cyanus</i>	White-chinned Sapphire	NEC	UND/MID/C	Present study	
<i>Amazilia lactea</i>	Sapphire-spangled Emerald	NEC	UND/MID/C	Guilherme (2009)	MPEG 63626
TROGONIDAE					
<i>Trogon melanurus</i>	Black-tailed Trogon	FR	C	Guilherme (2009)	MPEG 59928, WA3325343, 1462101, 1462097
<i>Trogon viridis</i>	Green-backed Trogon	FR	C	Guilherme (2009)	MPEG 63624
<i>Trogon ramonianus</i>	Amazonian Trogon	FR	UND	Guilherme (2009)	MPEG 63491, WA1462029
<i>Trogon curucui</i>	Blue-crowned Trogon	INV	UND/MID/C	Guilherme (2009)	MPEG 63492, WA3325342, 1371334
<i>Trogon collaris</i>	Collared Trogon	INV	MID	Present study	
<i>Pharomachrus pavoninus</i>	Pavonine Quetzal	FR	MID	Present study	WA1429156, 1433571
ALCEDINIDAE					
<i>Chloroceryle americana</i>	Green Kingfisher	VS	W	Present study	
<i>Chloroceryle aenea</i>	American Pygmy Kingfisher	VS	W	Present study	
<i>Chloroceryle inda</i>	Green-and-rufous Kingfisher	VS	W	Silva <i>et al.</i> (2015)	
MOMOTIDAE					
<i>Electron platyrhynchum</i>	Broad-billed Motmot	INV	MID	Guilherme (2009)	MPEG 59929

Family/Species/ Conservation status	English name	Guild	Stratum	Source	Voucher
<i>Momotus momota</i>	Amazonian Motmot	O	G/UND/MID	Silva <i>et al.</i> (2015)	WA952369
GALBULIDAE					
<i>Galbula cyanicollis</i>	Blue-necked Jacamar	INV	UND/MID	Present study	
<i>Galbula cyanescens</i>	Bluish-fronted Jacamar	INV	MID	Guilherme (2009)	MPEG 63486, 63625, WA3325279, 1460992, 1460987
<i>Galbula dea</i>	Paradise Jacamar	INV	C	Present study	
BUCCONIDAE					
<i>Notharchus hyperrhynchus</i>	White-necked Puffbird	INV	C	Present study	WA3324232
<i>Bucco macrodactylus</i>	Chestnut-capped Puffbird	INV	G/UND/MID	Guilherme (2009)	MPEG 63490, 63489, WA1460963
<i>Nystalus obamai</i>	Western Striolated Puffbird	INV	MID/C	Present study	
<i>Malacoptila semicincta</i> ^E	Semi-collared Puffbird	INV	UND	Present study	WA2787704
<i>Nonnula sclateri</i> ^{B, E}	Fulvous-chinned Nunlet	INV	G/UND	Present study	WA3229536, WA1371821, WA3249105
<i>Nonnula ruficapilla</i> ^B	Rufous-capped Nunlet	INV	G/UND/MID	Present study	
<i>Monasa nigrifrons</i>	Black-fronted Nunbird	INV	G/UND	Guilherme (2009)	MPEG 63488, WA3325029, 1326323
<i>Monasa morphoeus</i>	White-fronted Nunbird	INV	G/UND/MID	Present study	WA952320
<i>Chelidoptera tenebrosa</i>	Swallow-winged Puffbird	INV	AE	Guilherme (2009)	MPEG 63487
CAPITONIDAE					
<i>Capito auratus</i>	Gilded Barbet	FR	MID	Guilherme (2009)	MPEG 63501, 64566
RAMPHASTIDAE					
<i>Ramphastos tucanus</i> ^{**C}	White-throated Toucan	FR	C	Present study	WA3058758, WA3325334
<i>Ramphastos vitellinus</i> ^{**C}	Channel-billed Toucan	FR	MID	Present study	WA3325333, WA3204945
<i>Aulacorhynchus atrogularis</i>	Black-throated Toucanet	O	MID	Present study	
<i>Pteroglossus inscriptus</i>	Lettered Aracari	FR	C	Guilherme (2009)	MPEG 64564
<i>Pteroglossus mariae</i>	Chestnut-eared Aracari	FR	C	Guilherme (2009)	MPEG 59935
<i>Pteroglossus castanotis</i>	Brown-mandibled Aracari	FR	MID	Guilherme (2009)	MPEG 59934, WA3325332, WA2757307
<i>Pteroglossus beauharnaisii</i>	Curl-crested Aracari	FR	C	Guilherme (2009)	MPEG 63502, 63503, 63504, WA3325331, WA3206900
PICIDAE					
<i>Picumnus rufiventris</i> ^B	Rufous-breasted Piculet	INV	UND/MID	Present study	
<i>Melanerpes cruentatus</i>	Yellow-tufted Woodpecker	O	C	Guilherme (2009)	AC 190, 191, MPEG 63634
<i>Veniliornis affinis</i>	Red-stained Woodpecker	INV	MID	Silva <i>et al.</i> (2015)	
<i>Veniliornis passerinus</i>	Little Woodpecker	INV	UND/MID/C	Silva <i>et al.</i> (2015)	
<i>Piculus leucolaemus</i>	White-throated Woodpecker	INV	MID/C	Present study	
<i>Piculus laemosictus</i>	Spot-throated Woodpecker	INV	MID/C	Present study	

Family/Species/ Conservation status	English name	Guild	Stratum	Source	Voucher
<i>Celeus flavus</i> ^C	Cream-coloured Woodpecker	INV	MID	Present study	
<i>Celeus torquatus</i> ^{*,C}	Ringed Woodpecker	O	MID	Present study	WA972554
<i>Celeus spectabilis</i> ^{B,E,C}	Rufous-headed Woodpecker	INV	MID	Present study	WA3158715
<i>Dryocopus lineatus</i>	Lineated Woodpecker	INV	MID	Present study	
<i>Campephilus rubricollis</i>	Red-necked Woodpecker	INV	MID	Present study	WA3325286
<i>Campephilus melanoleucus</i>	Crimson-crested Woodpecker	INV	MID	Guilherme (2009)	MPEG 63632, WA3325285, 1460966
FALCONIDAE					
<i>Daptrius ater</i>	Black Caracara	VS	MID	Guilherme (2016)	
<i>Ibycter americanus</i>	Red-throated Caracara	INV	MID	Present study	WA3325284
<i>Milvago chimachima</i>	Yellow-headed Caracara	VS	G	Present study	
<i>Herpetotheres cachinnans</i>	Laughing Falcon	VS	G/UND/MID	Present study	
<i>Micrastur ruficollis</i>	Barred Forest Falcon	VS	G	Guilherme (2009)	MPEG 63472, WA3325023
<i>Micrastur mirandollei</i>	Slaty-backed Forest Falcon	VS	UND/MID	Present study	
<i>Micrastur semitorquatus</i>	Collared Forest Falcon	VS	G	Present study	
PSITTACIDAE					
<i>Ara macao</i> ^C	Scarlet Macaw	PS	MID	Present study	XC430740, WA3212607, WA3110803
<i>Ara chloropterus</i> ^C	Red-and-green Macaw	PS	MID	Present study	
<i>Ara severus</i> ^C	Chestnut-fronted Macaw	PS	MID	Present study	WA3334010, WA3058781, WA3331032
<i>Primolius couloni</i> **	Red-bellied Macaw	O	MID/C	Present study	WA3325323, WA3061151
<i>Orthopsittaca manilatus</i>	Blue-headed Macaw	FR	C	Present study	
<i>Psittacara leucophthalmus</i>	White-eyed Parakeet	PS	MID	Guilherme (2009)	MPEG 63475, 63476, 63461, WA3325330
<i>Aratinga weddellii</i>	Dusky-headed Parakeet	FR	C	Present study	WA3324083
<i>Pyrrhura rupicola</i> ^{*,E}	Black-capped Parakeet	FR	UND/MID	Present study	WA3333977
<i>Brotogeris cyanoptera</i>	Cobalt-winged Parakeet	FR	MID	Guilherme (2009)	MPEG 6361
<i>Brotogeris sanctithomae</i>	Tui Parakeet	FR	UND/MID	Present study	
<i>Pionites leucogaster</i>	White-bellied Parrot	PS	UND/MID	Guilherme (2009)	MPEG 63620
<i>Pionus menstruus</i>	Blue-headed Parrot	PS	MID	Present study	WA3325314
<i>Amazona farinosa</i> ** ^{,C}	Southern Mealy Amazon	O	MID	Present study	WA3324079
<i>Amazona ochrocephala</i> ^C	Yellow-crowned Amazon	PS	G/UND/MID	Guilherme (2009)	MPEG 63474, WA3324081
THAMNOPHILIDAE					
<i>Pygiptila stellaris</i>	Spot-winged Antshrike	INV	MID	Guilherme (2009)	MPEG 63545, 63637, 63638
<i>Microrhopias quixensis</i> ^B	Dot-winged Antwren	INV	MID	Silva <i>et al.</i> (2015)	
<i>Epinecrophylla leucophthalma</i>	White-eyed Antwren	INV	UND	Guilherme (2009)	MPEG 63635, 63636

Family/Species/ Conservation status	English name	Guild	Stratum	Source	Voucher
<i>Epinecrophylla amazonica</i>	Madeira Stipple-throated Antwren	INV	UND	Present study	
<i>Epinecrophylla ornata</i> ^B	Ornate Antwren	INV	MID	Guilherme (2009)	MPEG 59986, WA2301406, WA3064167
<i>Myrmophylax atrothorax</i>	Black-throated Antbird	INV	G	Present study	
<i>Myrmotherula brachyura</i>	Pygmy Antwren	INV	MID	Present study	
<i>Myrmotherula axillaris</i>	White-flanked Antwren	INV	MID	Guilherme (2009)	AC 196, MPEG 59976, 59977, 59978, 59979, 59980, 63542, 63543
<i>Myrmotherula longipennis</i>	Long-winged Antwren	INV	UND/MID	Guilherme (2009)	MPEG 59987, 59988, 59989
<i>Isleria hauxwelli</i>	Plain-throated Antwren	INV	G/UND	Guilherme (2009)	MPEG 59981, 59982, 59983, 59984, 59985
<i>Thamnomanes ardesiacus</i>	Dusky-throated Antshrike	INV	MID	Guilherme (2009)	MPEG 59969, 59972, 59973
<i>Thamnomanes schistogynus</i> ^E	Bluish-slate Antshrike	INV	MID	Guilherme (2009)	MPEG 59967, 59968
<i>Dichrozona cincta</i>	Banded Antbird	INV	G	Present study	
<i>Thamnophilus doliatus</i>	Barred Antshrike	INV	MID	Silva <i>et al.</i> (2015)	XC430732
<i>Thamnophilus schistaceus</i>	Plain-winged Antshrike	INV	MID	Guilherme (2009)	MPEG 63540, 63544, XC430733, WA1371282
<i>Thamnophilus aethiops</i>	White-shouldered Antshrike	INV	UND/MID	Guilherme (2009) Guimarães (2017)	AC 192, 193, 194, 195, 588, 590, MPEG 59961, 59962, 59963, 59964, 59965, WA146
<i>Cymbilaimus lineatus</i>	Bamboo Antshrike	INV	MID	Present study	
<i>Cymbilaimus sanctaemariae</i> ^B	Fasciated Antshrike	INV	MID	Present study	WA3058776, WA3212570
<i>Taraba major</i>	Great Antshrike	INV	G/UND	Present study	
<i>Hylophylax naevius</i>	Spot-backed Antbird	INV	UND	Guilherme (2009)	MPEG 59998, 59999
<i>Sclateria naevia</i>	Silvered Antbird	INV	G	Guilherme (2016)	MPEG 60012, WA969802
<i>Myrmelastes hyperythrus</i>	Plumbeous Antbird	INV	G/UND	Guilherme (2009)	MPEG 64567, WA3324194
<i>Myrmelastes humaythae</i>	Humaitá Antbird	INV	G	Guilherme (2009)	XC468213
<i>Myrmoborus myotherinus</i>	Black-faced Antbird	INV	G/UND	Guilherme (2009)	MPEG 60005, 60006, 60007, 60008, 60009, WA951093
<i>Myrmoborus leucophrys</i>	White-browed Antbird	INV	G	Guilherme (2009)	MPEG 60010
<i>Akletos goeldii</i> ^{B, E}	Goeldi's Antbird	INV	G/UND	Guilherme (2009)	MPEG 60011, XC430741, WA3324076
<i>Hafferia fortis</i>	Sooty Antbird	INV	G	Guilherme (2009)	MPEG 63539, 63639, 63640, WA3334071

Family/Species/ Conservation status	English name	Guild	Stratum	Source	Voucher
<i>Sciaphylax hemimelaena</i>	Southern Chestnut-tailed Antbird	INV	G/UND	Guilherme (2009)	AC 199, MPEG 60013, 60014
<i>Cercomacra cinerascens</i>	Grey Antbird	INV	MID	Present study	WA961150
<i>Cercomacroides fuscicauda</i>	Riparian Antbird	INV	G/UND	Present study	
<i>Cercomacroides seroa</i>	Black Antbird	INV	UND	Guilherme (2009)	MPEG 63549
<i>Hypocnemis subflava</i> ^{B, E}	Yellow-breasted Warbling Antbird	INV	UND	Silva <i>et al.</i> (2015)	WA3223640, WA2943326, WA3382943
<i>Hypocnemis peruviana</i>	Peruvian Warbling Antbird	INV	UND	Guilherme (2009)	AC 200, 201, 202, 586, MPEG 63547, 63548
<i>Willisornis poecilotus</i>	Common Scale-backed Antbird	INV	G	Guilherme (2009)	MPEG 59990, 59991, 59992, 59993, 59994, 59995, 59996, 59997
<i>Phlegopsis nigromaculata</i>	Black-spotted Bare-eye	INV	G	Guilherme (2009)	AC 204, MPEG 60022, 60023, 60024, 60025
<i>Oneillornis salvini</i> ^E	White-throated Antbird	INV	G	Guilherme (2009)	AC 203, MPEG 60019, 6002, 63546, WA1371811
<i>Rhegmatorhina melanosticta</i>	Hairy-crested Antbird	INV	G	Guilherme (2009)	MPEG 60021
CONOPOPHAGIDAE					
<i>Conopophaga peruviana</i>	Ash-throated Gnatcatcher	INV	G	Present study	CEMAVE E152474
GRALLARIDAE					
<i>Hyllopezus berlepschi</i>	Amazonian Antpitta	INV	G	Present study	
<i>Myrmothera campanisona</i>	Thrush-like Antpitta	INV	G	Present study	WA1371814, 1371815
FORMICARIIDAE					
<i>Formicarius analis</i>	Black-faced Antthrush	INV	G	Present study	WA1371813
<i>Formicarius colma</i>	Rufous-capped Antthrush	INV	G	Silva <i>et al.</i> (2015)	
SCLERURIDAE					
<i>Sclerurus mexicanus</i>	Tawny-throated Leaf-tosser	INV	G	Present study	
<i>Sclerurus caudacutus</i>	Black-tailed Leaf-tosser	INV	G	Guilherme (2009)	MPEG 59959
DENDROCOLAPTIDAE					
<i>Dendrocincla fuliginosa</i>	Plain-brown Woodcreeper	INV	G/UND/MID	Guilherme (2009)	MPEG 63522, 63523
<i>Dendrocincla merula</i>	White-chinned Woodcreeper	INV	G/UND	Guilherme (2016)	AC 205, MPEG 59936, 63521
<i>Deconychura longicauda</i>	Long-tailed Woodcreeper	INV	MID	Present study	
<i>Sittasomus griseicapillus</i>	Olivaceous Woodcreeper	INV	MID/C	Present study	
<i>Glyphorhynchus spirurus</i>	Wedge-billed Woodcreeper	INV	C	Guilherme (2009)	MPEG 59942
<i>Xiphorhynchus elegans</i>	Elegant Woodcreeper	INV	MID	Guilherme (2009)	MPEG 59943, 59944, 59945, 59946, 63524
<i>Xiphorhynchus guttatoides</i>	Lafresnaye's Woodcreeper	INV	MID	Guilherme (2009)	MPEG 63525, WA961216
<i>Campylorhamphus trochilirostris</i> ^B	Red-billed Scythebill	INV	UND	Guilherme (2009)	MPEG 59949, WA3061123

Family/Species/ Conservation status	English name	Guild	Stratum	Source	Voucher
<i>Dendroplex picus</i>	Straight-billed Woodcreeper	INV	MID	Present study	
<i>Lepidocolaptes fatimalimae</i>	Inambari Woodcreeper	INV	C	Present study	
<i>Dendrexetastes rufigula</i>	Cinnamon-throated Woodcreeper	INV	MID/C	Present study	WA1326333
<i>Dendrocolaptes certhia</i>	Amazonian Barred Woodcreeper	INV	MID	Present study	
<i>Dendrocolaptes picumnus</i>	Black-banded Woodcreeper	INV	G/UND	Present study	
XENOPIIDAE					
<i>Xenops minutus</i>	Plain Xenops	INV	UND/MID	Guilherme (2009)	MPEG 59960, 63526, AC 208, 209, 595
<i>Xenops rutilans</i>	Streaked Xenops	INV	MID	Present study	WA973883
FURNARIIDAE					
<i>Furnarius leucopus</i>	Pale-legged Hornero	INV	G	Present study	
<i>Automolus rufipileatus</i>	Chestnut-crowned Foliage-gleaner	INV	UND	Silva <i>et al.</i> (2015)	
<i>Automolus melanopezus</i> ^B	Brown-rumped Foliage-gleaner	INV	UND	Present study	
<i>Automolus subulatus</i>	Striped Woodhaunter	INV	UND/MID	Guilherme (2009)	MPEG 59958
<i>Automolus ochrolaemus</i>	Buff-throated Foliage-gleaner	INV	UND	Guilherme (2009)	MPEG 59954, 59955, 59956, 59957, WA1460958, 952365
<i>Anabacerthia ruficaudata</i>	Rufous-tailed Foliage-gleaner	INV	MID/C	Silva <i>et al.</i> (2015)	
<i>Philydor erythrocerum</i>	Rufous-rumped Foliage-gleaner	INV	MID/C	Present study	
<i>Philydor erythropterum</i>	Chestnut-winged Foliage-gleaner	INV	MID/C	Present study	WA1326311
<i>Synallaxis rutilans</i>	Ruddy Spinetail	INV	G/UND	Guilherme (2009)	MPEG 59950, WA2455713
PIPRIDAE					
<i>Pipra fasciicauda</i>	Band-tailed Manakin	FR	UND/MID	Guilherme (2009)	MPEG 60040, 60041, 60042, 60043, 60044, 60045, 60046, 60047, 60048, 60049, WA1371299
<i>Ceratopipra rubrocapilla</i>	Red-headed Manakin	FR	UND/MID	Guilherme (2009)	MPEG 60051
<i>Lepidothrix coronata</i>	Blue-crowned Manakin	FR	UND/MID	Guilherme (2009)	MPEG 63656, 63590, WA1460975
<i>Machaeropterus pyrocephalus</i>	Fiery-capped Manakin	FR	UND/MID	Guilherme (2009)	MPEG 63589, 63655
ONYCHORHYNCHIDAE					
<i>Onychorhynchus coronatus</i>	Amazonian Royal Flycatcher	INV	UND/MID	Guilherme (2009)	MPEG 60037, 60038
<i>Terenotriccus erythrurus</i>	Ruddy-tailed Flycatcher	INV	UND/MID	Guilherme (2009)	MPEG 60039, 63573, AC 583
<i>Myiobius atricaudus</i>	Black-tailed Flycatcher	INV	UND/MID	Present study	WA1460982
TITYRIDAE					
<i>Laniocera hypopyrra</i>	Cinereous Mourner	INV	UND/MID	Present study	

Family/Species/ Conservation status	English name	Guild	Stratum	Source	Voucher
<i>Tityra inquisitor</i>	Black-crowned Tityra	FR	MID	Present study	
<i>Tityra cayana</i>	Black-tailed Tityra	FR	UND/MID	Present study	
<i>Pachyramphus castaneus</i>	Chestnut-crowned Becard	INV	MID	Present study	
<i>Pachyramphus polychopterus</i>	White-winged Becard	O	MID	Present study	WA3324215
<i>Pachyramphus marginatus</i>	Black-capped Becard	O	MID	Present study	AC 593
<i>Pachyramphus minor</i>	Pink-throated Becard	O	UND/MID	Present study	
<i>Pachyramphus validus</i>	Crested Becard	INV	UND/MID	Present study	
COTINGIDAE					
<i>Querula purpurata</i>	Purple-throated Fruitcrow	O	UND/MID	Present study	
<i>Lipaugus vociferans</i>	Screaming Piha	O	UND/MID	Present study	XC430739
<i>Gymnoderus foetidus</i>	Bare-necked Fruitcrow	FR	UND/MID	Guilherme (2009)	MPEG 63591, 64576
<i>Conioptilon mcilhennyi</i> ^E	Black-faced Cotinga	FR	UND/MID	Guilherme (2009)	MPEG 63657, 64575, XC430736, WA1648888
PIPRITIDAE					
<i>Piprites chloris</i>	Wing-barred Piprites	INV	C	Guilherme (2009)	MPEG 64586, WA1371295, 951289
<i>Platyrinchus coronatus</i>	Golden-crowned Spadebill	INV	UND	Present study	
<i>Platyrinchus platyrhynchos</i>	White-crested Spadebill	INV	MID	Present study	
RHYNCHOCYCLIDAE					
<i>Cnipodectes superrufus</i> ^{**B,E}	Rufous Twistwing	INV	UND	Present study	WA2236547, 1462008, 1621627
<i>Mionectes oleagineus</i>	Ochre-bellied Flycatcher	FR	UND/MID	Guilherme (2009)	MPEG 60035, 60036, 63572, AC 594
<i>Leptopogon amaurocephalus</i>	Sepia-capped Flycatcher	INV	UND/MID	Guilherme (2009)	MPEG 60032, 60033, 63574, 64572, 600, AC 589
<i>Corythopsis torquatus</i>	Ringed Antpipit	INV	G	Present study	WA3325302
<i>Rhynchocyclus olivaceus</i>	Olivaceous Flatbill	INV	UND/MID	Present study	
<i>Tolmomyias sulphurescens</i>	Yellow-olive Flycatcher	INV	MID	Guilherme (2016)	AC 587
<i>Tolmomyias assimilis</i>	Yellow-margined Flycatcher	INV	MID	Guilherme (2009)	MPEG 64569
<i>Tolmomyias poliocephalus</i>	Grey-crowned Flatbill	INV	MID/C	Present study	
<i>Tolmomyias flaviventris</i>	Ochre-lore Flatbill	INV	C	Present study	
<i>Todirostrum maculatum</i>	Spotted Tody-Flycatcher	INV	MID	Present study	
<i>Todirostrum chrysocrotaphum</i>	Yellow-browed Tody-Flycatcher	INV	C	Guilherme (2009)	MPEG 64568, 64574
<i>Poecilatriccus latirostris</i>	Rusty-fronted Tody-Flycatcher	INV	UND	Present study	AC 592, WA1829296
<i>Myiornis ecaudatus</i>	Short-tailed Pygmy Tyrant	INV	C	Present study	
<i>Hemitriccus cohnhafti</i> ^{*B,E}	Acre Tody-Tyrant	INV	MID	Present study	WA2376966
<i>Hemitriccus flammulatus</i> ^B	Flammulated Bamboo Tyrant	INV	MID	Silva <i>et al.</i> (2015)	AC 722
<i>Hemitriccus iohannis</i>	Johannes's Tody-Tyrant	INV	MID	Silva <i>et al.</i> (2015)	

Family/Species/ Conservation status	English name	Guild	Stratum	Source	Voucher
<i>Lophotriccus eulophotes</i> ^{B, E}	Long-crested Pygmy Tyrant	INV	MID	Guilherme (2009)	MPEG 60030, 60031, 63641, AC 425, 426, WA952327
TYRANNIDAE					
<i>Zimmerius gracilipes</i>	Slender-footed Tyrannulet	INV	C	Present study	
<i>Ornithion inerne</i>	White-lored Tyrannulet	INV	C	Present study	
<i>Myiopagis gaimardii</i>	Forest Elaenia	INV	C	Present study	
<i>Myiopagis flavivertex</i>	Yellow-crowned Elaenia	INV	C	Guilherme (2009)	MPEG 64571
<i>Tyrannulus elatus</i>	Yellow-crowned Tyrannulet	INV	C	Guilherme (2009)	MPEG 63644, 64573
<i>Capsiempis flaveola</i>	Yellow Tyrannulet	INV	MID	Present study	WA2879673, WA3315889
<i>Phaeomyias murina</i>	Mouse-colored Tyrannulet	INV	UND/MID/C	Present study	
<i>Attila spadiceus</i>	Bright-rumped Attila	O	MID/C	Guilherme (2009)	MPEG 63571, WA951253
<i>Legatus leucophaeus</i>	Piratic Flycatcher	INS	C	Present study	
<i>Ramphotrigon megalcephalum</i> ^B	Large-headed Flatbill	INS	UND/MID	Silva <i>et al.</i> (2015)	WA1586489
<i>Ramphotrigon fuscicauda</i> ^B	Dusky-tailed Flatbill	INS	UND/MID	Guilherme (2009)	MPEG 63570, 63646, 63647, WA1462130, 1371338
<i>Myiarchus tuberculifer</i>	Dusk-capped Flycatcher	INS	UND/MID/C	Guilherme (2009)	MPEG 63642, 63643
<i>Myiarchus ferox</i>	Short-crested Flycatcher	O	C	Guilherme (2009)	MPEG 64570
<i>Sirystes albocinereus</i>	White-rumped Sirystes	INV	UND	Present study	WA1374005, 1462118, 1374005
<i>Rhytipterna simplex</i>	Greyish Mourner	INV	UND/MID	Guilherme (2009)	MPEG 63648, 63649, WA3325337, 1461000
<i>Casiornis rufus</i> ^{MA}	Rufous Casiornis	INS	UND	Guilherme (2009)	MPEG 63645
<i>Pitangus sulphuratus</i>	Great Kiskadee	O	G	Present study	
<i>Myiodynastes maculatus</i>	Sulphur-bellied Flycatcher	O	MID	Guilherme (2009)	MPEG 63650
<i>Megarynchus pitangua</i>	Boat-billed Flycatcher	O	MID	Present study	
<i>Myiozetetes cayanensis</i>	Rusty-margined Flycatcher	INV	G	Present study	
<i>Myiozetetes similis</i>	Social Flycatcher	O	MID	Present study	
<i>Tyrannus melancholicus</i>	Tropical Kingbird	INV	MID/C	Present study	
<i>Tyrannus savana</i> ^{MA}	Fork-tailed Flycatcher	INV	G/UND	Present study	
<i>Myiophobus fasciatus</i> ^{MA}	Bran-coloured Flycatcher	INV	UND	Present study	
<i>Pyrocephalus rubinus</i> ^{MA}	Vermilion Flycatcher	INV	UND/MID	Present study	
<i>Cnemotriccus fuscatus</i>	Fuscous Flycatcher	INV	G/UND	Present study	
VIREONIDAE					
<i>Cyclarhis gujanensis</i>	Rufous-browed Peppershrike	INV	UND/MID	Present study	
<i>Vireolanius leucotis</i>	Slaty-capped Shrike-Vireo	INV	C	Present study	
<i>Tunchiornis ochraceiceps</i>	Tawny-crowned Greenlet	INV	UND	Guilherme (2009)	MPEG 60052, 60053

Family/Species/ Conservation status	English name	Guild	Stratum	Source	Voucher
<i>Vireo chivi</i> ^{MA}	Chivi Vireo	INV	C	Present study	
HIRUNDINIDAE					
<i>Atticora fasciata</i>	Wing-banded Swallow	INV	UND/AE	Present study	
<i>Stelgidopteryx ruficollis</i>	Southern Rough-winged Swallow	INV	MID	Guilherme (2009)	MPEG 63658
TROGLODYTIDAE					
<i>Microcerculus marginatus</i>	Southern Nightingale-Wren	INV	G/UND	Present study	WA951261
<i>Troglodytes musculus</i>	House Wren	INV	UND	Present study	
<i>Campylorhynchus turdinus</i>	Thrush-like Wren	INV	UND/MID	Present study	
<i>Pheugopedius genibarbis</i>	Moustached Wren	INV	UND	Silva <i>et al.</i> (2015)	
<i>Cantorchilus leucotis</i>	Buff-breasted Wren	INV	UND	Present study	
POLIOPTILIDAE					
<i>Polioptila plumbea</i>	Tropical Gnatcatcher	INV	UND/MID/C	Present study	
TURDIDAE					
<i>Catharus swainsoni</i> ^{MN}	Swainson's Thrush	INV	G/UND	Present study	
<i>Turdus ignobilis</i>	Hauxwell's Thrush	O	UND/MID	Present study	
<i>Turdus hauxwelli</i>	Creamy-bellied Thrush	O	G	Guilherme (2009)	MPEG 60058, WA3324213
<i>Turdus amaurochalinus</i> ^{MA}	Black-billed Thrush	FR	MID/C	Present study	
PASSERELLIDAE					
<i>Ammodramus aurifrons</i>	Grassland Sparrow	PS	G	Present study	
<i>Arremon taciturnus</i>	Pectoral Sparrow	O	G/UND	Guilherme (2009)	MPEG 63607, 6360, WA1371289
PARULIDAE					
<i>Myiothlypis fulvicauda</i>	Buff-rumped Warbler	INV	G	Silva <i>et al.</i> (2015)	AC 719, WA1341374
ICTERIDAE					
<i>Psarocolius decumanus</i> ^C	Crested Oropendola	FR	MID	Present study	XC430735
<i>Psarocolius bifasciatus</i> ^C	Olive Oropendola	O	MID/C	Guilherme (2009)	MPEG 63668, XC430734
<i>Cacicus cela</i>	Yellow-rumped Cacique	FR	C	Guilherme (2009)	MPEG 63610
<i>Icterus croconotus</i>	Orange-backed Troupial	FR	MID/C	Present study	WA3324227
<i>Molothrus oryzivorus</i>	Giant Cowbird	FR	G/C	Present study	
<i>Sturnella militaris</i>	Red-breasted Meadowlark	O	G	Guilherme (2009)	MPEG 63667
MITROSPINGIDAE					
<i>Lamprospiza melanoleuca</i>	Red-billed Pied Tanager	O	C	Present study	
THRAUPIDAE					
<i>Cissopis leverianus</i>	Magpie Tanager	FR	UND/MID	Present study	
<i>Paroaria gularis</i>	Red-capped Cardinal	INV	UND	Guilherme (2009)	MPEG 63669
<i>Tangara schrankii</i>	Green-and-gold Tanager	FR	MID	Guilherme (2009)	MPEG 63662
<i>Tangara mexicana</i>	Turquoise Tanager	O	C	Guilherme (2009)	MPEG 64577, 64578, 64579
<i>Tangara chilensis</i>	Paradise Tanager	FR	C	Guilherme (2009)	MPEG 63662

Family/Species/ Conservation status	English name	Guild	Stratum	Source	Voucher
<i>Tangara callophrys</i>	Opal-crowned Tanager	FR	C	Present study	
<i>Tangara episcopus</i>	Blue-grey Tanager	O	MID	Silva <i>et al.</i> (2015)	
<i>Tangara palmarum</i>	Palm Tanager	FR	C	Present study	
<i>Tangara nigrocincta</i>	Masked Tanager	FR	C	Present study	
<i>Hemithraupis flavicollis</i>	Yellow-backed Tanager	INV	C	Present study	
<i>Hemithraupis guira</i>	Guira Tanager	INV	C	Present study	
<i>Volatinia jacarina</i>	Blue-black Grassquit	O	G	Silva <i>et al.</i> (2015)	
<i>Eucometis penicillata</i>	Grey-headed Tanager	INV	UND	Present study	
<i>Lanio versicolor</i>	White-winged Shrike-Tanager	INV	C	Present study	
<i>Lanio luctuosus</i>	White-shouldered Tanager	INV	MID	Guilherme (2009)	MPEG 60054, 63660, 63661, WA1456768
<i>Ramphocelus nigrogularis</i>	Masked Crimson Tanager	O	MID	Present study	
<i>Ramphocelus carbo</i>	Silver-beaked Tanager	O	UND	Silva <i>et al.</i> (2015)	WA3333978
<i>Tersina viridis</i>	Swallow Tanager	FR	MID	Guilherme (2009)	MPEG 64580
<i>Cyanerpes nitidus</i>	Short-billed Honeycreeper	O	C	Present study	
<i>Dacnis flaviventer</i>	Yellow-bellied Dacnis	FR	MID	Guilherme (2009)	MPEG 63663, 64585
<i>Dacnis lineata</i>	Black-faced Dacnis	FR	C	Guilherme (2009)	MPEG 63664
<i>Dacnis cayana</i>	Blue Dacnis	O	C	Guilherme (2009)	MPEG 63605
<i>Sporophila caeruleascens</i> ^{MI}	Double-collared Seedeater	PS	G	Present study	
<i>Sporophila castaneiventris</i>	Chestnut-bellied Seedeater	PS	UND	Present study	
<i>Sporophila angolensis</i>	Chestnut-bellied Seed Finch	PS	G	Silva <i>et al.</i> (2015)	
<i>Saltator coerulescens</i>	Greyish Saltator	INV	UND	Present study	
<i>Saltator maximus</i>	Buff-throated Saltator	INV	UND	Silva <i>et al.</i> (2015)	
<i>Saltator grossus</i>	Slate-coloured Grosbeak	INV	C	Guilherme (2009)	MPEG 63609, 63665, 63666, XC467605
CARDINALIDAE					
<i>Habia rubra</i>	Scarlet-throated Ant Tanager	INV	MID	Guilherme (2009)	MPEG 60055, 60056
<i>Cyanoloxia rothschildii</i>	Rothschild's Grosbeak	FR	G	Guilherme (2009)	MPEG 60057, 63606, WA2454852
FRINGILLIDAE					
<i>Euphonia chlorotica</i>	Purple-throated Euphonia	FR	C	Present study	
<i>Euphonia lanirostris</i>	Thick-billed Euphonia	FR	MID	Guilherme (2009)	MPEG, 64582, 64583, 64584
<i>Euphonia chrysopasta</i>	Golden-bellied Euphonia	O	C	Present study	
<i>Euphonia xanthogaster</i>	Orange-bellied Euphonia	FR	MID	Guilherme (2009)	MPEG 63670
<i>Euphonia rufiventris</i>	Rufous-bellied Euphonia	FR	MID	Present study	

The nest, eggs and nestling development of Fork-tailed Woodnymph *Thalurania furcata boliviana*

by Edson Guilherme & Jônatas M. Lima

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SUMMARY.—Fork-tailed Woodnymph *Thalurania furcata* is widely distributed in South America, but there are comparatively few data on its breeding biology. A nest found with two eggs in an urban forest fragment in Acre, south-west Amazonia, was monitored until the nestlings fledged. The use of fibres from rhizomes of the fern *Phlebodium decumanum* as the main material used in the nest is reported for the first time in this species. Similarly, daily variation in the mass and growth of the nestlings is presented for the first time. Nest and egg dimensions, as well as the nestling period, were similar to those reported previously.

The genus *Thalurania* comprises seven species distributed from Mexico to Argentina (Stiles *et al.* 2020). Fork-tailed Woodnymph *T. furcata* is the geographically most widespread species of the genus, occurring across most of tropical South America, including the Guianas, Paraguay, much of Brazil, eastern Venezuela, Colombia, Ecuador, Peru and Bolivia (Stiles *et al.* 2020). At least 13 subspecies of *T. furcata* are generally accepted (Stiles *et al.* 2020), 12 of which occur in Brazil (Piacentini *et al.* 2015) and at least three in the state of Acre (*T. f. jelskii*, *T. f. simoni* and *T. f. boliviana*) (Guilherme 2016). The species inhabits the edge and interior of forest, occasionally plantations and more open areas (Stiles *et al.* 2020). Although it occurs in a wide geographic range, information on reproduction of this species is quite limited (Stiles *et al.* 2020). Formal descriptions of Fork-tailed Woodnymph nests in the literature are available only from north-east Brazilian Amazonia (*T. f. furcata*) and Amazonian Ecuador (*T. f. viridipectus*) (Ruschi 1986, Greeney & Gelis 2008). We present here for the first time descriptions of the nest, eggs and nestling development of *T. furcata* in south-west Brazilian Amazonia.

Methods

Study area.—We studied a nest of *T. furcata* in the Zoobotanical Park of the Universidade Federal do Acre (UFAC) (09°57'03.22"S, 67°52'30.65"W), in the city of Rio Branco, capital of Acre state, in the south-western Brazilian Amazon. Descriptions of the ecosystems and avifauna of the area can be found in Guilherme (2001).

Measurements, monitoring and marking.—We measured the nest and eggs using digital callipers. Eggs and nestlings were weighed using a digital scale (0.05 g precision). We visited the nest every two days during the observation period. We banded the nestlings using numbered metal rings supplied by CEMAVE (Centro Nacional de Pesquisa e Conservação de Aves Silvestres), under the scope of project 1099, coordinated by EG (senior bird bander, reg. no. 324654). Once the nest was no longer active, we collected it and deposited it in the nest collection of the UFAC ornithology laboratory (reg. no. AC 0043).

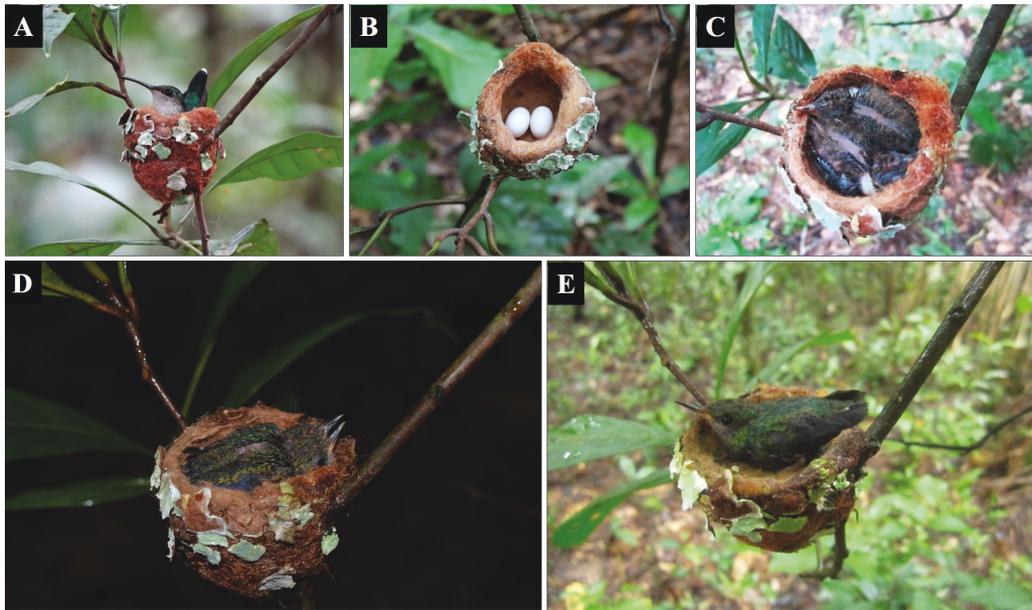


Figure 1. Nest, eggs and nestlings of Fork-tailed Woodnymph *Thalurania furcata boliviana* in south-west Brazilian Amazonia: (A) female incubating the eggs; (B) view of the nest showing the eggs; (C) nestlings with feathers growing on all body tracts; (D) feathered nestlings; (E) one of the nestlings the day prior to fledging (A, B and D: Edson Guilherme; C and E: Jônatas Lima)

Results

On 4 January 2016 we found a nest of Fork-tailed Woodnymph in the forest understorey at the Zoobotanical Park, when it contained two eggs (Fig. 1A). The nest was sited in the two-way fork of a small understorey sapling (*cf. Ocotea* sp.; Lauraceae), 1.55 m above ground. The branches where the nest was built were 4.05 mm (main) and 2.41 mm (secondary) in diameter, respectively. The low cup / fork nest (*sensu* Simon & Pacheco 2005) was constructed primarily of fern ramenta and lined internally with pale brown kapok seed down (*Ceiba* sp.; Bombacaceae) (Fig. 1A–B). Comparing the ramenta of *Cyathea* sp. and *Phlebodium* sp., both common in the Zoobotanical Park, with those used in the nest, it was clear that the material in the latter was the *Phlebodium decumanum* rhizome (Fig. 2). There were few lichens adorning the outer wall (Fig. 1A) and spider webs on the rim of the cup (Fig. 1B). The nest measured as follows: height of the outer wall 47.0 mm; depth of cup 19.0 mm; external diameter 53.2 mm; internal diameter of cup 37.6 mm, and wall thickness 7.8 mm (the latter an average of three different measurements).

On 11 January we measured and weighed the two white eggs (Fig. 1B): 13 × 9 mm, 0.8 g; and 13 × 9 mm, 0.5 g. The nestlings hatched sometime between 12 and 13 January but were weighed for the first time only on 14 January (Fig. 3). The only traces of plumage on hatching are beige-coloured feathers on the dorsal spinal tract which are pushed up and out by the developing contour feathers. By 26 January (*c.*14 days after hatching) the body was wholly covered in well-developed feather papillae on the remiges and other tracts (Fig. 1C). On 29 January the nestlings were completely feathered (Fig. 1D).

On 14 January the nestlings weighed 1.2 and 1.3 g, respectively (Fig. 3). Over the next 14 days (until 28 January) the nestlings gained on average 0.47 ± 0.37 and 0.53 ± 0.36 g per day reaching the asymptote at 4.5 and 5.0 g, respectively (Fig. 3). Over the next four days their mass declined by *c.*0.025 and 0.12 g per day, to 4.4 and 4.5 g, respectively, on

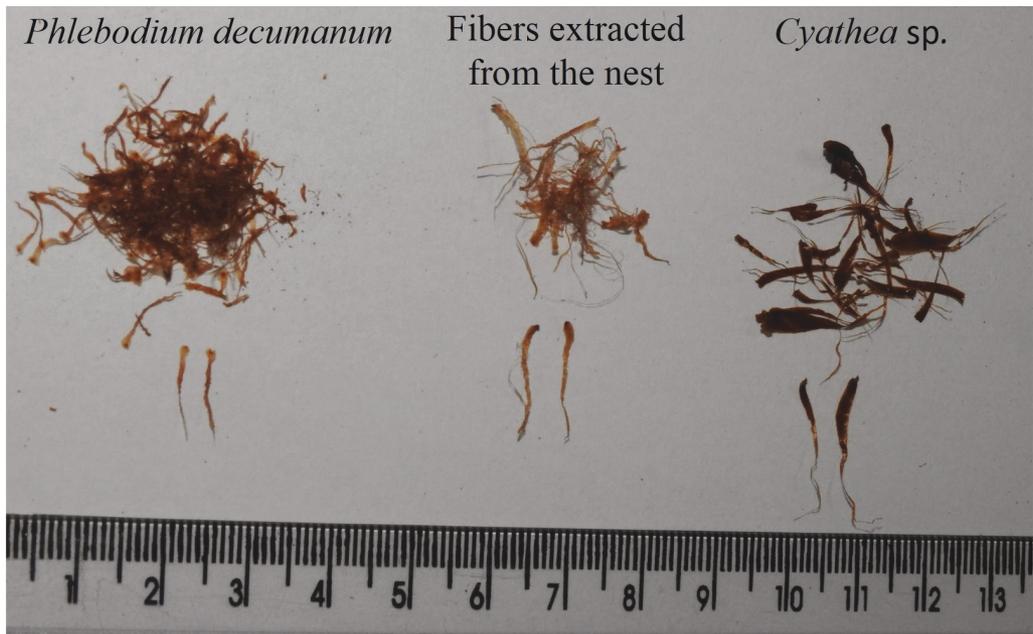


Figure 2. Comparison of ramenta used in the construction of a Fork-tailed Woodnymph *Thalurania furcata boliviana* nest with that of leaves of arborescent ferns (*Cyathea* sp.) and rhizomes of *Phlebodium* ferns that occur in the Zoobotanical Park; note the similarity between the material used to built the nest (centre) and the ramenta of *Phlebodium decumanum* (left) (Edson Guilherme)

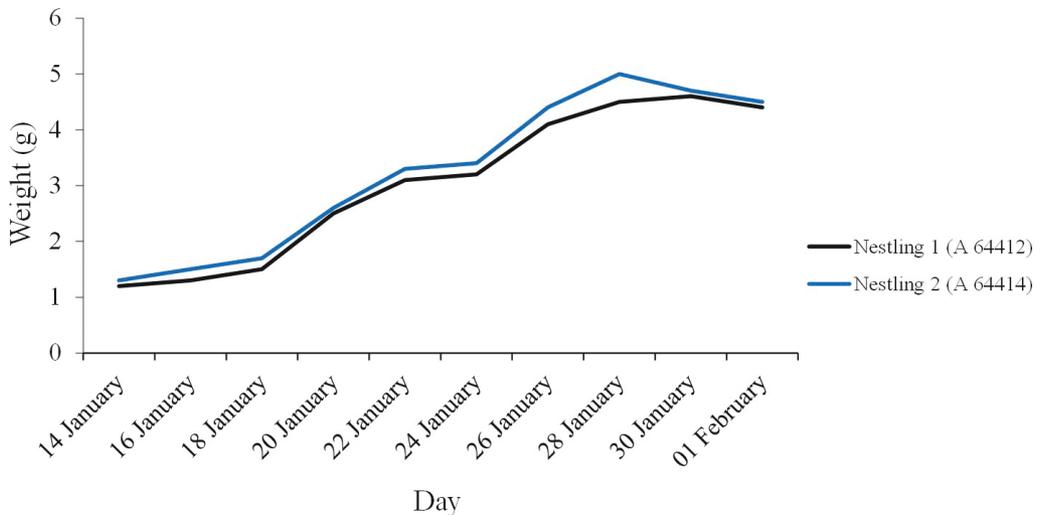


Figure 3. Mass gain of Fork-tailed Woodnymph *Thalurania furcata boliviana* nestlings in Acre, Brazil, over the development period (measurements taken every two days between 14 January and 1 February 2016).

1 February (Fig. 3) when they were last weighed. We ringed the nestlings the same day (ring codes A64412 and A64414). On 2 February just one nestling remained in the nest (Fig. 1E) and it was not present the next day. The max. duration of the nestling period was 21 days (assuming that the first nestling hatched on 12 January and fledged on 2 February 2016).

Discussion

Fork-tailed Woodnymph is common in south-west Amazonia, especially in Acre (Guilherme 2016), but it is poorly known ecologically. Although three races may occur in Acre, in the east of the state, where the Zoobotanical Park is situated, the subspecies is *T. f. boliviana* (Guilherme 2009). The species constructs its forked nest low above ground as reported elsewhere (Stiles *et al.* 2020). Almost all nest biometrics reported here were similar to those reported from Ecuador by Greeney & Gelis (2008), except internal diameter. In Acre and the nests from north-east Amazonian Brazil reported by Ruschi (1986), the internal diameter of the cup was relatively larger (almost double) than that of the Ecuador nests. This difference is perhaps explained by the time when the nests were measured: in our case, these were made when the nest had already been collected, whereas the measurements of the Ecuadorian nest were taken in the field during the incubation period (Greeney & Gelis 2008). The description of the eggs, and their sizes, were practically identical to those reported by Greeney & Gelis (2008) from Ecuador, and Brazil (Stiles *et al.* 2020). Unlike other hummingbird nests that are extensively decorated with lichens on their outer walls for camouflage (McCormac & Showman 2009), the Acre nest had practically no external decoration (Fig. 1), somewhat like that described by Greeney & Gelis (2008) in Ecuador.

The type of material used in the cup differed slightly from that reported in Ecuador, which contained much seed down in the external wall (Greeney & Gelis 2008). Ruschi (1986) stated that Fork-tailed Woodnymph constructs the outer walls with rameta of arborescent ferns, and lines the nest with fibres of Bromeliaceae, Gramineae and Brobaceae. This description is quite different from the Acre nest. Comparison of the material used to construct the cup of the latter nest with rameta of the unique arborescent ferns (*Cyathea* sp.) in the Zoobotanical Park was not compatible, but did match rhizome fibres of the epiphytic fern *Phlebodium decumanum* (Fig. 2). Use of fern rameta of *P. decumanum* is reported here for the first time for *T. furcata*, although this type of material (not identified to species) is often reported for other hummingbirds and passerines (Greeney *et al.* 2010, Fjeldså *et al.* 2020). Indeed, the material described in the Ecuador nest as 'brown plant fibres' (Greeney & Gelis 2008) was clearly fern rameta.

Development of the nestling is also presented here for the first time. Nestlings gain weight until the 16th day and then lose mass slowly until they fledge, which is similar to growth patterns in other families of birds (Seixas & Mourão 2003, Guilherme & Souza 2013) including hummingbirds (Muir & Butler 1925, Vereá 2016).

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Distribution, behaviour, and provenance of Oriental Dollarbirds *Eurystomus orientalis* in Micronesia, including the first two records from the Mariana Islands

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SUMMARY.—We document the status of Oriental Dollarbird *Eurystomus orientalis* in Micronesia, a region extralimital to the generally accepted geographic range of the species. Our review yielded 34 Micronesian records between 1938 and 2019, with 27 at Palau, four at Yap, and one at Pohnpei in the Caroline Islands, as well as one each at Guam and Saipan, which are the first for the Mariana Islands. Expanded observer effort since 2000 has produced an increase in regional sightings, with birds detected in ten of the 18 years from 2002 to 2019. Examination of museum specimens ($n = 3$) and photographs of wild dollarbirds ($n = 10$) confirmed all but one individual as belonging to the migratory Australasian subspecies *E. o. pacificus*. Timing of records, with nearly all between mid April and mid October, largely matches the known migration and overwintering periods for *E. o. pacificus*, further indicating that most records involved this taxon.

Oriental Dollarbird *Eurystomus orientalis* is one of the largest and most subtly coloured members of the family Coraciidae. Adults of both sexes exhibit blue-green body plumage, a dusky head, dark throat with bright purple streaks, red bare parts (bill, feet and thin eye-ring), and namesake pale blue ‘silver dollars’ in the outer primaries (Fig. 1a). Juveniles are not as brightly coloured as adults, particularly on the forehead and crown, with muted body plumage, restricted throat streaks, and bills that start all black and gradually turn red from the base (Fig. 1b, c). Adults often retain a small black tip to the bill.

The species is widely distributed across much of eastern Asia and Australasia (Fry *et al.* 1992, Fry & Boesman 2018). Ten subspecies are currently recognised, eight of which are non-migratory tropical populations that range from India and South-East Asia to western Melanesia (Fry & Boesman 2018, Gill & Donsker 2019). The other two subspecies are fully or partially migratory, with *E. o. cyanocollis*, formerly *E. o. calonyx* (Gill & Donsker 2019), breeding from south-eastern Siberia to eastern China and northern India, and wintering in South-East Asia and the Greater Sundas, and *E. o. pacificus* having migratory populations in northern and eastern Australia that spend the austral winter in New Guinea and the adjoining islands of western Melanesia and much of Wallacea (Coates 1985, Dutson 2011, Fry & Boesman 2018). These two subspecies differ sufficiently in plumage colour that adults can sometimes be distinguished in the field or from good photographs. Compared to *E. o. cyanocollis*, *E. o. pacificus* is somewhat paler with noticeably less colour saturation, a slaty-brown head, nape and upper back, and a paler turquoise belly. Juveniles of both subspecies are easily distinguished from adults in the field (HDP pers. obs.). For colour illustrations of representative subspecies, see Fry & Boesman (2018).

Dollarbirds typically forage in ecotones with an open component and prominent perches, including woodland, open forest, forest edge, roadsides, cultivation, and other areas with scattered trees, but sometimes also inhabit closed forest and forest canopy

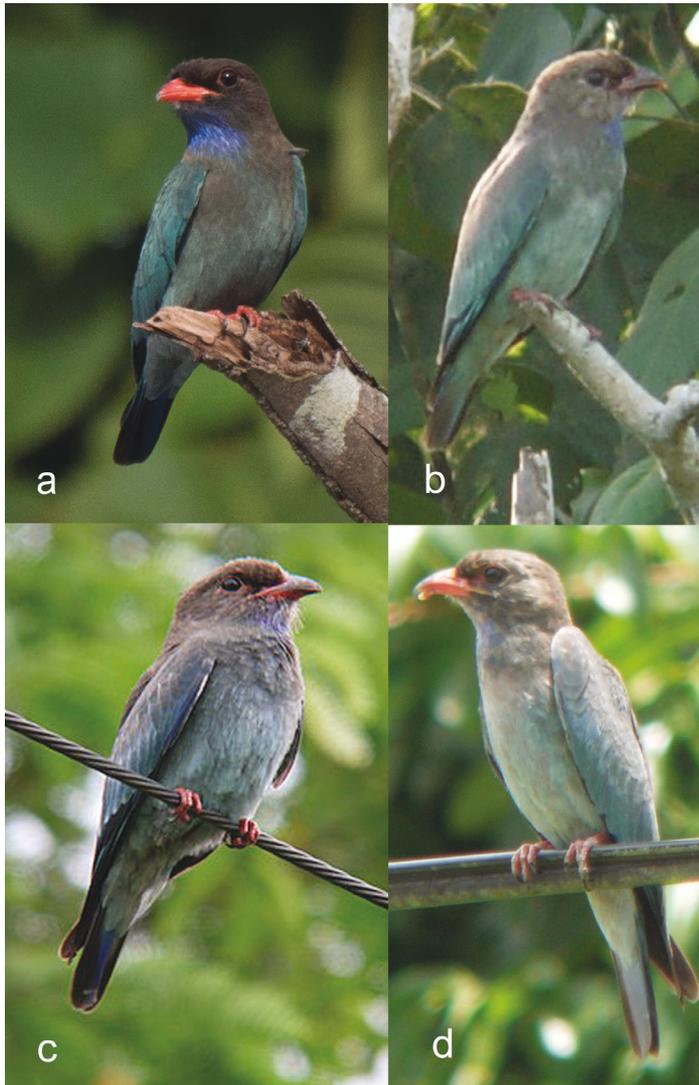


Figure 1. Plumage differences among four Oriental Dollarbirds *Eurystomus orientalis pacificus* of different ages photographed in Micronesia: (a) adult, Airai, Palau, 28 August 2019 (Glenn McKinlay), (b) juvenile, Ngeremlengui, Palau, 24–25 May 2008 (Alan Olsen, Palau National Museum), (c) older juvenile, Ngerekebesang Island, Palau, 7 June 2011 (Alan Olsen, Palau National Museum), (d) subadult, Aimeliik or Airai, Palau, 21 August 2008 (Alan Olsen, Palau National Museum). The subadult shows an all-red bill while retaining juvenile plumage.

(Coates 1985, Fry *et al.* 1992, Higgins 1999). Dollarbirds can be solitary, in pairs, or in loose feeding aggregations, and forage mainly by hawking large flying insects from high exposed perches, such as trees, snags and powerlines. They are most active from late afternoon to dusk, early morning, and during and after rain. The species is fairly common in much of its range and is not globally threatened (Fry & Boesman 2018).

The islands of Micronesia, which lie north and north-east of New Guinea and east of the Philippines, are considered outside the normal range of Oriental Dollarbird, with only 16 records previously published for the region. Over the past two decades, increased birding and biological field work in the region, plus the advent of eBird and other online databases, have produced more frequent reports of the species, many of which have not been published. Several authors have suggested that Micronesian records probably involve mostly *E. o. pacificus* (Engbring 1983, VanderWerf *et al.* 2006, Pratt & Etpison 2008, Pratt *et al.* 2010), but that hypothesis has not been confirmed, so the geographic provenance of Micronesian visitors is unknown. Here, we provide a listing of all known records of

Oriental Dollarbird made to date in Micronesia, summarise patterns of occurrence, and diagnose the subspecific identities of records where possible. We also provide supporting documentation for two records from the Mariana Islands, which are the first for that more northerly archipelago.

Methods

Review of records.—We reviewed all published reports, unpublished trip reports by visiting birders (www.cloudbirders.com), reports posted on eBird (<https://ebird.org>) and iNaturalist (www.inaturalist.org), records held in the Global Biodiversity Information Facility database (GBIF, www.gbif.org), and unpublished observations by birders living in Micronesia, to compile a comprehensive list of Oriental Dollarbird records for the region. We evaluated unpublished sightings for accuracy, and accepted those that came from experienced observers known to us and those supported by photographs. Because dollarbirds are so strikingly different from any resident bird species in Micronesia, with several obvious field marks, and because of their conspicuous behaviour, we also have high confidence in the accuracy of several reports from observers unfamiliar to us. When possible, we contacted observers to obtain supplemental information about their sightings and any photos they might have.

Subspecific evaluation of records.—HDP examined two of the three existing specimens (see Appendix) from Micronesia, which were loaned by their respective institutions (the Bernice P. Bishop Museum, Honolulu, Hawaii, USA [BPBH] and Brigham Young University, Hawaii, Laie, Hawaii, USA [BYUH]) to the National Museum of Natural History, Washington DC, USA, where adequate comparative specimens of the migratory and other subspecies are housed. He placed the specimens among series of *E. o. cyanocollis* and *E. o. pacificus* to determine visually their subspecific attribution. He also examined other specimens still in their cases and compared them directly with the two Micronesia ones to look for any matches. Additionally, HDP reviewed an online catalogue photograph of the third specimen, held at the Yamashina Institute for Ornithology, Chiba, Japan (YIO), as well as photographs taken of ten individuals in Micronesia, plus hundreds of images from other localities posted online, to assess subspecies identification of these birds. Photographs present several problems because they preserve an instant that may show deceptive coloration because of angles and intensity of light, whereas an observation of a live bird may better reveal true colours as the bird moves, but HDP has a lifetime of experience working with photographs as references for paintings, so we are confident of his comparisons.

Results

Summary of occurrence.—We compiled a total of 34 records of Oriental Dollarbird from Micronesia, 18 of which are previously unpublished (Appendix). Records were geographically distributed along a strong south-westerly gradient, with by far the largest number occurring in Palau (27 records; Fig. 2). Observations in Palau are primarily from Babeldaob ($n = 11$ records), the three main inhabited islands of Koror State ($n = 6$), Peleliu ($n = 3$), Angaur ($n = 3$) and the islets of the Southwest Islands ($n = 3$). Additional regional records were from Yap ($n = 4$), the Mariana Islands (Guam, $n = 1$; Saipan, $n = 1$), and Pohnpei ($n = 1$). Five records originated from atolls or atoll-like islands, including those from the Southwest Islands and Kayangel Atoll ($n = 1$) in Palau, and Ngulu Atoll ($n = 1$) in Yap.

Micronesian records spanned the period from 1938 to 2019, but have recently increased, with 23 in the past two decades (Appendix). Dollarbirds appeared in ten of the 18 years from 2002 to 2019 for the region as a whole, including in nine years in Palau alone. Records

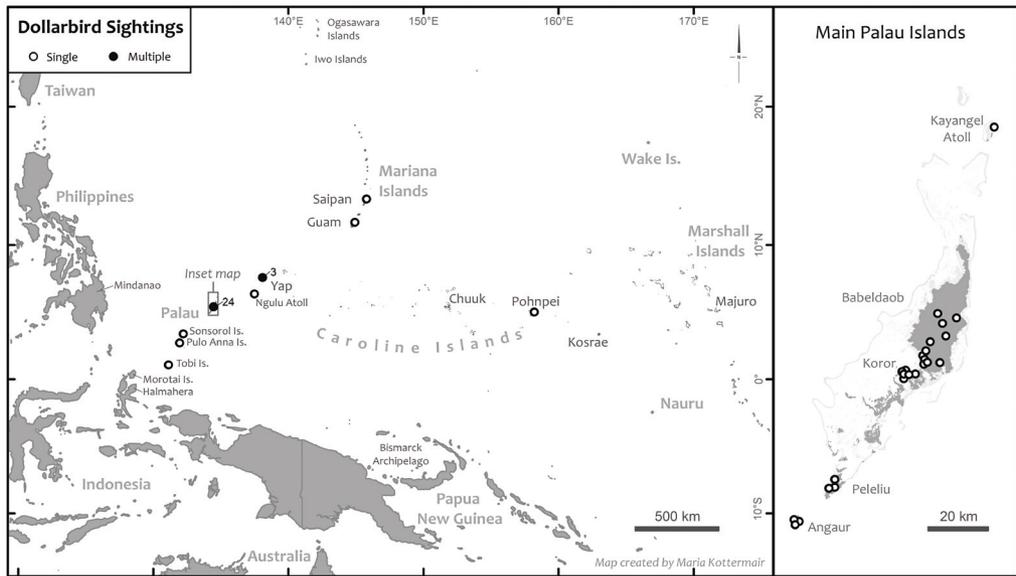


Figure 2. Locations of 34 known Oriental Dollarbird *Eurystomus orientalis* records from Micronesia.

demonstrated a highly seasonal pattern, all falling between 12 April and 17 December (Fig. 3). Numbers of records were highest between May and August, then dwindled through December. November was the only month in this period without a record.

Eighteen of the 22 dollarbird observations in which habitat was noted were in areas with a mix of open land (e.g., cultivated plots, roadsides, lawns or golf courses) and small or large patches of trees or forest (Appendix). Three individuals on atolls or atoll-like islets were in strand forest. Among described perch sites, powerlines were used about half the time ($n = 11$), while others included trees ($n = 6$), snags ($n = 3$) and a radio antenna ($n = 1$). The bias in favour of powerlines may reflect observer opportunity more than the birds' preference.

Adults predominated in our small sample of photographed individuals and museum specimens, with 11 adults, one subadult transitioning into adult plumage, and three juveniles recorded. All but three records involved singles, the exceptions being two pairs and a small group of unknown size (Appendix). One of the pairs was seen copulating, but the month of this observation was not reported. Twenty-nine records were of birds seen on one or several days only, while five others were of individuals that were present for longer periods ranging from c.17 to at least 50 days (Appendix). Multiple individuals were detected per year in the region in 1992 ($n = 2$ birds), 2005 ($n = 3$), 2008 ($n = 2$), 2014 ($n =$ probably ≥ 8), 2018 ($n = 2$) and 2019 ($n = 2$) (Appendix). The year 2014 was exceptional for sightings, with multiple birds found in southern Babeldaob (including four on one day) and Koror in Palau, as well as one bird in Yap.

Subspecific identification.—Both specimens examined by HDP were well within the range of colour variation for *E. o. pacificus*, and outside the range for *E. o. cyanocollis* or any other subspecies. The third specimen (YIO), the first from the region, was originally assigned to *E. o. connectens* (Yamashina 1940), now subsumed in *E. o. orientalis*, but Mayr (1945) considered it to represent *E. o. pacificus*, which is the designation the specimen tag now bears. Based on the online photo of the specimen, HDP concurs with that designation. Thus, all existing Micronesian specimens pertain to the migratory Australasian form.

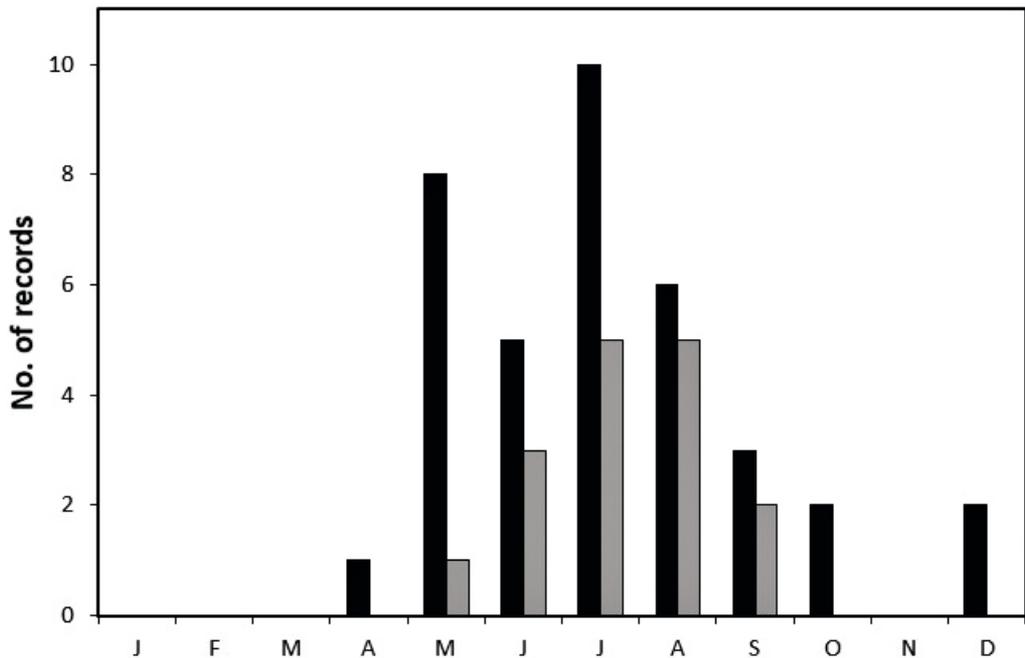


Figure 3. Monthly distribution of Oriental Dollarbird *Eurystomus orientalis* records in Micronesia in which the month(s) of occurrence is known (Appendix). Included are records for all individuals ($n = 34$, dark bars) and those confirmed as *E. o. pacificus* ($n = 12$, grey bars). Records over multiple months were tallied once for each month seen.

HDP identified nine of the ten dollarbirds documented by colour photographs as *E. o. pacificus* with certainty, the only exception being a bird photographed on Peleliu, Palau, by K. Swindle. The latter is borderline in the photos, which were apparently taken in deep shade, because it seems within the range of variation of both *E. o. pacificus* and *E. o. cyanocollis*. Given the May date and the shady conditions, it probably belongs to *E. o. pacificus*, but we cannot be 100% sure. Greyscale photos of an additional individual that were published in Engbring (1983) could not be identified to subspecies and the colour originals were not available. Results of both the specimen and photo examinations are shown in the Appendix. Records of confirmed *E. o. pacificus* generally corresponded with the same monthly pattern of occurrence documented among all dollarbirds, but without any observations made in April, October or December, and just one in May (Fig. 3).

First records for the Mariana Islands.—We describe the first two records of Oriental Dollarbirds in the Mariana Islands, both in 2018 and confirmed as *E. o. pacificus*. JC observed and photographed one at c.18.30 h in Marpi, northern Saipan, Commonwealth of the Northern Mariana Islands (15°15'19.4"N, 145°47'32.1"E) on 2 July. J. Fraser (pers. comm.) photographed the bird on 3 July 2018, and JC found it again on 4 July and 8 August. It was identified by its heavy bill, blue-green body plumage, red feet, a body size slightly larger and thicker than that of a Micronesian Starling *Aplonis opaca* perched nearby, pale patches in the primaries visible in flight, and undulating flight pattern (Fig. 4a). Based on photographs showing a half-black bill, no eye-ring and brown feathers on the forehead, HDP determined it to be an older juvenile. During the sightings, the bird perched on a powerline above a dirt road and repeatedly performed aerial sallies to catch insects in mid-flight. All observations occurred along the same 100-m stretch of road 40 m from the edge of a golf course. Habitat in the immediate area consisted of 50% open space and 50% native limestone forest mixed

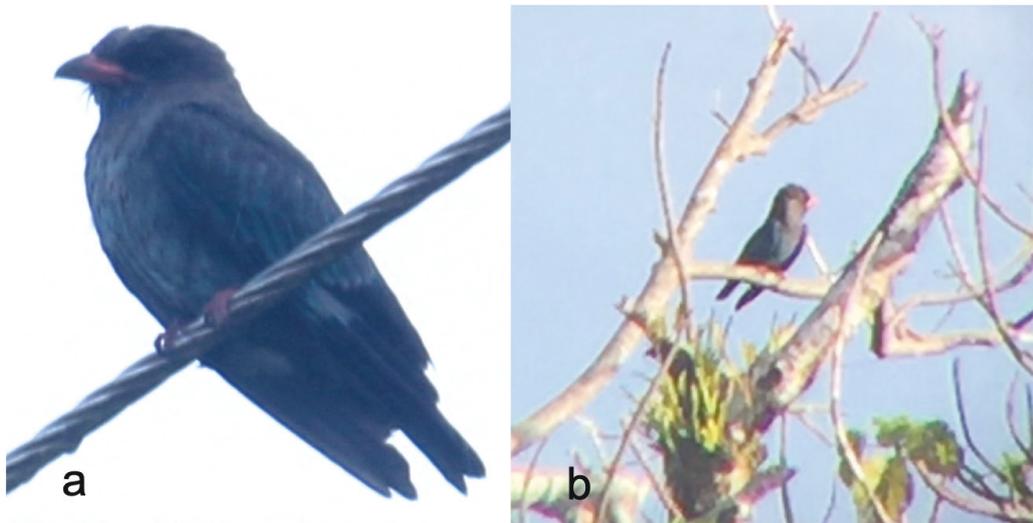


Figure 4. New records of Oriental Dollarbirds *Eurystomus orientalis* from the Mariana Islands: (a) a bird photographed on Saipan, 2 July 2018 (Janelle Chojnacki); lightening of shadows in Photoshop enabled HDP to categorise this individual as a juvenile; (b) an adult photographed on Guam, 24 September 2018 (Megan M. Pendred).

with non-native *Leucaena leucocephala* trees. JC's video, taken on 2 and 4 July, recorded the bird's short, raspy, squawk-like call.

In the late afternoon of 24 September, MMP & MK watched a dollarbird in native limestone forest 40 m from the edge of a golf course on Andersen Air Force Base, north-eastern Guam. They observed and photographed the bird for ten minutes from c.50 m as it perched above the forest canopy on an exposed branch of a *Macaranga thompsonii* tree. It then flushed suddenly and flew out of view towards the cliff to the east. Photographs show a medium-sized bird with turquoise-blue plumage over most of its upperparts and wings, a large, dark grey or brownish head with a short and slightly hooked orange-red bill tipped in black, bright red tarsi and feet, and long wings held below the body (Fig. 4b), indicating that it was an adult. The bird was noticeably larger than several Micronesian Starlings and Black Drongos *Dicrurus macrocercus* that later perched in the same tree. Although repeated visits to the site in the following days did not yield additional sightings, the observers heard a credible but unconfirmed report of a dollarbird on the edge of a golf course at the LeoPalace Resort in central Guam (K. Conroy pers. comm.) c.1 week later. Although timing would not preclude it, the Guam bird cannot be the same individual seen in July and August on Saipan because the latter was a juvenile, with much more black on its bill.

Discussion

Although most previous authors have described Oriental Dollarbirds as rare migrants to Micronesia (e.g., Pratt *et al.* 1987, Wiles *et al.* 2004, Pratt & Etpison 2008), our compilation and analysis of records provides significant new insights into the species' occurrence in the region. This study more than doubles the number of records known for Micronesia and establishes that the species is a regular visitor in very small numbers. Records originate predominately from Palau, where sightings have been documented in 50% of the years since 2002 (Appendix). However, because observer effort remains relatively low across Micronesia, we expect dollarbird occurrence to be more frequent than demonstrated

by available records, so the species probably reaches the region in most years. Presence is perhaps most under-estimated in Yap, which is 395 km north-east of the main Palau islands and is particularly under-watched. The lack of an indigenous Palauan name for the dollarbird (Engbring 1988; M. Eberdong pers. comm.), compared to other migrant landbirds such as Oriental Cuckoo *Cuculus optatus* and Barn Swallow *Hirundo rustica*, suggests that dollarbirds have always been rare there.

We identified 12 of 13 dollarbirds that were either photographed or collected as museum specimens in Micronesia as belonging to subspecies *E. o. pacificus*, with the lone unconfirmed bird probably also being this subspecies based on its May observation date. Additionally, all but two of the 34 regional records were between mid April and mid October, a pattern that aligns closely with the known migration and overwintering periods for *E. o. pacificus*. Australian populations move north to their austral wintering range in March–May and return south to their breeding range in September–November (Draffan *et al.* 1983, Coates 1985, White & Bruce 1986, Higgins 1999, Dutson 2011). Together, these results provide strong evidence that *E. o. pacificus* is the predominant subspecies reaching Micronesia.

Two other regional records are from December, but neither was identifiable to subspecies. Both could possibly represent lingering individuals of *E. o. pacificus* or members of the migratory East Asian race *E. o. cyanocollis* (Pratt *et al.* 2010). The latter scenario is supported by at least one dollarbird record from the Iwo Islands (Higuchi 1984, Brazil 1991), which are north of the Marianas and outside Micronesia, and are apparently too far north to be visited by *E. o. pacificus*. That individual, a specimen (YIO 30237) collected on 25 May 1929, is labelled as *E. o. calonyx* (now *E. o. cyanocollis*) and was confirmed as this subspecies via examination of the online catalogue photograph by HDP. This record gives credibility to the possibility that East Asian birds may rarely wander over the western Pacific Ocean during migration and perhaps reach Micronesia. Furthermore, the May collection date of this specimen indicates that occurrence of *E. o. cyanocollis* in the region could overlap with that of *E. o. pacificus*.

The northern lowlands of New Guinea serve as a major wintering area for *E. o. pacificus* (Schodde *et al.* 1975, Higgins 1999) and represent the most likely route of dollarbirds reaching Micronesia. In addition, the Moluccas, including the islands of Morotai and Halmahera in the north, appear to be another important non-breeding region for the subspecies (Coates & Bishop 1997) and may be a further source of birds arriving in Micronesia. Proximity to New Guinea and the northern Moluccas undoubtedly accounts for the significantly larger number of dollarbird records in Palau compared to other Micronesian archipelagos. Palau's main island complex lies 815 km north of New Guinea and 775 km north-east of Morotai, whereas the Southwest Islands, a string of small remote atoll-like islets and one atoll which are also part of Palau, are even closer to New Guinea (375–630 km) and Morotai (275–500 km) (Fig. 2). Although the Southwest Islands are rarely visited by observers, the three dollarbird sightings there represent nearly 10% of all records from Micronesia, suggesting that visitation rates may be higher there than elsewhere in the region. Distances from New Guinea to other Micronesian islands with dollarbird observations are Ngulu Atoll, 1,070 km; Yap, 1,200 km; Guam, 1,800 km; Pohnpei, 1,850 km; and Saipan, 2,020 km. These distances are much greater than the over-water distances of 150–600 km that *E. o. pacificus* must negotiate when migrating between Australia and New Guinea, or Australia and the nearest of the Moluccas or Lesser Sundas. Our Mariana records appear to be the northernmost records for *E. o. pacificus* and are probably two of the northernmost for any breeding Australasian landbird.

Neither Dickinson *et al.* (1991) nor Kennedy *et al.* (2000) mentioned any subspecies in the Philippines other than the resident form *E. o. orientalis* (reported therein as *E. o. cyanocollis*), which remains the case through 2019 (D. Allen *in litt.* 2019). Given the frequency and distances flown by dollarbirds reaching Micronesia, we speculate that small numbers of *E. o. pacificus* may also visit the southern Philippines on migration. The island of Mindanao is 470 km from Morotai, 660 km from the Southwest Islands and 830 km from Palau's main islands, and thus seems within the flight range of occasional *E. o. pacificus* migrants.

Observer effort, or lack thereof, probably influences several other patterns noted in Micronesia's dollarbird records. First, the brevity of most records, usually just one or several days, may be more attributable to a lack of extended observer coverage of birds than to ongoing movement or poor survival. Observations of dollarbirds during August–October, plus several records of individuals remaining three weeks or more, suggest that some successfully overwintered in Micronesia and departed on their southbound migration. Second, approximately half of Palau's records are concentrated in the Koror area and southern Babeldaob, where the human population and hence observer effort are much higher than elsewhere in the archipelago. Third, Palau records show a somewhat irruptive pattern with groups of sightings often clumped within a year or over several years. Many of these records, however, coincide with known periods of observer presence as follows: the late 1970s when J. Engbring conducted extensive bird observations in Palau; June 1992 when A. K. Kepler visited the Southwest Islands; April–May 2005 when Palau-wide bird surveys were conducted; and the broader period since 2002 when more biologists and birders began visiting or working in Palau and when eBird came into existence.

Habitat and perch use in Micronesia resembles that elsewhere in the species' range (Coates 1985, Fry *et al.* 1992, Higgins 1999), with open and edge habitats preferred and high natural or artificial perches used. Our small sample of Micronesian birds of known age was composed mainly of adults and indicates this age class may be more capable of moving substantially longer distances during migration than juveniles, or that adult survival rates are higher when migrating to and overwintering in the extreme northern edge of its winter range.

Among the few migratory landbirds that regularly visit Micronesia, most are of East Asian origin (Western Osprey *Pandion haliaetus*, Chinese Sparrowhawk *Accipiter soloensis*, Oriental Cuckoo, Barn Swallow, Grey-streaked Flycatcher *Muscicapa griseisticta* and Eastern Yellow Wagtail *Motacilla tschutschensis*) as are the majority of vagrants (Stinson *et al.* 1997, Wiles 2005, Pratt *et al.* 2010, Otobed *et al.* 2018). Confirmation of *E. o. pacificus* as a regular migrant of Australian origin is therefore noteworthy. Among other austral landbirds recorded in Micronesia, only Pacific Long-tailed Cuckoo *Urodynamis taitensis* (Pratt *et al.* 1987) and possibly Sacred Kingfisher *Todiramphus sanctus* (GM unpubl. data) occur regularly.

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Appendix: List of 34 known Oriental Dollarbird *Eurystomus orientalis* records documented in Micronesia between 1938 and 2019.

Date range	Island group	Location	Notes
11 Jul 1938	Palau	Babeldaob	Adult male specimen (YIO 30238; Yamashina 1940, Baker 1951). Photo available in the museum's online specimen catalogue. Confirmed as <i>E. o. pacificus</i> .
1950s	Palau	Koror, Koror State	One bird, observed by R. Owen, date unknown (Engbring 1983).
18 Jun 1976	Yap	near airport, Yap Island	Adult male specimen (BYUH 2000). Observed by HDP & P. L. Bruner perched on a high dead snag over an open garden. The carcass possessed moderate fat levels (Pratt <i>et al.</i> 1977). Confirmed as <i>E. o. pacificus</i> .
8 Oct 1977	Palau	Angaur	One bird, observed by J. Engbring (Engbring 1983).
20 Sep 1978	Palau	Angaur	One bird, observed by K. Axelson (Engbring 1983).
19 May 1979	Palau	Pulo Anna, Southwest Islands	Two birds, observed by J. Engbring (Engbring 1983).
May, Jun 1982	Pohnpei	near Kolonia	One bird, observed by R. R. Vega, photos (Engbring 1983). Exact dates unknown but first seen in May, captured and released in early June, then remained on-site for another week. It used trees at the edges of small fields, perching on exposed branches to hawk insects. At times, it harassed Hunstein's Mannikins <i>Lonchura hunsteini</i> . Subspecies was undetermined.
Sep or early Oct 1988	Yap	near Gitam, Yap Island	One adult, brought dead to M. Falanruw, but the specimen was not preserved, photo (Pratt <i>et al.</i> 2010). Precise date unknown; a conflicting date of occurrence in Pratt <i>et al.</i> (2010) was later confirmed by M. Falanruw (pers. comm.) as being in Sep or early Oct. Confirmed as <i>E. o. pacificus</i> .
2 Aug 1989	Palau	Ngcheangel Islet, Kayangel Atoll	One bird, observed by H. L. Jones, seen well as it flew south over the island with seven Barn Swallows (Pratt <i>et al.</i> 2010; H. L. Jones <i>in litt.</i> 2019; eBird).
4, 9 Jun 1992	Palau	Tobi, Southwest Islands	Adult specimen (BPBM 178864), sex undetermined. Observed by A. K. Kepler in good quality strand forest, perching in fairly dense foliage and making short foraging flights 8–13 m high (Kepler 1993, Wiles <i>et al.</i> 2004). Confirmed as <i>E. o. pacificus</i> .
15–16 Jun 1992	Palau	Sonsorol, Southwest Islands	One bird, observed by A. K. Kepler (Kepler 1993, Wiles <i>et al.</i> 2004). Perched in a <i>Tournefortia argentea</i> tree in strand forest.
Between 1999 and 2008	Palau	Malakal, Koror State	Two adults, observed by R. Leidich (<i>in litt.</i> 2018), date unknown but sometime within this period. Seen copulating on a powerline in town.
10 May 2002	Palau	Peleliu	Number of birds unreported, observed by M.-C. Tsai and C.-L. Hsueh (eBird).
Dec 2003	Palau	Peleliu	One bird, observed by A. Gupta and R. Leidich, date unknown (Pratt <i>et al.</i> 2010).
8 May 2005	Palau	Angaur	One bird, observed by M. Knecht (VanderWerf <i>et al.</i> 2006). Perched in a dead tree in the middle of an open area composed mostly of taro patches.
15 May 2005	Palau	Ngerekebesang Island, Koror State	One bird, observed by VanderWerf <i>et al.</i> (2006). Seen in flight, being mobbed by 10–12 Palau Swiftlets <i>Aerodramus pelewensis</i> .
17 May 2005	Palau	Ngechsar State, Babeldaob	One bird, observed by GJW (VanderWerf <i>et al.</i> 2006). Perched for lengthy periods on a roadside powerline through forest.
24–25 May 2008	Palau	Ngeremlengui State, Babeldaob	One juvenile, observed by A. Olsen (<i>in litt.</i> 2008) and M. Eberdong (pers. comm.), photo. Seen hawking insects from a perch in a tree next to a river. Confirmed as <i>E. o. pacificus</i> .
13 Jul–3 Aug 2008	Yap	Ngulu Islet, Ngulu Atoll	One adult, observed almost daily by D. W. Buden, photo (Pratt <i>et al.</i> 2010). Regularly perched atop a communications antenna protruding above the surrounding strand forest mixed with coconut. The bird died from an injury sustained on 3 August, but the specimen was not preserved. Confirmed as <i>E. o. pacificus</i> .

Date range	Island group	Location	Notes
21 Aug 2008	Palau	Aimeliik or Airai State, Babeldaob	One subadult transitioning to adult plumage, observed by A. Olsen (<i>in litt.</i> 2008) and M. Eberdong, photo. Perched on a powerline along the main highway through Airai and Aimeliik. Confirmed as <i>E. o. pacificus</i> .
12, 14 Apr 2010	Palau	Ngiwal State, Babeldaob	One bird, observed by A. Olsen (<i>in litt.</i> 2010) and D. Sargeant (<i>in litt.</i> 2019).
7 Jun 2011	Palau	Ngerekebesang Island, Koror State	One juvenile, observed by A. Olsen, photo (eBird). Perched on a powerline in mixed urban, forested and open agricultural habitat. Confirmed as <i>E. o. pacificus</i> .
12–14 Oct 2013	Palau	Ngerekebesang Island, Koror State	One bird, observed by GM. Seen several times and present for an unknown period before the observer's initial sighting. In an area with a mix of hillside forest, buildings and agricultural clearings.
19 Jul 2014	Palau	Aimeliik State, Babeldaob	One bird, observed by G. Pettigrew and M. Eberdong (pers. comm.; eBird). Perched on a powerline along the main highway in an area of farms with open areas, roadside and patches of forest. Different from three other individuals seen on this date (see other records for 19 Jul 2014).
19 Jul 2014	Palau	Aimeliik State, Babeldaob	One bird, observed by G. Pettigrew and M. Eberdong (pers. comm.; eBird). Perched on a powerline along the main highway in an area of farms with open areas, roadside and patches of forest. Different from three other individuals seen on this date (see other records for 19 Jul 2014).
19 Jul 2014	Palau	Airai State, Babeldaob	One bird, observed by G. Pettigrew and M. Eberdong (pers. comm.; eBird). Perched on a powerline along the main highway in an area of farms with open areas, roadside and patches of forest. Different from three other individuals seen on this date (see other records for 19 Jul 2014).
19 Jul 2014	Palau	Airai State, Babeldaob	One bird, observed by G. Pettigrew and M. Eberdong (pers. comm.; eBird). Perched on a powerline along the main highway in an area of farms with open areas, roadside and patches of forest. Different from three other individuals seen on this date (see other records for 19 Jul 2014).
23 Jul, 10 Aug 2014	Palau	Airai State, Babeldaob	One adult that was probably the same individual, observed on 23 Jul 2014 (GM photos) and 10 Aug 2014 (M. Eberdong pers. comm.; eBird), but probably different from the four seen on 19 Jul 2014 (see previous records). Perched on wires along the main highway in an area of farms with open areas, roadside and patches of forest. Confirmed as <i>E. o. pacificus</i> .
Jul 2014	Palau	Koror, Koror State	More than one bird, observed by G. Pettigrew (pers. comm.), date unknown. The birds comprised a small group, but other details lacking. Seen on the edge of town and forest.
17 Dec 2014	Yap	Yap Island	One bird, observed by R. Carlisle (eBird).
2–4 Jul, 8 Aug 2018	Marianas	Marpi, northern Saipan	One juvenile, observed by JC and J. Fraser, photos, vocal recording (eBird). See text for sighting details. Confirmed as <i>E. o. pacificus</i> .
24 Sep 2018	Marianas	north-eastern Guam	One adult, observed by MMP & MK, photos (eBird). See text for details. Confirmed as <i>E. o. pacificus</i> .
3 May 2019	Palau	north-western Peleliu	One adult, observed by K. Swindle, photos (eBird). Perched on a roadside powerline through forest. Repeatedly flew ahead of the observer before flying away. Subspecies undetermined.
Jul–18 Sep 2019	Palau	1.2 km north-east of airport, Airai State, Babeldaob	One adult, observed on 28 Aug 2019 by GM, photos (eBird). In an agricultural area near a river, with farm fields, several buildings and adjacent forest. Perched on a snag and live trees. A farm worker reported the bird was present most days between July and September, and that it had arrived after a storm with strong westerly winds. Confirmed as <i>E. o. pacificus</i> .

Historical breeding records of Chestnut-bellied Imperial Pigeon *Ducula brenchleyi* in the Ragnar Kreuger collection, with a description of the egg

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Chestnut-bellied Imperial Pigeon *Ducula brenchleyi* is endemic to the Solomon Islands (Baptista *et al.* 2019). The current distribution is apparently restricted to the largest islands in the south of the archipelago: Makira, Malaita and Guadalcanal. Previously the species was recorded *inter alia* on the Three Sister Islands, Ugi (now Uki) and Ulawa. On the latter two, the species was reported as common and abundant, respectively, in 1953 (Cain & Galbraith 1956). However, no recent records are available from any of the satellite islands, suggesting that the species is very rare there or locally extinct (BirdLife International 2019).

Chestnut-bellied Imperial Pigeon inhabits primary lowland and montane forest, and was reported to feed mainly on banyan figs at one study site (Baptista *et al.* 2019). In addition, it is found in degraded forests, and gardens, provided suitable fruiting trees are present (BirdLife International 2019). Recent records reveal that *D. brenchleyi* predominately occupies elevations of 200–700 m—but in the relatively near past it was frequently observed close to sea level (Cain & Galbraith 1956, Baptista *et al.* 2019). Due to wholesale deforestation of coastal areas, the species is now confined to higher altitudes in many regions (Baptista *et al.* 2019). The species is considered globally Vulnerable, and is threatened by hunting and habitat loss (BirdLife International 2019). However, following a ban on firearms in 2003 on Makira hunting pressure on that island has declined significantly (Mittermeier *et al.* 2018).

Virtually nothing is known concerning the breeding biology of *D. brenchleyi* (Mittermeier *et al.* 2018, Baptista *et al.* 2019). A nest was discovered only recently, in December 2016, on the south coast of Makira (Mittermeier *et al.* 2018). It was sited near a beach, in a small rosewood *Pterocarpus indicus* tree and concealed by epiphytes, c.10 m above ground. An adult was attending the nest, indicating that it was active (Mittermeier *et al.* 2018). Linear measurements of the eggs ($n = 3$) discussed below were already provided by Schönwetter (1963), but without data as to precise collecting location, their morphology, clutch size or seasonality. As no further information is currently available concerning the species' breeding biology, here we provide additional information concerning seasonality, clutch size and nests, along with a description of the egg, based on three clutches deposited in the LUOMUS (Finnish Museum of Natural History; MZH).

Historical breeding records

The following is based on three clutches collected by William M. French (1897–1960), a British planter with an intense interest in natural history, especially birds and their eggs. French began developing a coconut plantation on the Three Sisters Islands, after serving in Australia for several years and visiting New Guinea and India (RCS Library n.d.). In 1929 he was invited to collect on behalf of the American Museum of Natural History, New York, in the eastern islands of the Solomons. He assembled a large number of skins and bird eggs during the 1930s, until he was forced to leave the Solomons due to the advance of the Japanese army during World War II, leaving some specimens and personal possessions in a

TABLE 1

Overview of all three clutches of Chestnut-bellied Imperial Pigeon *Ducula brenchleyi* collected by William French on Malaupaina Island (Three Sister Islands) in 1938

Clutch size	Egg size (in mm)	Collection date	Catalogue no. (R. Kreuger catalogue no.)
1	46.4 × 32.7	25 August 1938	MZH 42424 (R. Kreuger 12422)
1	44.1 × 33.6	11 September 1938	MZH 42425 (R. Kreuger 12423)
1	43.5 × 33.0	15 September 1938	MZH 42426 (R. Kreuger 12424)

walled-up cave (RCS Library n.d.). Although he was unable to retrieve these specimens, others were donated by him to what is now the Natural History Museum, Tring, and other collections (RCS Library n.d.).

A substantial part of French's egg collection was subsequently acquired by Ragnar Kreuger (1897–1997), a Finnish industrialist and avid egg collector. Kreuger began to collect eggs in the 1910s, purchasing his first private collection in 1917 (<https://web.archive.org/web/20110716144551/http://www.luomus.fi/elaintiede/selkarankaiset/kokoelmat/munakokoelma.htm>). Over several decades he acquired one of the largest and most diverse, private egg collections in the world. In 1962 Kreuger gifted the entire collection, numbering *c.*60,000 eggs (E.-S. Hyytiäinen pers. comm.) to the University of Helsinki, where it is maintained in the Finnish Museum of Natural History (MZH).

Between 25 August and 15 September 1938 three active nests of Chestnut-bellied Imperial Pigeon were discovered by French on Malaupaina Island (*c.*10°14'52.80"S, 161°58'12.00"E; see Table 1). According to the label data associated with the eggs, the nests were simple platforms of sticks, placed on horizontal branches *c.*4.5–6.0 m above ground. All three nests were located in ridgetop forest and contained a single egg. Two of the three eggs were presumably collected during the mid to late incubation period, as their development was described as advanced.

The egg (see Fig. 1) is elliptical and white, typical of the genus *Ducula*. Mean size of the three eggs is 44.66 × 33.10 mm, range 43.5–46.4 × 32.7–33.0 mm. Mean shell weight is 1.681 g (*r* = 1.63–1.73 g; *n* = 3).

These data suggest that egg laying presumably peaked in August–September on the Three Sister Islands, and that clutch size is typically a single white egg. The latter is consistent with published information for congeneric taxa (Gibbs *et al.* 2001, del Hoyo *et al.* 2019).

These historic breeding records once more demonstrate the relevance of museum collections in contributing to a better knowledge of the biology of relatively little-known species. However, further research is essential for a fundamental understanding of the breeding biology, general ecology, and long-term conservation of this poorly known endemic.



Figure 1. Egg of Chestnut-bellied Imperial Pigeon *Ducula brenchleyi* (MZH 42424; R. Kreuger catalogue no. 12422) (Emma-Sofia Hyytiäinen © LUOMUS)

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Records of Brown Booby *Sula leucogaster* in the Pitcairn Islands with additional observations during 2015–19

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The Pitcairn Islands are a UK Overseas Territory comprising four islands (Oeno, Pitcairn, Henderson and Ducie) spanning >600 km in eastern Polynesia, in the South Pacific Ocean. Oeno and Ducie are low coral atolls, Henderson is a large raised coral island, and Pitcairn is volcanic in origin (Spencer 1995).

The islands' avifauna have received considerable scientific attention, mainly focused on Henderson Island, beginning in the early 20th century (North 1908, Ogilvie-Grant 1913), followed by the Whitney South Seas Expedition (Murphy 1924, Murphy & Mathews 1929). There was some work in the late 1980s on Henderson's landbirds (Graves 1992). The Sir Peter Scott Memorial Expedition in 1991–92 stationed researchers on Henderson Island for more than a year, and thoroughly studied the birds (Brooke 1995a,b, Brooke & Jones 1995, Imber *et al.* 1995, Jones *et al.* 1995, Trevelyan 1995). This was followed in the early 21st century by studies into the effect of introduced Pacific Rats *Rattus exulans* on Henderson's native fauna (Brooke *et al.* 2011, Amos *et al.* 2016, Opper *et al.* 2016, Bond *et al.* 2019b), and of the abundance of various species (Opper *et al.* 2017, Bond *et al.* 2019a). There are far fewer studies of the avifauna of Pitcairn (Williams 1960, Schofield & Bond 2016), Oeno (Brooke *et al.* 2018) and Ducie, although all were reviewed by Brooke (1995b) and Bourne & David (1983).

Ducie and Oeno possess no endemic species of birds, whilst Pitcairn is home to the endemic Pitcairn Reed Warbler *Acrocephalus vaughani* (Brooke 1995b), and Henderson supports five endemic species—Henderson Petrel *Pterodroma atrata*, Henderson Crake *Zapornia atra*, Henderson Fruit Dove *Ptilinopus insularis*, Henderson Lorikeet *Vini stephensi* and Henderson Reed Warbler *Acrocephalus taiti* (Graves 1992, Brooke 1995b, Opper *et al.* 2017, Bond *et al.* 2019a). The avifauna of the group as a whole has been described largely in three works (Williams 1960, Brooke 1995b, Thibault & Cibois 2017), and one review (Bourne & David 1983).

Of the 41 species recorded from the islands (Williams 1960, Bourne & David 1983, Brooke 1995b), a handful are vagrants or possible breeders, and could become established as breeding populations in the Pitcairn Islands, based on range and suitable habitat—Wedge-tailed Shearwater *Ardenna pacifica*, White-tailed Tropicbird *Phaethon lepturus* and Brown Booby *Sula leucogaster*.

Here we summarise records of Brown Booby across the island group and add three additional sightings from 2015–19.

Previous records

Williams (1960) described Brown Booby as the rarest of the sulids in the island group and mentioned two records. The first he observed himself: two birds at the north-western end of Pitcairn 'between (Down) Rope and St Paul's (Pool)' on 21 October 1956, and in relation to which he explicitly eliminated the possibility of dark-phase Red-footed Booby *Sula sula*, which also occurs in the group (Brooke 1995b). The other is a second-hand report from Pastor L. Hawkes, who ostensibly observed an individual at Henderson Island in

January 1957, but no further details are given. The Henderson record was repeated by Bourne & David (1983) and Fosberg *et al.* (1983).

During the Sir Peter Scott Commemorative Expedition in 1991–92, Brown Booby was not recorded on Henderson, or during any of the short visits to Oeno or Ducie (Brooke 1995b), with reference being made only to the earlier records of Williams (1960).

In their landmark work on the avifauna of eastern Polynesia, Thibault & Cibois (2017) described the extensive range of Brown Booby through the Line, Cook, Society, Tuamotu, and Marquesas archipelagos, and highlighted vagrant records from Rapa Nui (Flores *et al.* 2013) and the 1957 record from Henderson, but did not mention the bird observed directly by Williams on Pitcairn in 1956. They also included a report of a single at Oeno in 2014 (Scott 2014).

Recent records

In August–November 2015, as part of a Royal Society for the Protection of Birds (BirdLife in the UK) expedition to Henderson (Lavers *et al.* 2016), a single female Brown Booby was observed at North Beach regularly in September and November 2015 (Fig. 1).

During a birding tour, ‘a couple’ of Brown Boobies were observed at Pitcairn during the period 3–17 October 2017 (Morris & Beaman 2017). Unfortunately, no other details were noted at the time (M. Beaman pers. comm.).

During a three-week expedition to Henderson Island, including three days at Pitcairn, in June 2019, an adult female Brown Booby was observed soaring over North Beach, Henderson Island, on 10, 13, 16, 17 and 18 June 2019 (Fig. 2). Despite spending considerable time (12 days) on East Beach, Henderson Island, and on Pitcairn (three days), no others were seen.



Figure 1 (left). Adult female Brown Booby *Sula leucogaster*, North Beach, Henderson Island, 20 September 2015 (N. Duffield & S. Havery)

Figure 2 (right). Adult female Brown Booby *Sula leucogaster*, North Beach, Henderson Island, 19 June 2019 (A. L. Bond)

In the South Pacific Ocean, Brown Boobies breed throughout French Polynesia, although in the Gambier Islands they are recorded only in small numbers at Manui, in the south-east of the group, where no more than 15 nests were recorded annually from the 1990s to 2010 (Thibault & Bretagnolle 2001, Waugh *et al.* 2015), Kamaka (Ghestemme 2016) and Motu Teiku (Thibault & Cibois 2017), all of which are uninhabited. Brown Boobies are not historically common in eastern Polynesia, and are largely absent from the archaeological remains and early accounts of the islands (Thibault & Cibois 2012). They are much more common in northern Polynesia (Line, Marquesas, and Society Islands), and the northern Tuamotus, with the largest colony at Malden Island, in the Line Islands, which was home to 2,000 pairs in 1988 (Kepler *et al.* 1994), but most others are declining significantly or represented by just tens of breeding pairs (Thibault & Cibois 2017). Their high sensitivity to human disturbance often restricts colonies to uninhabited islets or inaccessible cliffs (Thibault & Cibois 2017).

Henderson is also home to breeding Masked *Sula dactylatra* and Red-footed Boobies, with 50 and 100–200 pairs estimated, respectively (Brooke 1995b), and boobies often breed sympatrically (Nelson 2005). To date, there is no evidence of breeding Brown Boobies in the Pitcairn Islands, however. This could be because of relatively high disturbance from human habitation, introduced mammals, and the islands' isolation (Brooke 1995b, Amos *et al.* 2016).

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