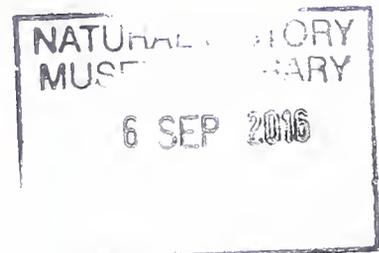
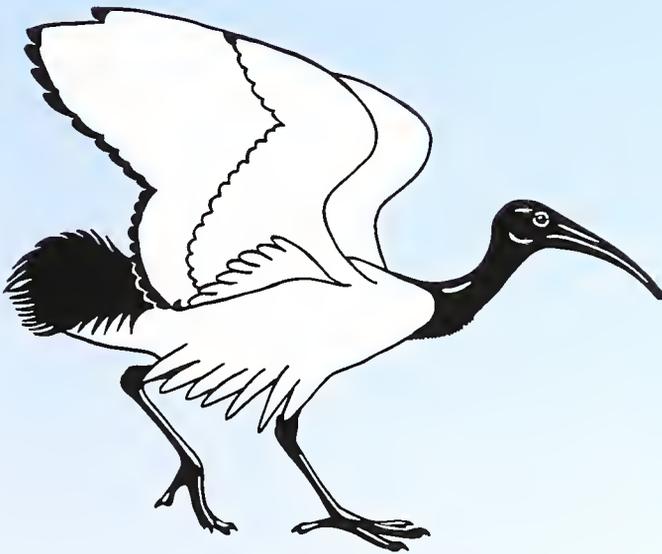


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# Bulletin of the British Ornithologists' Club

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Volume 136 No. 3  
September 2016



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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](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. The talk will start at 6.30 pm and, with questions, will last c.1 hour.

*It would be very helpful if those intending to come can notify the Chairman no later than the day before the meeting.*

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**Saturday 17 September 2016—One-day joint meeting with the Neotropical Bird Club and Natural History Museum** in the Flett Theatre, Natural History Museum, London SW7 5 BD. The nearest tube station is South Kensington and attendees should use the NHM entrance on Exhibition Road. There is **no charge** to attend and all are welcome. The programme is planned to include the following talks—see the BOC website [www.boc-online.org](http://www.boc-online.org) for any possible late alterations.

*How to save birds in the Brazilian Atlantic Forest on a shoestring*—Cristina Banks-Leite

*Bridging shortfalls in Brazilian ornithology*—Alex Lees

*What is a species and what is a subspecies? A new look at an old question, based on Colombian birds*—Thomas Donegan

*White-masked Antbird unmasked*—Fabrice Schmitt

*Changes and challenges in the HBW-BirdLife Checklist of Neotropical passerine species*—Nigel Collar

Access to the NHM is possible from 10.00 am, when coffee/tea will be available adjacent to the Flett Theatre. The meeting will begin at c.10.30 am, with a break for lunch around 12.30 pm—many food outlets are available both within the NHM and local to it in South Kensington. The afternoon session will begin at c.2.00 pm and, including a half-hour break for coffee/tea, should finish by 5.00 pm. The NHM closes at 6.00 pm. For up-to-date details, please check the BOC website: <http://www.boc-online.org>.

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**Tuesday 15 November 2016—6.30 pm—Guy Kirwan—When failure equals success: searching for the Critically Endangered Hooded Seedeater *Sporophila melanops* in central Brazil.**

*Abstract:* Known solely from the type specimen collected in the 1820s by Johann Natterer, in central Brazil, the Hooded Seedeater *Sporophila melanops* can be considered one of the greatest ornithological enigmas of the Neotropical region. As part of efforts to resolve this mystery, Guy Kirwan made two specific searches of the relevant region of Brazil, sponsored by BirdLife International, as well as conducting additional field work in the area during other years. This talk will describe the results of new investigations into the status of Hooded Seedeater, by Kirwan and co-workers (see also *PLoS ONE* 11(5): e0154231), as well as reporting other results stemming from his research into the avifauna of the Araguaia Valley region of central Brazil. A paper describing many of those general avifaunal results has already appeared, in *Bull. Brit. Orn. Cl.* 135: 21–60.

*Biography:* Guy Kirwan has travelled exceptionally widely throughout South America, especially Brazil, in which country he has spent more than ten years in the field. He is a freelance ornithologist and editor, notably of *Bull. Brit. Orn. Cl.*, with strong interests in avian taxonomy and the breeding biology of birds in the New World tropics. A Research Associate at the Field Museum of Natural History in Chicago and the Museu Nacional in Rio de Janeiro, he currently works for Lynx Edicions on the HBW Alive project.

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**The Chairman:** Chris Storey, 22 Richmond Park Road, London SW14 8JT UK. Tel. +44 (0)208 8764728. E-mail: [c.storey1@btinternet.com](mailto:c.storey1@btinternet.com)

# Bulletin of the BRITISH ORNITHOLOGISTS' CLUB

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## CLUB ANNOUNCEMENTS

### ANNUAL GENERAL MEETING

The Annual General Meeting of the British Ornithologists' Club was held in the upstairs room at the Barley Mow, 104 Horseferry Road, Westminster, London SW1P 2EE, on Tuesday 24 May 2016, with Chris Storey in the Chair. Twenty members were present.

**1. Apologies for absence** were received from Sir James Barlow, Anthony Bayliss, Mark Beaman, Bruce Beehler, Robert Cheke, Michael Dawson, Edward Dickinson, David Fisher, Tom Gladwin, Jeremy Greenwood, Kenneth Heron, Amberley Moore, Alex Randall, Frank Steinheimer, Simon Tonge and Frank Zino.

**2. Minutes of AGM 2015** The Minutes of the 2015 AGM held on 19 May 2015 which had been published (*Bull. Brit. Orn. Cl.* 135: 193, and on the BOC website) were approved and signed by the Chairman.

**3. Chairman's Review, Bulletin Editor's Report, Trustees' Report and Accounts for 2015** The Chairman introduced his Review and the Report and Accounts, copies of which were available at the meeting. In respect of the Review, he added that during the past year great progress had been made under David Wells' editorship on the next BOC checklist by Robin Woods on the Falkland Islands. The Club was also much in Nigel Redman's debt in its production.

The BOC had given notice at the end of 2015 of the termination on 31 December 2016 of the administrative agreement with the BOU. The decision to end this arrangement had been taken in light of the decline in the Club's subscription income and the continuing rise in BOU charges. The Club was grateful to the BOU, and Steve Dudley and Angela Langford, for their continuing help and advice over the years. Furthermore, the BOU and the Club had come to the view that the book / *Bulletin* storage facilities at Peterborough should be dispensed with, the stock digitised and any redundant copies disposed of. The precise details were yet to be finalised.

The meeting noted Dr Robert Prŷs-Jones' report on the Club meetings at the Barley Mow and the very successful joint meeting with OSME held at the Natural History Museum on 21 November 2015 (see below). Guy Kirwan's report on the Bulletin as set out in the Report and Accounts was also noted.

The *Hon. Treasurer* introduced the Financial Review and Accounts for the year ended 31 December 2015 and the accompanying independent examiner's statement. He reported that the Club had a surplus at the year-end of £1,035, almost identical to 2014. Recovery of the 2015 Gift Aid would be made in the current year. Overall the Club's funds stood at £428,073 at year-end and a satisfactory level of liquidity was maintained to enable commitments to be met with particular regard to future Checklist volumes and new developments for the Bulletin.

**4. The Way Forward** The Chairman outlined the sequence of events leading up to his letter to members in December 2015 and his letter of 20 April 2015, which accompanied the formal paper and proposal prepared by Matthew Boyer, solicitor, on behalf of the Committee. He said that he had received many replies, of which 27 were, subject in some cases to caveats, in favour and seven against. Concerns raised included lack of hard copies, poor internet coverage in certain parts of the world, the absence of a voting membership to monitor the trustees, and the dangers inherent in digital-only publications.

In summary the proposal addressed the following issues:

- Declining income, rising costs and falling readership.
- Requirement of trustees to further the Club's charitable objects, using the trust funds to that end.
- Academic publishing moving rapidly towards online open-access models.
- Reduction of costs by changing to a non-subscription basis (with members who so wish to become Friends of the BOC) and the use of investment income to finance an online *BBOC*.

He introduced Matthew Boyer to the meeting to speak to the paper and the formal resolution. Matthew Boyer said that the document entitled 'The Way Forward: the trustees' proposal for the future of the BOC', which had already been provided to members, set out the financial and commercial background to the trustees' conclusion that the charity needed to reform itself to become less reliant on members and more

reliant on the internet in order to continue and improve its charitable work. It was important to bear in mind that a charity must, as a matter of law, act for the benefit of the public.

To effect a transition from the current loose 'club' charitable structure to a more streamlined organisation it was necessary to create a new charity, with a new structure and constitution. Having created a new charity, it would then be necessary to transfer all of the assets of the existing charity to the new charity, and then dissolve the existing charity.

An important asset of the existing charity was the fund administered by a separate body, the Herbert Stevens Trust (HST). It was critical to ensure that this fund would be administered for the benefit of the new charity. Confirmation had been given by the Trustees of the HST that this would be the case, and nothing would proceed without this assurance being firm.

The most suitable legal structure for the new charity would be the Charitable Incorporated Organisation (CIO), on the Charity Commissioners' Foundation Model and described on p. 3 of *The Way Forward*. Matthew Boyer added that a CIO is a recently available type of charitable structure that is in every sense reputable and proper. The constitution of a CIO must be based on a pro forma provided by the Charity Commission, with any changes and, of course, the charity's objects, to be formally approved by the Charity Commission. Importantly, the trustees propose that the objects of the new charity will be as closely identical to those of the existing charity as possible, using essentially the same words, with the addition of confirmation that the work of the charity will be for the public benefit. Equally importantly, the new CIO will be regulated by the Charity Commission, whose statutory role is to foster the integrity of charities generally and to enforce proper governance.

Turning to p. 5 of *The Way Forward*—the formal resolution set out in italics would be put by the trustees to the members at the AGM. The essence of the proposal, which required members' approval, was that once four specifics had occurred, the existing charity would be dissolved. The charity would not and could not be dissolved unless and until all the following had occurred.

- (1) The successful creation and registration of a new CIO, with the existing trustees being the first trustees of that new charity.
- (2) The discharge of all of the existing charity's debts and other liabilities.
- (3) The agreement of the trustees of the HST to manage that fund for the benefit of the new charity.
- (4) The transfer of all other assets of the existing charity to the new charity.

Finally, Matthew Boyer and the trustees commended the resolution, with its four preconditions, to the members. Prior to putting the resolution to a vote, the Chairman took questions from the floor. In particular, Steven Gregory expressed his strong concerns as to the proposals, the speed of implementation and, in particular, the loss of the hard-copy *BBOC*, bearing in mind uncertainties as to the durability of digital formats.

The Chairman then asked the members to vote by a show of hands on the resolution. Those in favour: 18; those against: one; and abstentions: one. The resolution was duly passed.

**5. Any Other Business** The Chairman paid tribute to Keith Betton, whose term as trustee was ending and who had decided not to continue as a trustee of the proposed CIO. He said the BOC had benefited greatly from Keith's broad knowledge and contacts in the birding world. Keith had stressed that his wish to escape committee work in no way reflected on his support of the BOC and its plans for the future.

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### **Joint meeting on *Bird Monitoring in the Middle East with the Ornithological Society of the Middle East, the Caucasus and Central Asia, and the Natural History Museum, London, 21 November 2015***

Approximately 80 people attended this joint meeting between OSME, NHM and BOC, which was held at the Flett Theatre, NHM, London, as part of the continuing and successful annual series of one-day conferences involving BOC, NHM and a regional bird club. The meeting opened with an overview of *The value of BirdTrack as a bird recording tool in the OSME region* by Nick Moran, BirdTrack organiser. BirdTrack is a free global system via which birders can log, store and interact with their records. Nick introduced the tools that it offers to individual birdwatchers and how BirdTrack data can provide a valuable resource for conservation, monitoring and research.

The following talk by Richard Porter on *Bird recording and conservation in Iraq: a ten-year perspective* was based on his close involvement with biologists and conservationists in Iraq over the past decade, and was intended as a tribute to their labours under exceptionally difficult circumstances. The work of Nature Iraq featured prominently, especially its Key Biodiversity Areas Inventory—a monumental treatise that OSME helped sponsor. Other recent ornithological discoveries and conservation achievements were also highlighted, notably in the mountains of Kurdistan and relating to the striking and continuing ecological recovery of the formerly almost drained southern marshes.

The morning session closed with Andy Symes speaking on *Monitoring the threat status of birds and the implications for conservation management*. The BirdLife Secretariat is the Red List Authority for birds on the IUCN Red List, coordinating the process of evaluating all of the world's 10,000 or so bird species against Red List categories and criteria in order to assess their extinction risk. Monitoring changes in species threat status is a major tool in prioritising conservation management.

In 2014, the Wildfowl & Wetlands Trust (WWT) was approached to establish a waterbird monitoring programme for the East Jahra Reserve area of Kuwait under the UN-funded Kuwait Environmental Remediation Programme (KERP). In their talk on *Waterbird monitoring at Kadma Bay, Sulaiyikhat Bay and Jahra Pools, Kuwait*, Gareth Bradbury and James Drake described this innovative project. Following three successful coordinated counts in November 2014, January 2015 (timed to coincide with the International Waterbird Census) and April 2015, ten species of waterbird have been identified whose numbers exceed 1% of that species' flyway population.

Yoav Perlman used his talk on *35 years of bird monitoring in Israel* to describe the importance of Israel as a migration hotspot and a country with varied habitats, to outline the history of bird monitoring in Israel and the current structure of the national bird monitoring scheme. Flagship projects in Israel include the annual raptor counts in autumn and spring that have taken place since 1981, breeding atlas surveys, a long-term ringing network, and numerous focused monitoring projects of threatened species.

Finally, the conference closed with a presentation by Bob Elliot on *Monitoring illegal bird killing*. Many iconic and protected species continue to be under threat from illegal trapping, shooting and poisoning, and his talk drew on case studies to demonstrate why long-term monitoring of species and habitats is vital in fighting against wildlife crime.

Overall, the programme of talks successfully integrated information ranging from specific case studies at particular localities, via national overviews of avian monitoring, to regional assessments of conservation threat and approaches to help counteract it, resulting in a thoroughly worthwhile event much enjoyed by the audience.

*Rob Sheldon & Robert Prŷs-Jones*

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The 983rd meeting of the Club was held on Tuesday 24 May 2016 in the upstairs room at the Barley Mow, 104 Horseferry Road, Westminster, London SW1P 2EE. Eighteen members and four non-members were present. Members attending were: Mr D. Allen, Miss H. Baker, Cdr. M. B. Casement, RN, Mr S. Chapman, Mr S. M. S. Gregory, Mr R. Langley, Mr R. W. Malin, Dr C. F. Mann, Dr P. Morris (*Speaker*), Mr D. J. Montier, Mr R. Pritchett, Dr R. Prŷs-Jones, Mr N. J. Redman, Mr P. Sellar, Dr A. Simmons, Mr S. A. H. Statham, Mr C. W. R. Storey (*Chairman*) and Mr P. Wilkinson.

Non-members attending were: Mr J. Boorman, Mrs M. Gauntlett, Mrs J. McDonald and Mrs M. Montier.

Dr Pat Morris gave a talk entitled *Taxidermy: a peep into the parlour*, intended as a brief survey of a topic that has been long neglected. So called 'stuffed birds' form a significant part of the history of Britain's wildlife, but fell out of favour after World War II. But it is important to remember that in the 19th and early 20th centuries taxidermists performed a prominent role, embedded in the social history of their times. Preserved birds (and mammals to a lesser extent) were probably more important in Britain than in other countries because of their acceptance as part of the domestic scene. No respectable household was without a few specimens. This led to the establishment of hundreds of small taxidermy businesses throughout the country, with up to 18 operating simultaneously in Glasgow alone (with more in Birmingham and London). Much of their output was dire and gives taxidermy a bad name today. The great mansions often had taxidermy in the main hall or on otherwise prominent display, making a clear statement about the owners and their estate. Exotic species might be conspicuous, indicating foreign travels, or a selection of gamebirds indicative of the sporting opportunities in the environs. But even a modest middle-class home would have taxidermy as part of its decoration. This led to a demand for colourful displays in glass cases, often with the species of two or more continents mixed. There was no scientific intent, just the eye-catching colour of unfamiliar species.

A contrary approach was that of dedicated collectors who built up substantial displays of British and foreign birds, often motivated by a genuine interest in the study of plumage variations and patterns of distribution (with voucher specimens for the occurrence of rare species). This type of taxidermy frequently outgrew domestic space and required a whole room (or entire outbuilding!) to accommodate the birds. It is easy to forget how important such collections were in the compilation of the early county avifaunas and the illustrations needed for field guides that make such collections obsolete today. Supplying collectors led to George Bristow, taxidermist of St. Leonards in Sussex, being blamed for fraudulently distorting ornithological history by passing off imported birds as British, the so-called 'Hastings Rarities'. The evidence is strong but not incontestable, and it is hard to see how such a fraud could have been a practicable possibility. Nevertheless, the role and reputation of taxidermists were dealt a serious blow and to this day many assume that Bristow was one of the 20th century's greatest fraudsters. He is the only British taxidermist to have been awarded the accolade of a blue plaque on his former residence—for entirely the wrong reasons.

In modern times, with fresh perceptions and declining wildlife abundance, there has been a tendency to express regret that birds are seen stuffed in glass cases rather than alive in the wild. Taxidermists are blamed for present-day scarcity, the stuffed birds being evidence of their guilt. This is false logic. Taxidermists were simply doing a job. Blaming them for present-day scarcity is akin to blaming undertakers because people die. Modern taxidermists are tightly constrained by national and international legislation, although this creates expensive bureaucracy and probably achieves comparatively little in real terms.

# Breeding biology of Yellow-browed Antbird

## *Hypocnemis hypoxantha*

by Daniel M. Brooks, Pablo Aibar, Pam Bucur, Ron Rossi & Harold F. Greeney

Received 17 February 2016

**SUMMARY.**—We provide novel data concerning the nests, eggs and parental care of Yellow-browed Antbird *Hypocnemis hypoxantha* based on two nests in eastern Ecuador and Peruvian Amazonia, one of which was video-taped. Both adults participated in incubation, with earliest and latest feeding events at 06.11 h and 17.22 h, respectively. Feeding behaviour is described, with intervals of 1–114 minutes (mean = 38.3 minutes) and tettigoniid cicadas the primary prey. Nestlings frequently produced faecal sacs (interval range = 4–132 minutes, mean = 37.8 minutes) immediately following food delivery, and the sac was always carried from the nest by an adult. Two events involving a parent bird being chased from the nest are described, the first involving a male Fulvous Antshrike *Frederickena fulva*. Systematics are discussed in light of nest morphology and architecture.

Yellow-browed Antbird *Hypocnemis hypoxantha* is a distinctive Amazonian thamnophilid that comprises two currently recognised subspecies: nominate *hypoxantha* in western Amazonian lowland and foothill forests from southern Colombia south to central Peru, and *H. h. ochraceiventris* in south-east Amazonian Brazil (Zimmer & Isler 2003). Generally found below 400 m, the nominate subspecies occasionally ranges as high as 900 m (Zimmer & Isler 2003, Ridgely & Tudor 2009).

The species' reproductive biology is almost completely unknown (Zimmer & Isler 2003). Willis (1988) provided a cursory description of a nest with nestlings from Colombia, but included few details of the nest and no description of the eggs or behaviour. Here, we provide details of nest architecture and describe the eggs and parental care behaviour for the first time, based on two nests, in eastern Ecuador and Amazonian Peru.

## Methods

The first nest (hereafter Ecuadorian nest) was found on 5 October 2012, at the Shiripuno Research Center in Pastaza province (210 m; 01°06'S, 76°43'W). Shiripuno is within Yasuní Biosphere Reserve, floristically described as wet-evergreen Amazonian lowland forest comprising a mix of *terra firme* and *várzea* (see Loiselle *et al.* 2007 for details of a nearby locality).

The second nest (hereafter Peruvian nest) contained a single nestling and was located near the Amazon Conservatory for Tropical Studies, dpto. Loreto, Peru (c.120 m; 03°15'S, 72°55'W). Habitat is typical Amazonian lowland forest, with a mix of *várzea* and *terra firme* (see Brooks *et al.* 2005 for a more complete site description). On 4 July we bracket-mounted a motion-triggered Stealthcam (model G42NG) 76 cm from the nest and recorded ten-second video clips with a minimum of 30-second intervals between clips for two full days (5–6 July). The only exception to 5–6 July was the description of the antshrike invading the nest (see last paragraph of Results regarding *Frederickena fulva* invasion) on 4 July as it was a unique situation.

## Results

*Description of nest and eggs.*—The Ecuadorian nest was 1.4 m above ground, in an area of relatively level-ground mature *terra firme* forest, c.30 m from the edge of a large swampy area with a broken canopy dominated by palms. Canopy height was 30–40 m above the nest, with an open understorey composed of small saplings. The nest was a deep pouch, suspended from the rim of one side to the central rachis of an epiphytic fern growing on a c.8 m-tall sapling. Some of the rootlets and flexible fibres that attached the nest to the substrate were also wrapped around the adjacent leaflets and to another fern frond that crossed over the supporting frond, providing some overhead cover. The nest was composed predominantly of dicot leaves, bound with rootlets and fungal rhizomorphs. Externally, the nest was decorated with additional, loosely attached dead leaves, small sticks and leaf petioles, some of which formed a loose tail hanging c.20 cm below the nest and increased its resemblance to naturally collected detritus. Internally, the egg cup was neatly lined with dark, flexible fibres and fungal rhizomorphs.

The Peruvian nest was similar in form and attachment, 81 cm above ground and attached to the pinnately compound leaf of a small legume sapling (*Inga* sp.). It was constructed of similar materials, but these were somewhat less uniformly distributed in the external portion. The right side was constructed predominantly of leaves, and the other almost exclusively of twigs and thin, flexible black or green fibres. The base of the nest also contained more leaves than other portions.

Measurements of the Ecuadorian and Peruvian nests, respectively, were: external width 8.0 cm and 10.0 cm; external depth (front to back) 8.5 cm and c.11 cm; external height (from front rim to bottom) 8.5 cm and 13.0 cm; internal diameter (measured at perpendicular angles), 4.5 cm wide by 5.0 cm front to back and 4.0 cm by c.4.5 cm; internal depth 4.5 cm and 7.5 cm.

The two eggs at the Ecuadorian nest were completely undeveloped. They were white with fairly evenly distributed pale cinnamon flecks and scrawls, intermixed with darker,

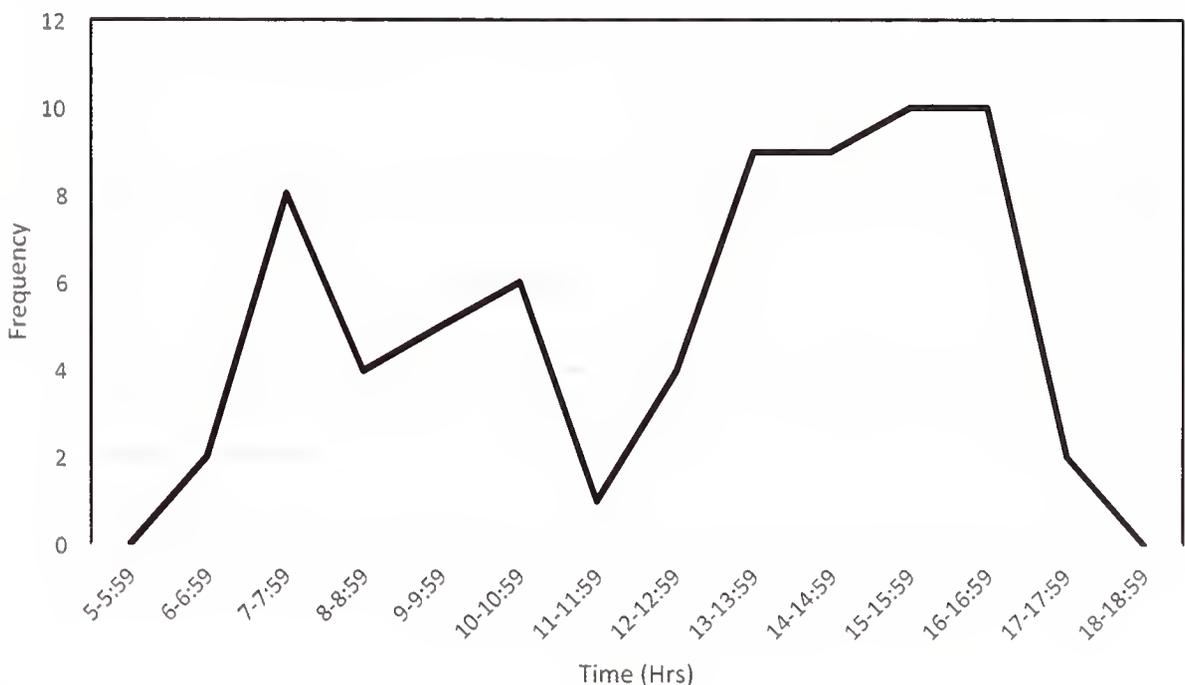


Figure 1. Activity periods of Yellow-browed Antbird *Hypocnemis hypoxantha* in Peru based upon video camera activity.

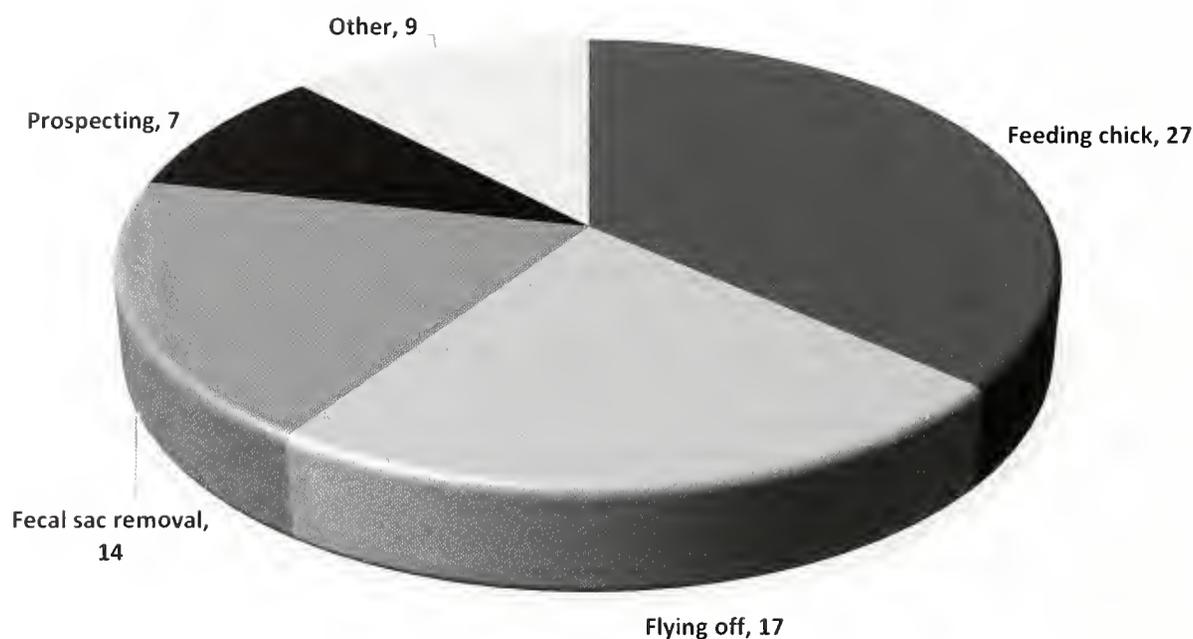


Figure 2. Video clip captures of adult Yellow-browed Antbird *Hypocnemis hypoxantha* in Peru based upon video camera activity.

red-brown blotching. They measured  $19.0 \times 13.8$  mm and  $19.7 \times 13.4$  mm, mass 1.99 and 1.95 g, respectively.

**Activity patterns.**—Video at the Ecuadorian nest revealed that both adults participated in incubation. At the Peruvian nest, we recorded 73 video clips, with the earliest and latest feeding events occurring at 06.11 h and 17.22 h, respectively, with temperatures of 25–29°C. The first burst of activity was generally around 07.00 h, following nocturnal quiescence, with a second period of activity in the afternoon at 13.00–17.00 h, (Fig. 1). Video clips of adults were allocated as follows: feeding chick = 37%, flying off = 23%, faecal sac removal = 19% and prospecting nest = 10% (Fig. 2, Table 1).

**Feeding behaviour.**—The most frequently recorded behaviour was food swallowing by the chick ( $n = 31$ , Table 1). The chick was recorded swallowing large prey items (i.e., prey that were large enough to be seen, e.g., orthopterans) on 17 occasions and small prey items on 14 occasions, which were not significantly different ( $X^2 = 0.29$ ,  $P = 0.59$ ). Adults were recorded delivering large prey on 14 occasions and small prey on 13 occasions, which were also not significantly different ( $X^2 = 0.3$ ,  $P = 0.84$ ). All 14 large-insect prey delivered to the chick were orthopterans, of which ten were identified as katydid (Tettigoniidae) and one as a grasshopper

Table 1  
Behaviours with associated frequency and % occurrence at the Amazon Conservatory for Tropical Studies, dpto. Loreto, Peru.

Parent behaviour	Frequency	%
Feeding chick	27	37
Flying off	17	23
Faecal sac removal	14	19
Prospecting	7	10
Probing chick's mouth	4	5
Chased off by another bird	2	3
Resting on nest, inactive	2	3
Removing katydid leg from nest	1	1
Chick behaviour	Frequency	%
Swallowing food items	31	84
Begging	6	16

% is percentage frequency of 73 clips, where some video clips may have recorded >1 behaviour.



Figure 3. Yellow-browed Antbird *Hypocnemis hypoxantha* in eastern Ecuador. A: adult perched on rim of nest; B: *in-situ* photo of nest showing resemblance to naturally collected material; C: nest lining and eggs; D: adult (H. F. Greeney)

(Acritidae). Intervals between feedings were variable, ranging from 1–114 minutes (mean = 38.3 minutes).

**Other behaviours.**—The nestling produced a faecal sac during 14 of 27 prey deliveries, and the sac was always carried from the nest by the adult (Table 1). The intervals between faecal sac production were 4–132 minutes (mean = 37.8 minutes).

Twice, the attending adult was chased from the nest by a second bird (Table 1). The first chase was by a male Fulvous Antshrike *Frederickena fulva* on 4 July 2015 at 14.15 h. The clip began with two birds fighting just above the nest, followed by the antbird flying off while the male antshrike perched on the edge of the nest inspecting it. Although tiny vertebrate prey are sometimes consumed by small passerines (*cf.* Delgado & Brooks 2003), the antbird chick was not eaten. The second chase was on 6 July 2015 at 06.11 hrs when another bird (unidentified), about the same size as the parent, flew towards the nest, appearing to make contact with the adult on the nest. Both birds flew away quickly and out of view.

## Discussion

Nest architecture and egg coloration of *H. hypoxantha* is similar to related species (Bates *et al.* 1999, Zimmer & Isler 2003, Isler *et al.* 2007) in the *H. cantator* clade (Oniki & Willis 1982, Tostain *et al.* 1992, Cadena *et al.* 2000, David & Londoño 2013). However, the one-sided attachment points on the nests of *Hypocnemis* differ from the genus *Drymophila* (Bates *et al.* 1999, Isler *et al.* 2013, Tello *et al.* 2014), whose nests are rim-supported but from multiple sides (Zimmer & Isler 2003, Greeney 2007), and strikingly so from the base-supported nests of *Sciaphylax* (Hennessey 2002) (previously placed in *Myrmeciza*, see Isler *et al.* 2013). *Hypocnemis* do, however, appear to share this nest construction trait with species of *Cercomacra* and *Cercomacroides* (Huber 1932, Snethlage 1935, Skutch & Eckelberry 1969, Kratter 1998, Pinho *et al.* 2006, Florez-V. & Londoño 2014), the final two genera placed together with *Hypocnemis*, *Drymophila* and *Sciaphylax* in the tribe Pithyini (Tello *et al.* 2014). Indeed, direct comparisons by HFG of the nests of multiple species of *Cercomacra* / *Cercomacroides*, with those of several species of *Hypocnemis* (including the present) suggest that, architecturally, nests of these three genera are nearly indistinguishable, despite descriptions in the literature (see citations above and discussion in Tello *et al.* 2014). In sum, the nest architecture of *H. hypocnemis* and other members of the genus provides support for a close relationship with *Cercomacra* and *Cercomacroides*, as opposed to other members of the Pithyini (Tello *et al.* 2014).

Incubation at the Ecuadorian nest was starting during the middle of the drier period in that region (Loiselle *et al.* 2007), suggesting that fledging would have occurred near the start of the local rains. The Peruvian nest held a single nestling during the earlier half of the dry season (Brooks *et al.* 2005). These records suggest that *H. hypoxantha* may be a dry-season breeder across its range, though Ecuadorian breeding records for other thamnophilids suggests that, as a whole, these understorey insectivores may breed year-round (Tallman & Tallman 1997, Greeney *et al.* 2004, Greeney 2007.). In south-east Peru *H. subflava* and *H. peruviana* also breed during the dry season (August–November: Tobias *et al.* 2011, David & Londoño 2013).

### Acknowledgements

HFG is indebted to Fernando Jarol Vaca Branstein and the staff of Shiripuno Research Center for their logistical support. His visit to Shiripuno was funded by Ryan P. Killackey and Pollywog Productions LLC during work on the documentary feature film, Yasuní Man. In Peru, this study would have been impossible without the assistance of Tom & Lynne Williams, who provided the camera, and Aniano Benavides, who found the nest. We are indebted to Conservación en la Amazonía Peruana (CONAPAC) and Amazon

Conservatory for Tropical Studies (ACTS) for permission to work in the region. Kind thanks also to Elaine Hong for helping with data analysis, and to Mort Isler and Guy Kirwan for helpful comments and edits.

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# New records of distribution and nesting of two species of Cypseloidine swifts in western Panama, with notes on additional species

by Eric G. Horvath & Craig C. Bennett

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**SUMMARY.**—We searched for nesting Cypseloidine swifts at 22 waterfalls in western Panama during April 2013 and April–August 2014. Three nests of Spot-fronted Swift *Cypseloides cherriei* were found, providing the first record of occurrence in Panama. White-chinned Swift *C. cryptus* was found at five sites, which is the first report of nesting in Panama. Chestnut-collared Swift *Streptoprocne rutila* nests were found at three waterfalls. White-collared Swift *S. zonaris* was found nesting at two sites and a roost site was found at a third waterfall. Nesting phenology and nest elevations are discussed. Field identification marks for *C. cryptus* are reviewed.

Scant information and few reliable sight records exist for swifts of the genus *Cypseloides* in Panama. This is due in large part to the difficulty of identifying swifts in flight and their habit of nesting in hard-to-see locations at waterfalls. In North America, regional searches have been undertaken for nesting Black Swifts *Cypseloides niger* (Knorr 1961, Foerster & Collins 1990, Levad *et al.* 2008, Horvath 2012). The primary reference for Cypseloidine swift nesting data in Central America is the detailed study by Marin & Stiles (1992) at one site in Costa Rica.

This paper presents data from a widespread survey of waterfalls in western Panama that provide new records of distribution and nesting details for Spot-fronted Swift *Cypseloides cherriei*, White-chinned Swift *C. cryptus*, Chestnut-collared Swift *Streptoprocne rutila* and White-collared Swift *S. zonaris*.

## Methods

In April 2013 and from April until August 2014 we searched for nesting Cypseloidine swifts at 22 permanent, year-round waterfalls in western Panama (Fig. 1) by carefully scanning wet rock faces around and behind waterfalls using binoculars and telescopes. The precise locations of the study sites are presented in the legend to Fig. 1. Nearly all searches were conducted in the middle of the day when sunlight provided bright conditions for observation. At six sites where nests were found, we returned on subsequent days to conduct follow-up observations; on some visits, misty conditions prevented us from determining nest contents.

At all but two nesting sites, we observed from a distance to avoid flushing or otherwise disturbing the birds. We observed only from eye level and did not climb to nests or use a mirror on a pole to inspect nest contents, so in most cases we were unable to determine if the adult on the nest was incubating eggs or brooding young. At site QW an adult swift was mist-netted, measured and released. Measurements were taken using a metal wing rule and callipers following standard parameters (Pyle 1997). An infrared camera was set up to record activity for 72 consecutive hours at the same site.

We conducted five evening watches at waterfalls following the methodology of Levad *et al.* (2008) which was developed for surveying Black Swift nests in the USA. However, because our study area is within the range of three swift species with similar

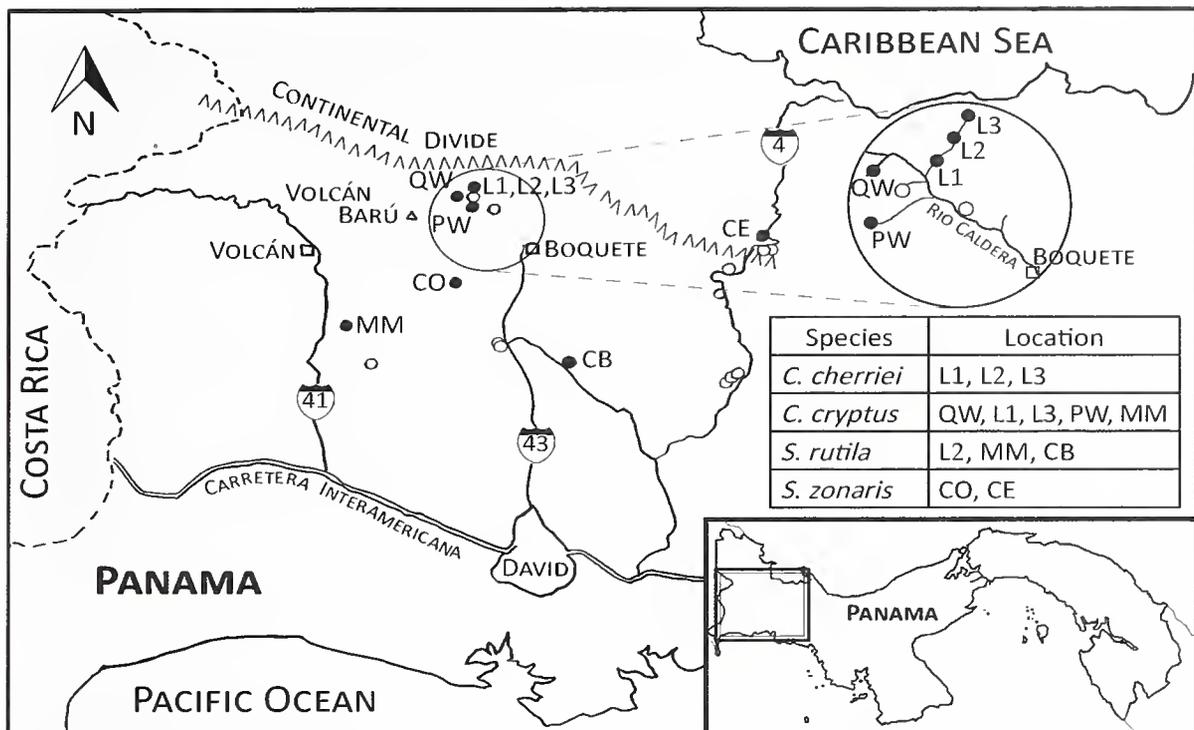


Figure 1. Map of survey sites in western Panama: black dots = occupied waterfalls, open circles = unoccupied sites. Location of the sites: L1 = 08°50'30"N, 82°28'35"W; L2 = 08°50'35"N, 82°28'26"W; L3 = 08°50'41"N, 82°28'19"W; MM = 08°41'06"N, 82°36'23"W; CO = 08°44'02"N, 82°29'56"W; CE = 08°47'07"N, 82°11'16"W; QF = 08°50'49"N, 82°29'24"W; PW = 08°49'01"N, 82°29'35"W; CB = 08°38'55"N, 82°23'45"W.

flight silhouettes (Spot-fronted Swift, White-chinned Swift, Chestnut-collared Swift), we determined that the evening watch was not a useful survey technique in Panama because low light conditions prevented accurate species identification as they flew to roost.

## Results

We found swifts nesting at nine of 22 waterfalls surveyed; the remaining 13 waterfalls appeared to be unoccupied. We cannot eliminate the possibility of nesting at the unoccupied waterfalls, since many were surveyed only once. However, most of these 13 waterfalls lacked either potential nest platforms that would be inaccessible to ground predators or the cliff overhangs necessary to protect nests from inclement weather.

### SPOT-FRONTED SWIFT *Cypseloides cherriei*

Three nests were found, each at a different waterfall along the same tributary of the Caldera River in an area of steep slopes and primary montane forest, at elevations of 1,745 m, 1,830 m and 1,945 m (Fig. 1: sites L1, L2, L3). Horizontal distance between waterfalls was c.300 m. The nests were located on vertical cliff faces 10 m, 8 m and 7 m above the base of the falls, which had approximate heights of 25 m, 15 m and 15 m, respectively. Each nest was in the zone of continuous mist within 3 m of the 'curtain' of falling water, in a dark location but unobscured by vegetation, protected from above by a rock overhang, and rarely received direct sunlight. We observed a torrential rainfall event in June 2014 when the creek flooded, but at each nest the rock roof prevented the nest from washing away. Two nests were on ledges (Figs. 2–3) and one was in a 'pocket'; in each case, the swifts entered and left the nest by direct flight from the nest rim.

Despite searching flocks of swifts in flight, we only observed Spot-fronted Swifts on the nest or flying directly along the canyon to the nest; we saw none in flight away from their



Figure 2. Adult Spot-fronted Swift *Cypseloides cherriei* incubating or brooding, site L3, western Panama, 13 June 2014 (Eric G. Horvath)



Figure 3. Spot-fronted Swift *Cypseloides cherriei* incubating, site L2, western Panama, 15 May 2014 (Lloyd Cripe)

nesting waterfalls. We were able to track the success of these three nests and each appeared to successfully fledge one young. Our observations have enabled us to create an outline of nesting phenology for 2014: egg laying in May, hatching in June, and fledging in late July to August.

#### **WHITE-CHINNED SWIFT** *Cypseloides cryptus*

Five occupied sites were found at elevations of 880 m, 1,745 m, 1,840 m, 1,945 m and 1,980 m; each was at a separate waterfall and had just one pair of swifts nesting (Fig. 1: sites MM, L1, QW, L3, PW). One nest was easily visible while the others were partially concealed behind ferns and other vegetation; all were in wet areas beside or under falling water (Figs. 5–7).

The nest at site L3 was monitored regularly throughout the nesting season. An adult was first observed incubating on 5 May 2014, and the first observation of a chick in the nest was on 13 June. The developing chick was viewed in the nest until 28 July when it appeared large, healthy and was flapping its wings. It was absent on our next visit on 7 August.

At site QW on 11 June 2014 an adult White-chinned Swift was trapped (Fig. 4)



Figure 4. White-chinned Swift *Cypseloides cryptus*, site QW, western Panama, 11 June 2014 (Eric G. Horvath)



Figure 5. Adult White-chinned Swift *Cypseloides cryptus* incubating, site L3, western Panama, 15 May 2014 (Lloyd Cripe)

and measured: flattened wing 132 mm, tail 43 mm, exposed culmen 5.4 mm. Wing moult was underway, with pp1–3 new and fully grown, pp4–5 in sheath and partially grown, and the outer pp6–10 old and worn. The tail was worn with frayed tips; no exposed rachis was present on any of the rectrices.

The infrared camera placed adjacent to the nest at site QW took one photo every five minutes and whenever motion was detected, resulting in 1,160 photos during the period 18–21 June 2014. On 18 June 2014 the single chick in the nest was covered in dark grey semi-plumes (Collins 1963) and gave a raised-wing threat display. It was estimated to be 15–20 days old. The chick had a skin temperature of 30°C, measured using an infrared thermometer 10 cm away; the chick's core temperature was probably higher. Ambient temperatures 1 m from the nest varied at 12–17° C. The photo sequence enabled us to document the following nest activity. The chick was brooded near-continuously by one adult at night, while the other adult roosted 1 m from the nest. Nest change-overs occurred during the night, and at times two adults were present at the nest simultaneously with the chick. Apparent nocturnal provisioning of the chick was visible in some photos. By day, the adults were largely absent, especially in the morning, when the chick was unattended for up to seven hours. The chick was alert and moved about in the nest when it was alone and did not exhibit torpor.

#### **CHESTNUT-COLLARED SWIFT** *Streptoprocne rutila*

We found three nests at geographically widely separated waterfalls at elevations of 350 m, 880 m and 1,830 m (Fig. 1: sites CB, MM, L2). Two nests were on cliffs next to waterfalls in somewhat drier locations than the *Cypseloides* nests and the third nest was at the back of an 8 m-deep cave located at the base of a waterfall. The cave nest, site L2, was observed during construction in mid April, and the first egg was noted on 15 May. A second egg was seen on 20 May, but by 22 June the nest had collapsed. We suspect that the nest was disturbed by humans, as it was in an easily accessible location on a popular hiking trail. The swifts started rebuilding the nest in July, later in the rainy season, but did not lay a second clutch. The other two nests were not regularly monitored, so we lack data on nest success.

#### **WHITE-COLLARED SWIFT** *Streptoprocne zonaris*

We observed one nest of this species at site CO (1,350 m elevation, Fig. 1) on 12 June 2014. The nest held two large, well-feathered young and a single adult. There was also a large colony of White-collared Swifts nesting at site CE, at 600 m elevation. Here c.100 adults were observed flying to and from their nests at midday on 16 June 2014, but we were unable to see and therefore count the nests due to access difficulties. At Cañon Macho de Monte (site MM), a night roost of c.100 White-collared Swifts was observed in April 2013 and April 2014 but, despite a thorough search of the canyon interior, no White-collared Swift nests were found.

## **Discussion**

The discovery of the three nests of Spot-fronted Swifts reported here provides the first documented record of the species' occurrence in Panama (G. Angehr, Panama Bird Records Committee, pers. comm.). The distinctive white facial markings of Spot-fronted Swifts were photographed (Figs. 2–3). This little-known species has been reported nesting at 1,900 m elevation in central Costa Rica (Marín & Stiles 1992), 1,900 m on the west slope of the Andes in Ecuador (Marín & Stiles 1993), 2,050 m on the east slope of the Andes in Ecuador (Greeney 2004), 1,100 m in the central Coastal Cordillera of northern Venezuela (Collins 1980) and at 1,745–1,945 m in western Panama (this study). Spot-fronted Swift has

also been observed in Colombia (Chávez-Portilla *et al.* 2007) at 1,800 m. It is notable that we found three pairs nesting close to each other along just one tributary of the Caldera River, and not elsewhere in Chiriquí province, despite searches of other waterfalls. More surveys are required to clarify the species' distribution, but present data indicate that Spot-fronted Swift nests at montane waterfalls at 1,100–2,050 m elevation and is rare and local with a disjunct range.

This study also yielded the first report of nesting White-chinned Swifts (Figs. 5–7) in Panama. Although White-chinned Swift is widely distributed, with records from Belize to Peru, there are few published reports of nesting: in Costa Rica at 700 m elevation (Sardinal River: Stiles & Skutch 1989) and 1,900 m (Tiribí River: Marín & Stiles 1992), in Amazonas, Brazil (Whittaker & Whittaker 2008) at 100 m, in Acre, Brazil (Biancalana & Magalhães *in press*) at 286 m, and in eastern Venezuela (Ayarzagüena 1984) at 860 m. In Surinam, the species is suspected of nesting at c.500 m (Ottema 2002). In Panama, we found them nesting at sites ranging from 880 m to 1,980 m. The two previous records from Panama (Wetmore 1968) are both of specimens: one taken in San Blas province in July 1932, and one on Coiba Island in March 1957. The lack of subsequent sight records in Panama may reflect the difficulty of identifying this species in flight. The data presented here indicate that White-chinned Swift nests at 100–1,980 m elevation, and is uncommon but not rare near mountain waterfalls in Chiriquí province, Panama.

Because both White-chinned Swifts and Black Swifts have dark, unpatterned plumage and subtle facial markings, field separation of these two species at the nest is not straightforward, and we were initially unsure which species was involved in our observations. Marín & Sánchez (1998) reported Black Swifts nesting along the Tiribí River, Costa Rica, 300 km from our study area; White-chinned Swift also nests at this locality (Marín & Stiles 1992). To resolve identification, we captured an adult swift at site QW and found that its wing and tail measurements were within the range of White-chinned, but smaller than Black Swift (Marín & Stiles 1992). In addition, the trapped swift was in wing moult. Black Swifts breeding in North America are not known to moult their flight feathers during the breeding season (Pyle 1997), whereas White-chinned Swifts moult during the nesting season in Costa Rica (Marín & Stiles 1992). The original species description by Zimmer (1945) indicates that a diagnostic feature of White-chinned Swift is that the pale markings on the top of the head are restricted to the sides of the forehead. Both adult White-chinned Swifts at the QW nest displayed a small amount of white below the bill and some whitish fringes to the feathers on the side of the forehead (Fig. 4). The other six presumed White-chinned Swifts that we saw at nests possessed a similar face pattern (Figs. 5–7). Black Swifts nesting in North America vary in the amount of white feather fringes on the lores, superciliary area and forehead (C. Gunn *pers. comm.*) and, in particular, adults can show pale dusky fringes to the chin and crown. It appears from our observations that adult White-chinned Swifts in Panama lack pale feather fringes to the centre of forehead and crown, which can often be seen in adult Black Swifts, and that White-chinned Swifts can have markedly white chins, unlike the dusky chins sometimes observed in Black Swifts.

An additional morphological feature that has been noted as a difference between White-chinned and Black Swifts is the presence of an exposed rachis projecting from the tips of the rectrices in *C. cryptus*, which is absent in *C. niger* (Marín & Stiles 1992, Pyle 1997) except on worn rectrices (C. Gunn *pers. comm.*). The heavily worn tail of the swift we trapped shows that while this may be a useful character for fresh and unworn rectrices, it is not useful for identification during the nesting season, when adult White-chinned Swifts have worn tails. Nostril shape has also been demonstrated to separate these species (Zimmer 1945, Marín & Stiles 1992), with Black Swifts possessing elliptical nostrils and White-chinned



Figure 6. Adult White-chinned Swift *Cypseloides cryptus* incubating, site L3, western Panama, 30 May 2014 (Lloyd Cripe)

Figure 7. Adult White-chinned Swift *Cypseloides cryptus* incubating or brooding, site MM, western Panama, 19 June 2014 (Eric G. Horvath)

Figure 8. Probable White-chinned Swift *Cypseloides cryptus*, 20 km from known nest sites, Chiriquí River, western Panama, 15 April 2014; at least one photographed within a flock of Chestnut-collared Swifts *Streptoprocne rutula* foraging low over riparian canopy trees. Note white chin and white scaling on belly that eliminates Chestnut-collared Swift. Compared to Black Swift *Cypseloides niger*, White-chinned Swift has relatively shorter wings, but this field mark varies considerably in both species, depending on whether they are gliding or stalling, and should not be considered diagnostic (Eric G. Horvath)

Swifts having more rounded nostrils. We were unable to evaluate this character in the field, despite using high-quality telescopes, because the nostrils are so small and field conditions precluded close approach to nests.

Shape in flight has been noted as another means to separate Black Swifts from White-chinned Swifts by Howell & Webb (1995), who emphasised the cleft tail (diagnostic) and relatively longer tail and wings of Black Swifts. However, Pyle (1997) demonstrated that only older male Black Swifts display a notched tail; the tail is square-ended in females and

first-years of both sexes. Photographs of Black Swifts in flight at nesting areas in North America (EGH unpubl.) indicate that wing shape varies substantially between slender and sickle-shaped to broader. For separating White-chinned from Black Swifts, we found flight shape useful only with the aid of good photographs and, in the case of swifts lacking a forked tail, we consider shape alone to be an unreliable means of specific identification for most observations of *Cypseloides* in flight, particularly at localities where three *Cypseloides* species occur.

Chestnut-collared Swift is readily identified in the field under good lighting by their broad chestnut collar and upper breast-band, a feature shown by all males. Females also possess a bright collar, but often it is 'abbreviated' dorsally or absent there (Stiles & Skutch 1989, Howell & Webb 1995). There are many sight records in Panama, but breeding distribution is poorly known. As we found nests at widely scattered locations and at highly variable elevations, we suggest that Chestnut-collared Swift is probably a commoner nesting bird in western Panama than previously recognised.

Our data on nesting phenology of Spot-fronted, White-chinned and Chestnut-collared Swifts in Panama reveal a pattern of nest initiation in late April, egg laying in May (following the start of the wet season) and fledging in late July / August. In Costa Rica, Marín & Stiles (1992) found that these three species all breed at the same time of year, from the start of the rainy season and continuing from May into August. In Venezuela, Collins (1980) observed a Spot-fronted Swift nest with eggs in mid July. The length of the nestling period for Spot-fronted Swifts observed in our study was *c.*60 days, similar to the 65 days reported by Marín (2008). In contrast, White-collared Swifts appear to start nesting at the end of the dry season, *c.*1 month earlier, as we observed large young in the nest in June. This places egg laying in early April for Panama, matching *S. zonaris* phenology in Costa Rica (Marín & Stiles 1992).

The Cypseloidine swift habit of nesting at shaded, cool and humid cliffs near or behind waterfalls is well known (Knorr 1961, Collins 1968, Marín & Stiles 1992, Leivad *et al.* 2008), and probably has adaptive significance. Three hypotheses, which are not mutually exclusive, have been proposed regarding the selective advantage of waterfall nesting.

The first hypothesis relates possible torpor to nest site location. Torpor in Black Swifts was proposed by Udvardy (1954) who extrapolated from the Koskimies (1948) torpor study of Common Swift *Apus apus*. While the adults are away from the nest, the nestling may survive the period of cold by temporarily becoming torpid; by reducing body temperature the loss of body weight from starvation is diminished. Boyle (1998) linked possible torpor and nest ambient temperature by hypothesising that the constantly cool temperatures would aid in slowing the metabolism of the Black Swift nestling when it was alone. Air temperature at Black Swift nests has been documented to be especially stable, varying little (Gunn *et al.* 2012). Foerster (1987) observed that older Black Swift nestlings are typically left unattended for long periods during the day, which could suggest possible use of torpor. At dusk adult Black Swifts return to the nest and brood the chick, making torpor unnecessary at night. Field observers have searched for torpor-like behaviour in adult and nestling Black Swifts, but torpor has not been observed (Legg 1956, Gunn *et al.* 2012). Although there is an absence of experimental or behavioural studies demonstrating torpor in Cypseloidine swifts, they may possess this capacity. While torpor cannot be eliminated, to date no studies have demonstrated its regular use.

A second hypothesis, developed by Marín & Stiles (1992), relates high humidity to nest stability and adhesion to the cliff. *Cypseloides* construct their nests on ledges or niches in vertical cliffs, and sometimes these ledges are precariously small. For Black, White-chinned and Spot-fronted Swifts, nests are often constructed of live mosses that 'root' to the cliff with their anchoring rhizoids, enhancing nest stability on insecure ledges. The high humidity

found near and behind waterfalls permits the mosses that form the nest cup to continue growing after having been plucked from the cliff during nestbuilding. Nests composed of mosses rooted to the cliff are more secure and less apt to fall. In coastal areas, Black Swift nests were found to be constructed of seaweed (Legg 1956), so rooting by mosses is not a requirement at all localities. For White-collared Swift, often the egg is simply laid on a rock ledge with little or no nest material (Marín & Stiles 1992). Overall, the nest adhesion hypothesis can be seen as an additional supporting factor but not explanatory for all Cypseloidine waterfall nesting situations.

The third hypothesis is avoidance of predation. It has been proposed that Black Swift nests are associated with waterfalls to limit predator access (Knorr 1961, Marín & Stiles 1992, Levad *et al.* 2008). Nest success for most small, open-nest birds is 40–60% (Ricklefs 1969) even though they have short nesting cycles of 25–30 days. However, among the four species of Cypseloidine swifts studied by Marín & Stiles (1992) in Costa Rica, nest success rates averaged 71%, despite the long nesting cycle of 80–90 days. Data from our study in Panama suggests that nest success among Spot-fronted Swifts may be relatively high, although our sample size is tiny ( $n = 3$ ). The most comprehensive study of Black Swifts, in Colorado, USA, revealed a nest success rate of 72% (Hirshman *et al.* 2007). The low reproductive rate of Cypseloidine swifts, with clutches of either two eggs in *Streptoprocne* or one in *Cypseloides* (Marín & Stiles 1992), combined with the long nesting cycle, strongly suggests that all require extraordinarily safe places to nest.

We propose that waterfall nesting locations provide uniquely high levels of safety from predation for the following reasons. First, snakes and small mammals (i.e. rodents and procyonids) that routinely climb dry, vertical rock faces cannot scale the slippery algae and moss on the vertical, permanently wet cliffs at waterfalls. Second, waterfalls are loud and mask sounds at the nest. Third, the strong moist winds generated by waterfalls may disperse nest odours. Finally, Cypseloidine swifts often nest behind the ‘veil’ of falling water and these dripping locations help to visually conceal the nests from avian nest predators such as corvids and raptors. We predict that experimental studies of nest predation that compare waterfall locations to dry-cliff sites not associated with waterfalls will demonstrate lower predation rates at waterfall nesting locations.

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- Addresses: Eric G. Horvath, P.O. Box 721, South Beach, OR 97366, USA, e-mail: horvath@pioneer.net. Craig C. Bennett, PTY 50066, P.O. Box 25207, Miami, FL 33102, USA, e-mail: craiginlagrande@aol.com

# The history and morphology of Lord Howe Gallinule or Swampen *Porphyrio albus* (Rallidae)

by Hein van Grouw & Julian P. Hume

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**SUMMARY.**—The extinct Lord Howe Gallinule or Swampen *Porphyrio albus* (White, 1790) is known from a number of written accounts, from at least ten contemporary paintings and from two skins, but the provenance of the specimens is confused and the taxonomic literature riddled with error. We present a review of the evidence and its reliability, demonstrate that the two extant specimens were collected on Lord Howe Island, provide details about when they were taken and by whom, and how they subsequently arrived in England. We further present evidence to demonstrate that Lord Howe Gallinule possessed several unique morphological characters.

‘Although generally believed to be absolutely extinct, I should not be surprised to hear of a specimen being taken in the recesses of the mountains, many parts of which have not yet been explored’ (Bassett-Hull 1909).

Lord Howe Gallinule or Swampen *Porphyrio albus* (White, 1790) was endemic to remote Lord Howe Island, a small island c.10 km long and 0.3–2.0 km wide, located c.600 km east of Australia. It was considered common when initially discovered in 1788, but quickly succumbed to over-hunting, and had disappeared by 1834 (Hindwood 1940, Hume & Walters 2012, Hume & van Grouw 2014). The population contained all-blue and all-white birds, as well as individuals with a variable mix of blue and white feathers. Just two specimens are extant: the type (NMW 50.761), in the Naturhistorisches Museum, Vienna, has reliable documentation linking it to Lord Howe Island. There is no doubt that this specimen is the type, as White (1790) stated that the bird on which his Lord Howe Gallinule drawing was based was deposited in the Leverian Museum (Pelzeln 1860, 1873). The specimen was purchased during the sale of the Leverian collection in 1806 by the Vienna Museum (Pelzeln 1860, 1873, Forbes 1901), being catalogued as ‘Lot 2782: White fulica, *Fulica alba*, New Holland’. However, the provenance of the second specimen held in the World Museum, Liverpool (WML D3213), is uncertain. The discovery and subsequent descriptions of Lord Howe Gallinule have resulted in a wealth of confusing literature, exacerbated by uncertainty over provenance. We provide evidence to suggest that some of the accounts were based on hearsay, and provide historical and morphometric evidence to ascertain that the Liverpool skin was indeed collected on Lord Howe. We further show that *P. albus*, although exhibiting several unique characters, was most similar morphometrically to Purple Swampen *P. porphyrio melanotus* of Australia and New Zealand. Finally, we show that *P. albus* was uniquely coloured in its natural purple-blue plumage-variant, of which no specimen exists.

## The early literature

To clarify a complicated situation, we compiled all of the contemporary literature describing or illustrating the species and have listed it chronologically, providing information concerning the reliability of each account and illustration. The accounts describing live birds on Lord Howe Island and collection of specimens occurred in March–

May 1788 by crew members on visiting ships, and the paintings were executed between 1788 and 1790. Five ships arrived on Lord Howe in 1788, the outgoing *Supply*, as well as the *Sirius*, which was supplying a newly founded penal colony on Norfolk Island from Sydney in 1788–90, and the returning transports of the First Fleet, the *Scarborough*, *Charlotte* and *Lady Penrhyn* (Hindwood 1940). After the first landing on 19 March 1788 by the *Supply* en route from Norfolk Island, the *Supply* returned to Lord Howe again together with the *Sirius* and the three transports on 16–18 May 1788, during which period the crews from each ship plundered the avifauna. There are no more reports detailing landings on Lord Howe or ornithological observations until 1853 (see below).

## The accounts

Lieutenant Henry Lidgbird Ball, commander on the ship *Supply*, who first observed Lord Howe Island on 17 February 1788, en route to Norfolk Island to establish the penal colony, and named and claimed Lord Howe for Britain on his return trip (Nichols 2006). Ball went ashore on 19 March, and according to Arthur Bowes Smythe, who also wrote about Ball's discovery (see below), members of the crew captured Lord Howe Gallinules for the first time, as Ball did not provide any details himself.

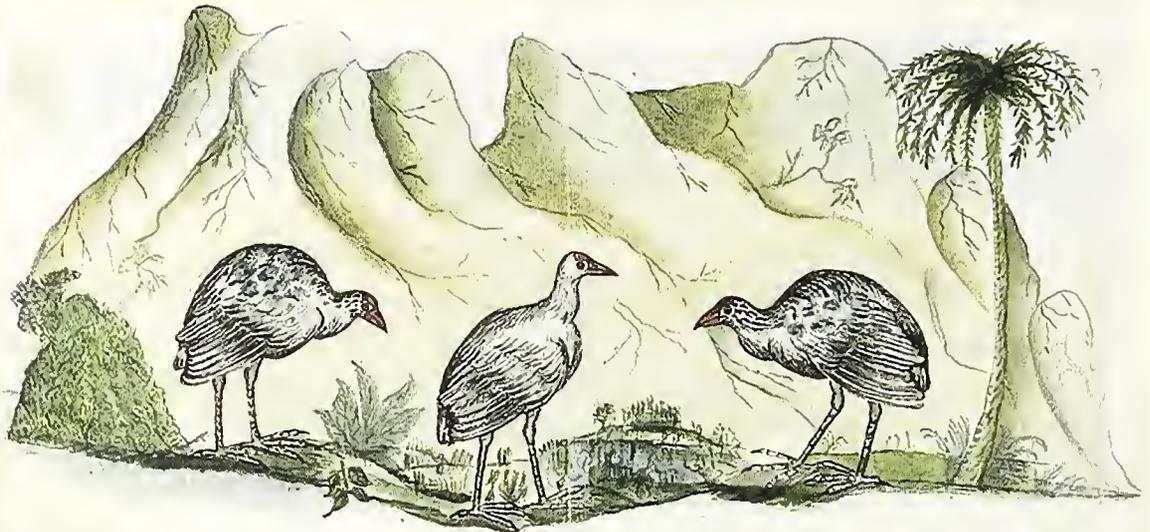
### *First-hand accounts*

1. David Blackburn (landed 19 March 1788 and 16 May 1788) was Master on the *Supply* and apparently part of the first landing party on Lord Howe on 19 March, as well as the second on 16 May, on both occasions when the *Supply* was returning from Norfolk (Hindwood 1940). His account was written in a letter to a friend in England (Blackburn 1934). He was the only person to mention the diet of Lord Howe Gallinule: '...on the shore we caught several sorts of birds, ... and a white fowl – something like a Guinea hen, with a very strong thick & sharp pointed bill of a red colour – stout legs and claws – I believe they are carnivorous they hold their food between the thumb or hind claw & the bottom of the foot & lift it to the mouth without stopping so much as a parrot'.

2. Arthur Bowes Smythe (landed 16 May 1788) was surgeon on the *Lady Penrhyn* and mentioned Lieutenant Ball's discovery in his journal (Bowes Smythe MS 22 March 1787–August 1789). He stated: 'The *Supply* in her return [from Norfolk] landed at the island [Lord Howe] she made in going out & were very agreeably surpris'd to find great numbers of fine Turtle on the beach, & on the Land amongst the trees great Nos. of fowls like a Guinea hen [Lord Howe Gallinule], & another species of fowl [Lord Howe Woodhen *Gallirallus sylvestris*] not unlike the landrail in England, & all so perfectly tame that you cd. frequently take hold of them with your hands but cd. at all times knock down as many as you thought proper wt. a short stick'.

Bowes Smythe finally experienced the naivety of the Lord Howe avifauna himself on the morning of 16 May 1788 (Bowes Smythe 1787–89) and stayed overnight (Hindwood 1940). After going ashore, he remarked: 'When I was in the Woods amongst the Birds I cd. not help picturing to myself the Golden Age as described by Ovid to see the Fowls (or Coots) some white, some blue & white, others all blue wt. large red bills & a patch of red on the top of their heads, ...'. Bowes Smythe also executed the first illustration of Lord Howe Gallinule at this time (*in* Hindwood 1932), when he depicted three individuals, one completely white and the others tinged with blue (Fig. 1).

3. Thomas Gilbert (landed 16 May 1788) was commander on the *Charlotte* and wrote a detailed account of the avifauna on Lord Howe, including Lord Howe Gallinule (Gilbert



Representation of a Bird of the Coot kind, found at Lord Howe Island, in the South Sea.

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Figure 1. Watercolour of three Lord Howe Gallinules *Porphyrio albus* by Arthur Bowes Smythe, c.1788, based on live birds that Bowes Smith observed during his visit to Lord Howe Island in May 1788. The handwritten note reads 'Representation of a Bird of the Coot kind, found at Lord Howe Island, in the South Sea' (National Library of Australia, Canberra)



WHITE GALLINULE.

*Published by J. Stoddart.*

2

Figure 2. White Gallinule, pl. 44 in Phillip (1789), probably based on a live specimen (Hein van Grouw, Natural History Museum, Tring)

1789): 'Among the different kinds of birds we met with, there was one about the size of a large barn-door fowl, quite white, with long yellow legs, and a remarkably strong beak. I caught six of them by running them down among the low bushes. The cocks were very beautiful, their white feathers being tipped with azure blue'.

4. Arthur Phillip (account written in 1789) was the first Governor of New South Wales and sailed with the first fleet in 1787 (Phillip 1789). Governor Phillip received Lord Howe bird specimens in Sydney, including live individuals, possibly collected by Lieutenant Ball or his crew. Some were sent to Lady Mary Elisabeth Chatham in England aboard the *Alexander* in 1788, whereupon they were probably purchased by Sir Joseph Banks (Barton 1889, Bladen 1901, Hindwood 1940). Lady Chatham was married to John Pitt, Second Earl of Chatham, and sister-in-law to the Prime Minister, William Pitt the Younger (Stanhope 1861). Phillip never visited Lord Howe Island, so he almost certainly based the first part of his account on those of Blackburn, Lieutenant Ball and / or Bowes Smythe, in which they compare Lord Howe Gallinule with a guineafowl. Phillip stated (p. 182): 'There are also many very large pigeons, and the white birds resembling the Guinea fowl, which were found at Norfolk Island, were seen here also in great numbers. The bill of this bird is red, and very strong, thick, and sharp pointed'.

Phillip (1789) illustrated the bird and also provided a detailed description, which strongly suggests that they were based on a live gallinule he received in Sydney (Fig. 2): 'WHITE GALLINULE. This beautiful bird greatly resembles the purple Gallinule in shape and make, but is much superior in size, being as large as a dunghill fowl. The length from the end of the bill to that of the claws is two feet three inches; the bill is very stout, and the colour of it, the whole top of the head, and the irides red; the sides of the head around the eyes are reddish, very thinly sprinkled with white feathers; the whole of the plumage without exception is white. The legs the colour of the bill. This species is pretty common on Lord Howe's Island, Norfolk Island, and other places, and is a very tame species. The other sex, supposed to be the male, is said to have some blue on the wings.'

Phillip (1789) referred to the gallinule occurring on 'Norfolk Island and other places', but does not indicate where the 'other places' are. His provenance of Norfolk Island is also in error (see below).

5. John Hunter (present early 1790?) was Captain on the *Sirius* and later replaced Phillip as Governor of New South Wales (Percival 1949). Captain Hunter did not mention visiting Lord Howe, but presumably landed there while supplying the penal colony on Norfolk. The *Sirius* was wrecked on Norfolk on 19 March 1790, and Captain Hunter and George Raper (see below), along with the rest of the crew, were marooned there for 11 months until a rescue ship arrived from Sydney (Percival 1949, Hindwood 1964, 1965). Hunter was a keen naturalist and artist, and illustrated a Lord Howe Gallinule (Hunter MS; Fig. 3). The painting forms part of Hunter's *Birds & flowers of New South Wales drawn on the spot in 1788, '89 & '90*, so the Lord Howe Gallinule illustration must have been executed sometime between 1788 and 1790 (Wheeler & Smith 1988). It is not known if his illustration is based on a live bird when on Lord Howe, or from memory when marooned on Norfolk.

6. George Raper (present early 1790?) was Midshipman on the *Sirius* (Hindwood 1964) and, like Captain Hunter (Hindwood 1965), illustrated Lord Howe Gallinules presumably while on Lord Howe or while marooned on Norfolk. Raper's depiction of a single bird is dated 1790 (Fig. 4). G. P. Whitley (*in* Hindwood 1940) examined a volume of drawings in the Alexander Turnbull Library, Wellington, and discovered an unsigned painting of two Lord Howe Gallinules (Fig. 5), which has been assigned to George Raper and is also dated 1790. This painting is particularly important as it details two plumage variations of the gallinule.



Figure 3. Ground Bird of Lord Howe Island; a Lord Howe Gallinule *Porphyrio albus* depicted by John Hunter (1788–90) (National Library of Australia, Canberra)

### *Second-hand accounts*

1. John White (account written in 1790) was a ship's surgeon and in his book (White 1790: 135), which was more or less a journal of his time in New South Wales, he also presented descriptions of the animals on Lord Howe based on either Lieutenant Ball's or Bowes Smythe's accounts, or on those of other sailors, as he apparently never visited Lord Howe Island himself. White may have questioned the sailors in Sydney, as they had first been to Norfolk Island on the *Supply*, and had stopped at Lord Howe Island on their return: 'They



GROUND-BIRD of LORD-HOWE-ISLAND. Natural size. 1790

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Figure 4. Ground Bird of Lord Howe Island; a Lord Howe Gallinule *Porphyrio albus* depicted by George Raper (1790), presumably after a live bird; drawing No. 71, George Raper Drawings Collection, Library and Archives, NHMUK London (Natural History Museum, London)

[sailors] also found on it, in great plenty, a kind of fowl, resembling much of the Guinea fowl in shape and size, but widely different in colour; they being in general all white, with a red fleshy substance rising, like a cock's comb, from the head, and not unlike a piece of sealing-wax. These not being birds of flight, nor in the least wild, the sailors availing themselves of their gentleness and inability to take wing from their pursuits, easily struck them down with sticks'.

In his book's appendix, White described the Lord Howe Gallinule, giving it the name *Fulica alba* and the provenance as Lord Howe Island, and illustrated it with a painting by Sarah Stone from a specimen in the Leverian Museum (Fig. 6). It is not known with certainty if White had seen the specimen, but his account categorically states that he was describing a skin. The editor of White's book approached Stone to illustrate the gallinule once the specimen became available at the Leverian Museum (White 1790: A2): 'THE WHITE FULICA. *Fulica alba*. White Fulica, with the bill and front red, shoulders spined, legs and feet yellow? The body is about the size of a domestic fowl. The shoulders [wrists]



Figure 5. Illustration of two Lord Howe Gallinules *Porphyrio albus*, one all white and one still variegated, by George Raper (1790); this painting is particularly important as it clearly shows two stages of the colour aberration progressive greying (Alexander Turnbull Library, Wellington)

are furnished with a small crooked spine. In the dried specimen the legs and feet are yellow; but, perhaps, in the living bird might have been of the same colour with the beak.'

2. Anon. artist (Thomas Watling collection) (illustration dated c.1792, almost certainly incorrectly). Two Lord Howe Gallinule illustrations, executed by an anonymous artist, referred to as the 'Port Jackson artist' (Macinnis 2012), formed part of the Thomas Watling collection, and are now at the Natural History Museum, London (NHMUK-L-Watling-329-M-1 and NHMUK-L-Watling-330-M-1). Watling was a convict and artist who assisted John White by copying natural history illustrations (Pearce 1989). It is not certain if Watling was the artist of these Lord Howe Gallinule paintings, and the date of c.1792 that accompanies the paintings is a later addition that is almost certainly incorrect. The mystery is that White (1790) used engravings in his book that possess matching paintings in Watling's collection, yet Watling did not arrive in Sydney until 1792 (Macinnis 2012), hence the c.1792 attribution. It is probable therefore that Watling obtained illustrations by other artists after his arrival, and subsequently copied them; this is almost certainly the case with the Lord Howe Gallinules. However, the handwritten notes on the paintings suggest that the artist had either seen a live bird himself, or obtained information from someone else. The note on no. 329 reads: 'This bird is of Lord Howe and when young is intirely [sic] black, from that to a bluish grey and from that to an intire [sic] white. The bird feeds itself with its feet like a parrot' (Fig. 7). The second painting no. 330 states: 'Three stages of this Bird, taken at Lord Howes Island, before it arrives at maturity' (Fig. 8).



Figure 6. The White Fulica, pl. 27 in White (1790), as depicted by Sarah Stone based on the mounted specimen in the Leverian Museum (Hein van Grouw, Natural History Museum, Tring)

## Extinction

The period between the discovery of Lord Howe and the date of the last mention of living Lord Howe Gallinules spanned only 1788–90. Lord Howe Island was first settled in 1834, but whalers and sealers regularly used the island for supplies prior to this (Hume & Walters 2012). Foulis (1853) was on the island from 1844 until 1847 with 16 other residents.



Figure 7. Illustration by an anonymous artist of a Lord Howe Gallinule *Porphyrio albus* from Thomas Watling's collection, NHMUK-L-Watling-329-M-1; the handwritten notes read 'This bird is of Lord Howe and when young is intirely [sic] black, from that to a bluish grey and from that to an intire [sic] white. The bird feeds itself with its feet like a parrot' (Natural History Museum, London)

He made an ornithological report, the first survey of the avifauna of Lord Howe Island for 63 years, but did not mention the gallinule (Foulis 1853, Hindwood 1940). No doubt a poorly volant, chicken-sized gallinule quickly fell prey to whalers and sealers, and disappeared extremely rapidly, possibly even by the end of the 18th century. And, although Bassett-Hull (1909) hoped for its rediscovery, the confirmed existence of the Lord Howe Gallinule spanned just two years.

### Confusion over provenance

There is no doubt that there was once a population of predominantly white gallinules on Lord Howe Island, with the discovery of subfossil remains confirming this (Hume & Walters 2012). However, there is no substantiating evidence to suggest that a white gallinule historically occurred on Norfolk Island (*contra* Pelzeln 1860, 1873, Gray 1862, Sharpe 1894, Rothschild 1907, Mathews 1928), but subfossil *Porphyrio* remains pre-dating European discovery of the island have been recovered (Holdaway & Anderson 2001). Norfolk Island lies c.900 km north-east of Lord Howe and was visited by the capable naturalists the Forsters in 1774 during Cook's discovery of the island; they did not mention a white



Figure 8. Illustration by an anonymous artist of three Lord Howe Gallinules *Porphyrio albus* from Thomas Watling's collection, NHMUK-L-Watling-330-M-1; the handwritten note reads 'Three stages of this Bird, taken at Lord Howes Island, before it arrives at maturity (Natural History Museum, London)

gallinule (cf. Iredale 1910, Hindwood 1932). Despite this lack of first-hand evidence, several commentators confused the provenance, even leading to the description of supposed Norfolk Island birds as a second species of white gallinule.

Confusion was initiated when Arthur Phillip mentioned white gallinules on Lord Howe, Norfolk 'and other places' (Phillip 1789), which was followed by Latham (1790, 1801), who gave only Norfolk Island as their provenance. Latham based his locality on the accounts of Phillip (1789) and White (1790) alone, but White gave Lord Howe as the provenance (p. 135). There is some doubt as to the accuracy of the accounts of both Phillip and White, as they were published in popular books (Phillip 1789, White 1790), in which much information was gleaned from official and semi-official documents (Hindwood 1940). White and Phillip also never landed on Lord Howe or Norfolk themselves, so both authors discussed the observations of others in describing the islands, although Phillip did see live Lord Howe Gallinules in Sydney. White (1790: 238) confirmed his lack of field observation when he stated: 'in the dried specimen the legs and feet are yellow; but, perhaps, in the living bird might have been of the same colour with the beak'.

Pelzeln (1860, 1873) repeated Latham's (1790, 1801) statement that the Vienna specimen was obtained on Norfolk Island, and in the Leverian sale it was catalogued as originating in New Holland (= Australia), presumably in reference to it having been sent from Sydney, rather than any suggestion that it had been collected there. These errors almost certainly arose from misinterpretation of the collectors' voyages. Supply ships regularly sailed between Sydney and Norfolk, often stopping at Lord Howe, making confusion over provenance extremely likely.



Figure 9. Illustration of *Porphyrio stanleyi*, based on the Liverpool specimen, by J. G. Keulemans *in* Rowley (1875), as Rowley thought the Liverpool bird was a different species; it is probable that the present pose of the Liverpool specimen (see Fig. 11) is modelled on this picture (Hein van Grouw, Natural History Museum, Tring)

White (1790) sent his manuscript to England prior to 1790, as he did not return to England until after 1794 (Nelson 1998). As Sarah Stone was able to illustrate the Lord Howe Gallinule pre-1790 for White's volume based on a specimen in the Leverian Museum (White 1790, Pelzeln 1860), it is plausible that White had sent a Lord Howe Gallinule along with the manuscript from Sydney. This was the specimen obtained by Sir John Lever for the Leverian Museum and now in Vienna. Alternatively, this skin might have arrived earlier, possibly also sent by Governor Phillip with the Liverpool bird (see below). Unfortunately, there is no surviving correspondence, as far as is known, from White or Phillip to clarify this conundrum.

The Liverpool skin was probably obtained, without date or provenance, on its arrival in England by Sir Joseph Banks, one of the naturalists on Cook's first voyage, but it was supposed to have come from New Zealand (Rowley 1875, Forbes 1901). It is extremely likely that a Lord Howe Gallinule was included with the 1788 consignment sent by Governor Phillip to Lady Chatham in England, after which it was presumably purchased by Banks and eventually reached Liverpool. Nothing is known as to the whereabouts of the specimen until it eventually came into the possession of William Bullock, whose collection, including the gallinule, was auctioned in 1819 (Forbes 1901), when it was catalogued as 'Lot 60, White



Figure 10. Illustration of a Takahe-like Lord Howe Gallinule *Notornis alba* in Salvin (1873) by J. G. Keulemans, based on a sketch provided by Pelzeln of the Vienna specimen (Hein van Grouw, Natural History Museum, Tring)

Gallinule (*Fulica*) *alba*); New Zealand, rare; brought by Sir J. Banks'. The specimen was purchased by Lord Stanley and, along with his Knowsley collection, bequeathed to the people of Liverpool and finally donated to the free public museums of Liverpool by the 13th Lord Derby around 1850 (Rowley 1875, Forbes 1901).

### Taxonomic muddle

Confusion over provenance resulted in Rowley (1875: 37, pl. 9; Fig. 9) providing a new name for the Liverpool bird, *Porphyrio stanleyi*, in honour of Lord Stanley, and giving the type locality as Lord Howe Island or New Zealand. He also considered the specimen to be a probable juvenile. Based on the Vienna specimen, Pelzeln (1860: 331) was first to assign Lord Howe Gallinule to the genus *Notornis*, but thought Norfolk was the provenance, as did Latham (1790), Rowley (1875) and Rothschild (1907); all failed to note the Lord Howe provenance of the Vienna specimen recorded by White (1790). Salvin (1873) agreed



Figure 11. Liverpool specimen of *Porphyrio albus* (WML D3213), probably collected March or May 1788 on Lord Howe Island, and the type of *Porphyrio stanleyi* Rowley, 1875, which was probably re-prepared (modelled) after Keuleman's illustration (see Fig. 9) (Hein van Grouw)

with Pelzeln (1860) that Lord Howe Gallinule was more similar to New Zealand Takahe *Notornis mantelli* and therefore should be placed in *Notornis*, as shown in the accompanying illustration by J. G. Keulemans (Fig. 10). However, Salvin apparently never saw the Vienna specimen and based his attribution purely on a drawing of it provided to him by Pelzeln, stating: 'I therefore (depending, of course, upon the accuracy of the drawing sent me, which has been placed on stone by Mr. Keulemans on a slightly larger scale than the original sketch) have little hesitation in adding this species to the genus *Notornis*, thereby confirming the position pointed out for it by Herr von Pelzeln...'. Salvin's caution seems justified as, in our opinion, Pelzeln must have been biased towards Takahe when he provided the sketch.

Rowley (1875) described a number of superficial differences between the two specimens to support his assignation, stating that *P. stanleyi* of Lord Howe was morphologically similar to Purple Gallinule *P. porphyrio*, whereas *Notornis alba* of Norfolk was more akin to Takahe. Rowley probably also never saw the Vienna specimen himself and based his conclusions on the descriptions by Phillip (1789), White (1790), Pelzeln (1860, 1873) and the illustration in Salvin (1873). Here again, it seems that Pelzeln's inaccurate reproduction of the bird confused matters. Furthermore, Forbes (1901) noted that the Liverpool specimen had probably been 'remade' since the time of Bullock, and that its pose had been modelled on the plate in White (1790; Fig. 6). However, the present pose of the Liverpool bird (Fig. 11) is nothing like the illustration in White, but Rowley's plate (Fig. 9), which was also prepared



Figure 12. Lateral (top) and dorsal views of the specimen at the Naturhistorisches Museum Wien (NMW 50761), probably collected March 1788 on Lord Howe Island, the type specimen of *Porphyrio alba* (White, 1790) (A. Schumacher, © Naturhistorisches Museum Wien)

by Keulemans, is identical in pose to the Liverpool mount. So either Forbes was in error, or the specimen has been remade (again) since Forbes, based on the plate in Rowley. Sarah Stone's illustration of the Vienna bird was probably derived from the original pose of the mounted specimen, rather than the specimen being modelled on her painting; the skin is now demounted with legs outstretched (Fig. 12).

Rowley (1875) also noted that the wings were longer in the Liverpool specimen and considered that this individual, his *P. stanleyi*, was clearly volant. Remarkably, Rothschild (1907) recorded that the wings of both specimens were of the same length (nine inches), but also remarked that the wing-coverts of the two specimens differed in length, and then muddled the situation even further by stating that *stanleyi* and *alba* were both flightless. Following Forbes (1901), Rothschild (1907) assigned them to *Notornis*, but disagreed with Forbes that both specimens represented *alba*. Rothschild (1907) was of the opinion that the bird described and pictured in Phillip (1789) was *N. stanleyi* of Lord Howe Island (= Liverpool specimen), while White's bird (1790) was *N. alba* from Norfolk Island (= Vienna specimen). He distinguished them only by the difference in length of the wing-coverts, based solely on the inadequate details in the figures of Phillip (1789) and White (1790). Although Rothschild (1907) had seen the Vienna specimen personally, the reproduction of *N. alba* (Fig. 13), a third depiction by Keulemans, also seems slightly biased towards Takahe, rather than a gallinule. Furthermore, dark-coloured primaries were added to the figure and, as this was supposed to represent the Vienna bird (all white), their inclusion was borne wholly out of Rothschild's muddled imagination. Therefore, both the figures provided by Pelzeln (*in* Salvin 1873) and Rothschild (1907) were probably reconstructed to justify a relationship with *Notornis*.

If this was not already sufficiently confusing, Mathews (1928) decided that the above-mentioned painting of Lord Howe Gallinule by George Raper (Fig. 4) was sufficiently distinct from *Porphyrio albus* that another name should be applied to it, describing *Porphyrio*



Figure 13. Illustration of a Takahe-like Lord Howe Gallinule *Notornis alba* in Rothschild (1907) by J. G. Keulemans, based on how Rothschild thought the species would have appeared in life; although it is based on the Vienna specimen, artistic license permitted Rothschild / Keulemans to erroneously picture the bird with coloured primaries (Hein van Grouw, Natural History Museum, Tring)

*raperi* in recognition of the artist. His grounds were extremely dubious to say the least and, subsequently, when Mathews (1936) had reproduced the Raper painting (Fig. 14) and compared it to the Vienna skin, he admitted his error and synonymised *P. raperi* under *P. albus*.

Some authors questioned the validity of the white gallinule skins altogether. Temminck (1820), Gray (1844) and Mayr (1941) considered *N. alba* to be an albino of New Zealand Purple Swamphen *P. melanocephalus*, as did Rowley (1875) with respect to his *P. stauleyi*, despite describing it as a new species in the same publication! Buller (1888), Sharpe (1894) and Hindwood (1932) all synonymised *P. stauleyi* under *P. melanocephalus* and also considered it to be an albino. The Norfolk Island provenance was finally and correctly refuted by Iredale (1910), who provided plausible evidence to suggest that a white gallinule had not occurred on any island in recent times, other than on Lord Howe. It is almost certain therefore that *P. albus* was endemic to Lord Howe and historical records of its occurrence on Norfolk Island are in error.

### Records of Purple Gallinule on Norfolk and Lord Howe

The eastern subspecies of Purple Gallinule *P. p. melanocephalus* has been noted as a straggler to Lord Howe Island for at least 130 years, but has become established as a breeder only



Figure 14. Reconstruction of Raper's painting 1790 in Mathews (1936) (Hein van Grouw, Natural History Museum, Tring)

since 1987 (Ripley 1977, Hutton 1990). Also on Norfolk Island, the species is probably self-introduced and has been recorded since the earliest European occupation (Christian 2005). In early 1900 it was not uncommon and recorded as breeding (Bassett-Hull 1909), but since the 1990s the number of breeding birds has increased dramatically (Christian 2005).

As *P. p. melanotus* was prone to white feathering, Mayr (1941) considered Lord Howe Gallinule nothing more than a 'partially-albinistic' population of the widespread Purple Gallinule; the survival of blue individuals was due to them being less conspicuous, following the disappearance of the original population of white birds. That Mayr was incorrect is demonstrated by our reconstruction of normal-coloured Lord Howe Gallinule, which was nothing like *P. p. melanotus* or any other *Porphyrio* subspecies. Hindwood (1940) considered that the island population was white but that occasional blue birds arrived from Australia and interbred with *P. albus*, but this was due to a misunderstanding of the cause of blue and white coloration in the resident *P. albus* population (see below). Furthermore, the distinct mtDNA, morphology and behaviour of *P. albus* strongly suggests that Lord

Howe birds no longer hybridised with *P. p. melanotus*. Taylor & van Perlo (1998), following Hindwood (1940) and Hutton (1991), also considered the blue-and-white birds to be hybrids of Lord Howe Gallinule with Purple Gallinule, rather than pure Purple Gallinules with aberrant white feathers, which was also not true (see below). Whether the odd white-feathered *P. p. melanotus* visited Lord Howe Island in the past is unknown, but it appears that, since establishing as a breeder, only normal-coloured *P. p. melanotus* has occurred on Lord Howe (Hutton 1991).

### Inadequate knowledge of colour aberrations

As Lord Howe Gallinule exhibited white plumage, at least in adults, it was considered by several authorities to represent an aberration of an existing species. Aberrant white feathering is a rather common phenomenon in wild birds, but knowledge of colour aberrations and inheritance was poorly known until recently. For example, the term 'albino' was, and still is, widely used for many different colour aberrations. The aberration albino is far less common than previously thought, and aberrant white plumage is rarely caused by albinism. In general, it is a result of either a form of inheritable leucism or a phenomenon termed progressive greying (see van Grouw 2012, 2013). In both leucism and progressive greying, white feathers are produced by the absence of melanin pigment-producing cells (van Grouw 2014). In leucism the absence of melanin cells is congenital and inheritable, therefore the white pattern is already present in juvenile plumage and the amount of white feathering does not change with age. In progressive greying, however, loss of pigment-producing cells results in age-related white feathering, so juvenile plumage is always normal-coloured (van Grouw 2013, 2014). Furthermore, the loss of pigment cells appears to be progressive; the bird will gain an increasing number of white feathers following every moult, and in many birds the entire plumage eventually becomes white.

Different forms of progressive greying appear to exist, but the causes of most of these are unknown. Some are clearly inheritable and based on a single mutation. Other forms, however, do not seem to be directly related to inheritance and may be entirely age-related, while in others the progressive loss of pigment cells can be a result of (heritable) disorders such as vitiligo (pigment disease) or related to environment (van Grouw 2012, 2013).

The handwritten notes on the painting in Thomas Watling's collection (Fig. 7) that state 'young were all black, turning bluish grey, then pure white with maturity', are probably based on observations of live birds by the artist or first-hand information. This observation demonstrates that the adult white plumage in Lord Howe Gallinule is caused by a form of progressive greying. Furthermore, as all adult Lord Howe Gallinules exhibited white feathers to a certain degree, we can safely assume that in this case the progressive greying was a heritable form.

Progressive greying is the most common cause of white feathers in birds. It has been recorded in many different species including several Rallidae, e.g. Common Coot *Fulica atra*, Common Moorhen *Gallinula chloropus*, Weka *Gallirallus australis* and Corn Crake *Crex crex* (Figs. 15–18). In some of these taxa it occurs frequently, especially Common Coot, and in Australian / New Zealand *P. p. melanotus* it is, or at least was, also fairly common (Buller 1888, 1905, Mayr 1941, Austin 1955). Buller (1888) mentioned several *melanotus* specimens in his own collection (Fig. 19) and others in the Colonial Museum (now Te Papa Museum, Wellington). More recent examples are also available at Te Papa and in other collections in both New Zealand and Australia. Although Buller incorrectly described them as 'albino' and 'partial albino', the aberrant white feathers of these all-white and variegated birds were all the result of different stages of progressive greying. Buller (1905) subsequently mentioned a few more (partly) white specimens, and also specifically quoted Mr Robert Wilson, who



Figure 15. Two specimens of Weka *Gallirallus australis* showing different stages of progressive greying; top: NHMUK 2004.15.419 (in the final stage of progressive greying), below: NHMUK 1939.12.9.3710 (Harry Taylor, © Natural History Museum, London)

wrote to him from Rangitikei: 'I obtained two specimens of Pukeko [Swamphen] which are partial albinos, but the pure white one I had seen I was not able to get, though he was seen again'.

### Morphological comparison of *P. albus* with subspecies of *P. porphyrio*

Our data show that wing chord and tail lengths of the Vienna *Porphyrio albus* are the shortest, whereas the Liverpool *P. albus* has a similar wing and tarsus length to Philippine *P. p. pulverulentus* and African *P. p. madagascariensis*, which have the shortest wings and tarsi of all subspecies examined (Table 1). However, the Philippine and African subspecies are also the smallest subspecies, so proportionately their wings and tarsi are longer than in *P. albus*,

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Figure 16. Two specimens of Common Moorhen *Gallinula chloropus* showing different stages of progressive greying; left: NHMUK 1996.41.2095, right: NHMUK 1996.41.2359 (Harry Taylor, © Natural History Museum, London)

Figure 17. Two specimens of Corn Crake *Crex crex* showing different stages of progressive greying; top: NHMUK 1939.12.9.3702, below: NHMUK 2004.15.413 (in final stage of progressive greying (Harry Taylor, © Natural History Museum, London)



Figure 18. Two Common Coots *Fulica atra* showing different stages of progressive greying; top: Tolkamer, the Netherlands, 29 June 2006 (© Harvey van Diek), below (in final stage of progressive Greying): Capelle aan den IJssel, the Netherlands, 28 March 2004 (© Chris van Rijswijk)

Figure 19. Pl. 31 in Buller (1888); full image (left) and inset (right) of New Zealand Swamphean *P. p. melanotus* with progressive greying based on a specimen in Buller's collection (Hein van Grouw, Natural History Museum, Tring)



TABLE 1

Measurements of *Porphyrio* specimens used in our analysis. Unless stated, all specimens are held at the Natural History Museum, Tring. All measurements were made using dial callipers (to the nearest 0.1 mm) and a 300-mm rule (to the nearest 1.0 mm). Measurements of wing chord (bend of 'wrist' to primary tip) were obtained from the flattened wing. Tarsus was measured from the top of the tarsi at the junction with the tibia (heel joint) to the joint of tarsi with the first phalanx of the middle toe. Tail was measured from the skin at the base of the tail to the tip of the two central rectrices.

<i>Porphyrio p. porphyrio</i> (Europe)					<i>Porphyrio p. melanotus</i> (New Zealand)				
Specimen	Wing	Tarsus	Tail	Middle toe	Specimen	Wing	Tarsus	Tail	Middle toe
♂ 1891.8.1.40	260	99.9	88	99.9	♀ 1889.11.1.285	266	93	95	84.5
Ad. 1905.6.28.1010	263	104.8	95	104.8	♀ 1926.10.10.8	272	91.2	100	85.2
Ad. 1934.1.1.2049	259	102.8	94	102.9	♂ 1849.12.12.7	258	88.2	85	84
Ad. 1851.4.29.2	256	100	94	100.9	♂ 1889.11.1.287	285	100.1	96	95
Mean	259.5	101.9	92.8	102.1	Mean	270.3	93.1	94	87.2
<i>Porphyrio p. madagascariensis</i> (Africa)					<i>Porphyrio p. melanotus</i> (Norfolk Island)				
Specimen	Wing	Tarsus	Tail	Middle toe	Specimen	Wing	Tarsus	Tail	Middle toe
♀ 1904.10.23.76	234	88.8	79	88.8	Ad. WML 11950	254	91.4	91	80.5
♀ 1935.10.16.107	234	87.9	86	88.2	Ad. WML 16090	270	99.9	95	93.7
♂ 1940.4.7.96	241	87.8	93	88.8	Mean	262	95.7	93	87.1
♂ 1955.6.N.1736	242	89	89	91					
Mean	237.8	88.4	86.8	89.2	<i>Porphyrio p. pulverulentus</i> (Philippines)				
<i>Porphyrio p. poliocephalus</i> (India)					Specimen	Wing	Tarsus	Tail	Middle toe
Specimen	Wing	Tarsus	Tail	Middle toe	Ad. RMNH 99515	235	85	80	88
♀ 1889.11.3.187	252	87.2	93	89	Ad. 1896.6.6.1255	234	88	80	82.6
♀ 1938.7.15.1396	237	92.3	81.3	92.6	Ad. 1842.2.15.140	241	87	-	88.9
♂ 1889.11.1.256	237	90	92	89.5	Ad. 1881.5.1.5677	233	85	-	86.3
♂ 1881.12.29.31	258	94	102	96.8	Mean	235.8	86.3	80	86.5
Mean	246	90.9	92.1	92	<i>Porphyrio albus</i> (Lord Howe Gallinule)				
<i>Porphyrio p. melanotus</i> (Australia)					Specimen	Wing	Tarsus	Tail	Middle toe
Specimen	Wing	Tarsus	Tail	Middle toe	NMW 50.761	218	86	73.3	77.7
Ad. 1887.5.2.66	263	95.6	97	89	WML D3213	235	88.4	-	66.5
♀ 1969.4.4.8	243	87.1	98	80	Mean	226.5	87.2	73.3	72.1
♂ 1969.4.4.9	275	97.2	96	93.3					
♂ 1898.5.17.179	274	105.5	99	97.6					
Mean	263.8	96.4	97.5	90					

and their wing load (relation between wing area and body mass, in g / cm<sup>2</sup>) is lower. Lord Howe Gallinule was comparable in size to *P. p. melanotus* (Phillip 1789; pers. obs. based on specimens), up to 50 cm in total length, which, together with nominate *P. p. porphyrio*, is one of the largest subspecies (Taylor & van Perlo 1998). Therefore, the wings of *P. p. melanotus* are proportionately longest (Table 1), as they are large and heavy birds, whereas the longest tarsus is exhibited in *P. p. porphyrio*. Although we do not know its body weight, as *P. albus* was such a large bird, its wing load was probably the highest of all. To support relationships between populations, morphological ratios, e.g. wing-tail index, tarsus-toe index and/or wing-tarsus index can be compared between taxa (see Table 2). However, as there was such a significant difference in body mass between *P. albus* and many *P. porphyrio* subspecies, this tool appears unreliable for our dataset. For example, both the wing-tail index and tarsus-toe index are smallest in *P. albus*, suggesting that Lord Howe Gallinule was not only absolutely but also relatively the smallest representative of all populations, but this is incorrect.

TABLE 2

WTI: wing-tail index (ratio wing / tail lengths); TarsI: tarsus-toe index (ratio tarsus / toe lengths); WTarsI: wing-tarsus index (ratio wing / tarsus lengths). For specimen details, see Table 1.

Subspecies	WTI
<i>P. albus</i>	32.4
<i>P. p. pulverulentus</i>	33.9
<i>P. p. melanotus</i> NZ	34.8
<i>P. p. melanotus</i> Norfolk	35.5
<i>P. p. porphyrio</i>	35.8
<i>P. p. madagascariensis</i>	36.5
<i>P. p. melanotus</i> AUS	37.0
<i>P. p. poliocephalus</i>	37.4
Subspecies	TarsI
<i>P. albus</i>	84.1
<i>P. p. pulverulentus</i>	92.7
<i>P. p. melanotus</i> AUS	93.4
<i>P. p. melanotus</i> Norfolk	97.2
<i>P. p. porphyrio</i>	100.2
<i>P. p. madagascariensis</i>	100.9
<i>P. p. melanotus</i> NZ	101.0
<i>P. p. poliocephalus</i>	101.2
Subspecies	WTarsI
<i>P. p. melanotus</i> NZ	34.4
<i>P. p. melanotus</i> Norfolk	36.5
<i>P. p. melanotus</i> AUS	36.5
<i>P. p. pulverulentus</i>	36.6
<i>P. p. poliocephalus</i>	37.0
<i>P. p. madagascariensis</i>	37.2
<i>P. albus</i>	38.5
<i>P. p. porphyrio</i>	39.3

The ratio wing/tarsus length of *P. albus*, however, is second largest, indicating a substantial proportional change towards a terrestrial lifestyle. This is also supported by the high wing load.

The most striking difference between *P. albus* and other *Porphyrio*, except *P. p. melanotus*, is the short middle toe, which is especially reduced in the Liverpool specimen. In all other *P. porphyrio* subspecies, the middle toe is the same length or even slightly longer than the tarsus, but in *P. p. melanotus*, however, the middle toe is shorter than the tarsus, just as in *P. albus*. The tail of the Vienna



Figure 20. 'Shoulders' (left and right side) of Liverpool specimen of Lord Howe Gallinule *Porphyrio albus* (WML D3213) showing a few remnant purple-blue feathers, a colour not found in the shoulder/upperparts plumage of any subspecies of Purple Swamphen *P. porphyrio* (Hein van Grouw)

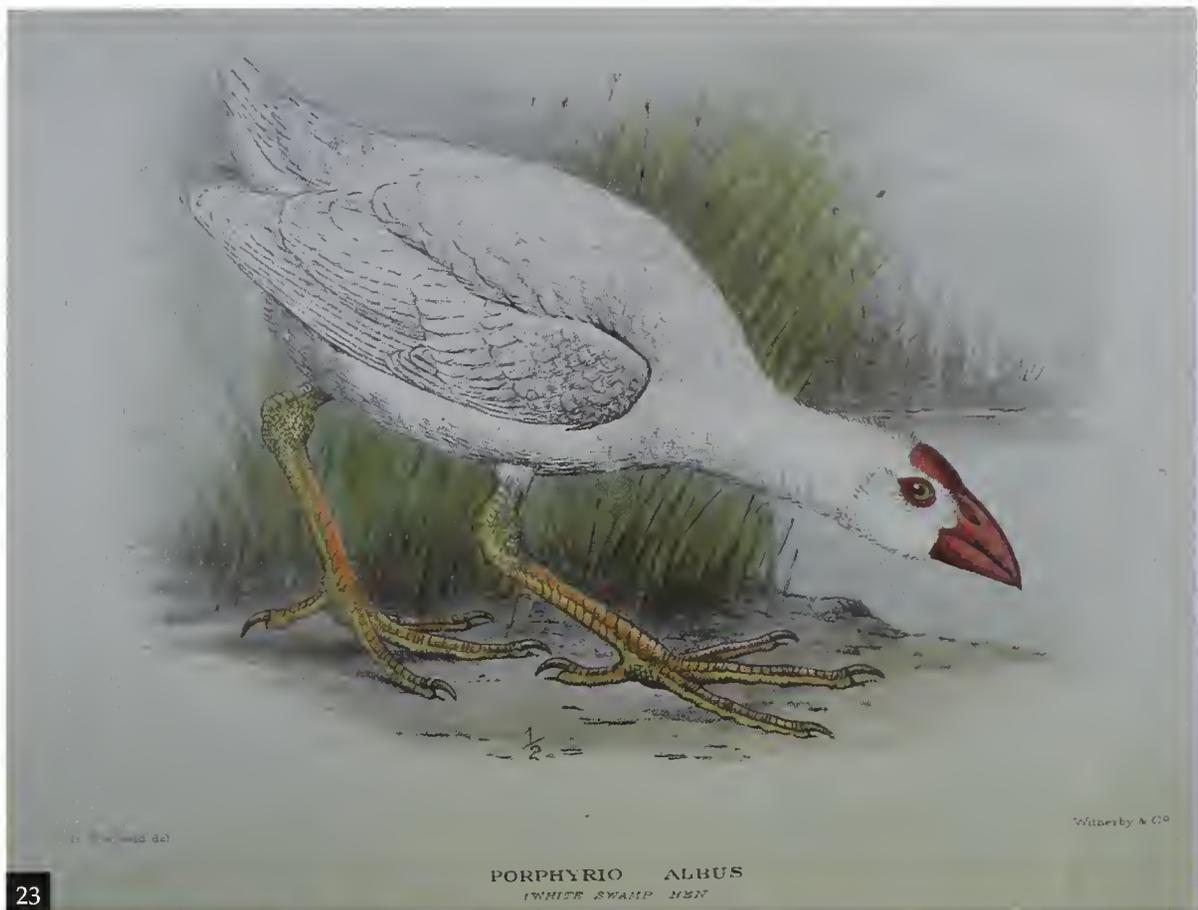


Figure 21. Reconstruction of a blue-coloured (i.e. younger) Lord Howe Gallinule *Porphyrio albus*, before it becomes white (Julian P. Hume)



Figure 22. Coloration of different subspecies of Purple Swamphen *Porphyrio porphyrio*, dorsal (above), ventral (below), from left to right: *P. p. porphyrio* (NHMUK 1905.6.28.1010), *P. p. madagascariensis* (NHMUK 1955.6.N.17.38), *P. p. poliocephalus* (NHMUK 1881.12.29.31), *P. p. pulverulentus* (NHMUK 1842.2.15.140) and *P. p. melanotus* (NHMUK 1887.5.2.66) (Harry Taylor, © Natural History Museum, London)

specimen (tail lacking in Liverpool skin) is also the shortest of all specimens examined. Further confusion has arisen from measurements of the Liverpool bill (exposed culmen) compared to the Vienna bird; e.g. Ripley (1977) and Taylor & van Perlo (1998) reported a culmen length of 63 mm and 79 mm, respectively. Rowley (1875) described the bill as badly broken, but our study has shown that the rhamphotheca has entirely disappeared in the Liverpool skin, a fact that has not been previously reported, and that the underlying bony core of the bill has been painted red, simulating an undamaged bill. This explains



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Figure 23. White Swamphen *Porphyrio albus* in Mathews (1928); for Mathews the spur was motive to remove the species to a new genus, *Kentrophorina*, as, according to him, no wing claw was present in the type of the genus *Porphyrio* (Hein van Grouw, Natural History Museum, Tring)

Figure 24. Detail of the right wing of the Vienna specimen of Lord Howe Gallinule *Porphyrio albus* showing the spur (Hans-Martin Berg, © Naturhistorisches Museum Wien)

the 16 mm difference in culmen length between the specimens; consequently, only the bill measurement of the Vienna bird is reliable.

In coloration, the Vienna skin is pure white, whereas the Liverpool skin has individual blackish-blue feathers on the head and neck, blue feathers on the breast and a few purple-blue feathers on the back and shoulders (Fig. 20). From the distribution of the coloured feathers, we were able to reconstruct the natural purple-blue coloration of this extinct species (Fig. 21). It differed primarily from other *Porphyrio* (Fig. 22) in having the lores, forehead, crown, nape and hindneck blackish blue, the mantle, back and wings purple-blue, rump and uppertail-coverts darker, and underparts all dark greyish blue.

A wing claw or spur was used as a discernible taxonomic character in *P. albus* by White (1790), Rowley (1875), Forbes (1901) and Mathews (1928). It is remarkable, however, that of all of the depictions of *P. albus* based on the Vienna specimen, only those in White and Mathews (Figs. 6, 23) show the spur. Mathews (1928) considered the spur sufficiently diagnostic to place *alba* in a new genus, *Kentrophorina*, as no wing claw is evident in the type of the genus *Porphyrio*. We compared the wing claw of *P. albus* with *P. porphyrio* subspecies, and noted that the claw is longest and most distinct in the Vienna *P. albus* specimen (Fig. 24), but extremely variable in all material examined. In some it is small and pointed, in others longer and less sharp, and in a few completely absent. In the Liverpool *P. albus*, it is sharp but buried below the wing feathers (Rowley 1875). Therefore, the variability of the claw is such that it cannot be used as a reliable taxonomic character.

We conclude that both extant specimens of Lord Howe Gallinule exhibited reduced wing length with correspondingly more robust legs and short toes, all characteristics of an increasingly terrestrial mode of life, and in the process of becoming flightless. Although wing and tarsus length differ slightly between the specimens, and the Vienna bird possesses larger wing spurs, both are *Porphyrio albus*. The Liverpool specimen is also a younger bird than that of Vienna, of which the latter had become entirely white, having completely passed through the progressive loss of pigment cells to final moult.

## Discussion

Recent DNA work suggests that the Vienna specimen of *P. albus* is a distinct taxon (Garcia-R. & Trewick 2015). Morphometrics further demonstrate that Lord Howe Gallinule had evolved into a terrestrial species and support the hypothesis that it was distinct from *P. porphyrio*. According to Garcia-R. & Trewick (2015), however, Lord Howe Gallinule may have been most closely related to the Philippine subspecies (*P. p. pulverulentus*) but as many clades in their phylogeny, including those containing *P. albus*, show weak statistical support, this result may change significantly should a more complete dataset become available. Furthermore, this relationship is not supported by morphometrics or by coloration (this paper). The short middle toe of the Australian / New Zealand bird and tendency to white feathering are shared with *P. albus*, although the former was clearly volant. Garcia-R. & Trewick (2015) suggested that *P. albus* arose from a small number of migrants of *P. p. pulverulentus* during the late Pleistocene (c.500 MYA), but expressed some caution in drawing this conclusion, as dispersal from the Philippines required dispersal beyond other islands en route.

Wing length of Lord Howe Gallinule suggests it was probably capable of flight, but may have become behaviourally flightless; a characteristic observed in some other island endemics, notably parrots (Hume 2007, Hume & Winters 2015). Tarsus length in *P. albus* is much more reduced and this characteristic, along with the short toes, is also indicative of a terrestrial lifestyle or flightlessness (Livezey 2003). In coloration, Lord Howe Gallinule was a variable population comprising all-white and variable white-and-blue individuals, all indicative of birds exhibiting progressive greying (Hume & van Grouw 2014). The large number of white individuals was presumably due to an inheritable form of the condition (Hume & van Grouw 2014), probably linked to a small founding population. Based on a middle toe that is shorter than the tarsus, close proximity geographically, the fact that progressive greying is not uncommon in *P. p. melanotus*, and that Lord Howe and Norfolk have both been naturally re-colonised by this subspecies, we suggest it is more likely that *P. albus* derived from Australian / New Zealand *P. p. melanotus*, rather than Philippine *P. p. pulverulentus*.

Garcia-R. & Trewick (2015) were unable to retrieve amplifiable DNA from the Liverpool specimen, but our data suggest that it also originated on Lord Howe Island. The distribution of blackish-blue feathers on the head and neck and purple-blue feathers on the upperparts of the Liverpool specimen enabled us to reconstruct the purple-blue plumage variant of *P. albus*, which demonstrates that this coloration was unique in *Porphyrio* (Fig. 21). The Liverpool specimen was also a younger bird than that of Vienna (see above).

It appears that the wealth of illustrative and documentary evidence made available to 18th- and 19th-century scientists, some of it riddled with errors, clearly muddled the provenance of Lord Howe Gallinule. However, our data show that the Liverpool specimen was collected on Lord Howe along with the Vienna bird between March and May 1788, and that the former differs from the Vienna specimen in being younger in age and preserving some of the original purple-blue coloration.

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Address: Bird Group, Dept. of Life Sciences, Natural History Museum, Akeman Street, Tring, Herts. HP23 6AP, UK, e-mails: h.van.grouw@nhm.ac.uk, j.hume@nhm.ac.uk

# Breeding biology and natural history notes for White-collared Swift *Streptoprocne zonaris* in Costa Rica

by Manuel Marín

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**SUMMARY.**—The breeding biology of White-collared Swift *Streptoprocne zonaris* was studied in Costa Rica. Eggs were laid between mid April and mid May, and fledging occurred between late June and mid July. There are three clear nesting patterns for this wide-ranging species, which can be termed 'northern', 'central' and 'southern', all associated with the onset of the rainy season. My study was consistent with the breeding pattern elsewhere in the Northern Hemisphere. All nests were placed in sites with high humidity and were from 10 cm to 30 m or more above ground or water level. Nests were reused in subsequent seasons, and one nest was in use for at least 13 years. All observed clutches had two eggs and mean egg mass was 9.9 g. Egg ( $n = 23$ ) were dull white and sub-elliptical (39%), long sub-elliptical (35%), short sub-elliptical (17%) or short oval (8%) in shape. Incubation period was 26 (25–27) days. Mean hatching mass was 8.8 g, and max. mass was reached at age 33 days (127% of adult size), thereafter it declined slightly. Fledging occurred at 47 (43–51) days. The growth constant  $k = 0.225$  and  $T_{(10-90)}$  period was 19.5 days. Most mortality occurred at the egg stage or in the early days of a nestling's life. The major cause of nest failure was weather-related: flooding and starvation, but egg infertility and predation also occurred. Adult primary feather moult started in tandem with egg laying and lasted 6–7 months.

White-collared Swift *Streptoprocne zonaris* is the most widespread New World swift, ranging from Mexico (Guerrero in the west and Tamaulipas in the east), south through Middle America, and east to the Greater Antilles, as well as over much of South America, while the species is also a vagrant to the southern USA (AOU 1998).

Despite this broad distribution, almost nothing is known about the species' breeding biology, mainly because access to nest sites is often difficult, and it has a prolonged breeding cycle. Consequently, most of what is known about the species concerns its distribution and breeding sites; for a summary, see Marín & Stiles (1992). Passeggi (2011) recently published information concerning breeding phenology and incubation from a site in north-west Argentina and Biancalana (2014) reported breeding data from south-east Brazil, both near the southern end of its breeding distribution at 23–24°S. Here I present new information on breeding phenology, nest sites, nests, eggs, incubation, growth, development, moult, mortality, etc.

## Study area and Methods

The data reported here were gathered in Costa Rica, mostly in the gorge of the Tiribí River, San José province, at 09°57'N, 83°55'S, between 1,880 m and 2,100 m (see Marín & Stiles 1992 for details). In June–August 1995 and May–August 1996 and 1997, visits were made at 1–5-day intervals to nest sites, while some data from visits in 1984–86 are also included and, when relevant, data from other sites and other countries are also integrated.

I assessed nestling body mass to 0.1 g using an AVINET spring balance of 10, 30, 50, 100 and 300-g graduations depending on nestling age. I measured wing length (flattened)

and tail length to 0.5 mm using a metal wing rule with a perpendicular stop at zero. Tarsus length and exposed culmen were measured to the nearest 0.1 mm using dial callipers, following Baldwin *et al.* (1931) and Marín & Stiles (1992). Nestlings were measured only in the morning, between 08.00 and 11.00 h. Egg dimensions and mass were measured in the field to the nearest 0.1 mm using dial callipers. Egg-shape assessments are based on Preston (*in* Palmer 1962). The duration of 10–90% of body mass growth or  $T_{(10-90)}$  period (Case 1978) and the growth rate constant  $K$  (Ricklefs 1976) were determined. Body masses and measurements of adult birds banded in the area were supplemented with data from museum specimens from the same geographic area (see Acknowledgements). Swifts possess ten primaries and their moult is bilaterally symmetrical, with the sequence from the innermost to the outermost primary feather. To assess moulting season, I assigned a numerical value or moult score of 0–1 for each feather, a fresh feather would have a score of 1, while a half-grown one would score 0.5, and a bird with all ten primaries replaced will score 10, these values based on % grown, following Stiles & Wolf (1974) and Marín & Stiles (1992). I used data from mist-netted birds at the study site as well as museum specimens (see above) from the general area to obtain moult scores. During incubation, nest attendance was measured using a temperature data-logger that operated between  $-5^{\circ}\text{C}$  to  $+37^{\circ}\text{C}$  (Stow Away XTI-8K, ONSSET Computer Corporation, Pocasset, MA). An external sensor was attached to three nests, next to or below the eggs to record temperature at five-minute intervals. The number of days of useful data from each nest varied at 7–12 days, because adult activity occasionally dislodged sensors from the nests.

## Results and Discussion

**Breeding phenology.**—Egg laying in the Greater Antilles (Cuba and Dominican Republic) occurs in April and May (Bond 1980, 1984, Stockton de Dod 1981, Montes Espin & Garcia Rivera 2010). In southern Mexico egg laying is also from mid April to May (Rowley & Orr 1965, Whitacre 1989; West. Found. Vert. Zool. egg data cards). In Ecuador egg laying starts in December–January (Marín & Carrion 1994; MM unpubl.), i.e. 5–6 months earlier than more northerly populations. My limited Ecuadorian data on breeding, including inferences from moult patterns (see below), suggest that populations east and west of the Andes possess a similar breeding phenology. At the southern end of the species' breeding range, in north-west Argentina (Tucumán and Córdoba) and in south-east Brazil, the onset of the breeding season is mid October to late November, 2–3 months earlier than populations near the equator (de la Peña 2005, Passeggi 2011, Biancalana 2014; MM unpubl.). At the main study site in Costa Rica the onset of egg laying occurred between mid April and mid May, with 69% of eggs ( $n = 36$ ) being laid by late April, following the northern breeding pattern. The nesting pattern in the Northern Hemisphere is similar among all of the areas for which I have data—southern Mexico, Greater Antilles and Central America (see above). There are three clearly different timings of breeding throughout the species' range: northern, central and southern. The fledgling period in Costa Rica occurred between late June and mid July, and once the nestlings left the nest they did not return to the area, even to roost. Banded nestlings were never recaptured. In contrast, in the slightly larger Biscutate Swift *Streptoprocne biscutata*, Pichorim (2002) reported that fledglings stayed around the cave for a few days before fully departing. This difference might reflect the nature of the study site itself, Pichorim's was a large cave that might act as a roosting site as well, while in the present study the nests were scattered in small cavities (see below) and if the birds roosted in a nearby area they went unnoticed.

**Nest.**—All nests found were closely associated with water and in sites with high humidity (never <95%) on caves or ledges behind or beside waterfalls. The caves may be

mere niches or holes no more than 50 cm deep, although some were in narrow caves 2–3 m deep, but no more than 1 m wide. These caves were formed naturally by large boulders along the river. Isolated nests were found, but also up to three nests within a single cavity. Along the river in one linear area of c.10 m up to nine nests were found. Most aggregations and colonies at the study site and elsewhere in the species' range are small in contrast to some of the large colonies of several thousand birds described in Mexico (Whitacre 1989, 1991). In Costa Rica, many of the caves and waterfalls that host large numbers of birds are mainly roosting sites, although some of them might also harbour nests. As far as is known, all of the large colonies in Mexico are occupied year-round as both roost and nest sites (D. F. Whitacre *in litt.* 2016).

Nests were located 10 cm to 30 m above ground or water level. Most were placed on level horizontal surfaces and were in total darkness. Three exceptions were: (1) four nests sited in a deep ravine on a small ledge c.3 m above the water level and 4 m from a waterfall; (2) two nests in a small cavity behind a large waterfall; and (3) one nest on a narrow shelf c.1 m above water level. However, the first four nests were in a semi-dark area of the ravine that was completely covered by tall vegetation forming a 'tunnel', and the nests received a constant fine spray from the waterfall. Only the second exception, behind the large waterfall, might have received some direct light during several hours of each day. All nests found were a saucer-shaped platform, constructed of mud, roots with some mosses, and were constantly moist. Depending on substrate, the amount of material placed on the base of the nest varied. One nest (of 13) in 1984–86 and one nest (of 36) in 1995–97 had no material, with the eggs being placed directly in small, sandy, narrow depressions, c.1–2 m above water level. In southern Mexico, Whitacre (1989) also found nests without materials, but in larger numbers. Absence of nest material has not yet been reported anywhere in South America for any *Streptoprocne* spp., e.g., Andrade *et al.* (1985), Pichorim (2002), Passeggi (2011) and Biancalana (2014).

I was unable to measure the duration of nest construction. However, during the early part of the nestling period, the adults sometimes added additional material, usually dry mosses and sometimes leaves, to the centre of the nest, when nestlings were hatching, presumably to keep the recently hatched young drier.

Most nests studied in 1995–97 were c.500–1,000 m higher along the river than the main study area of 1984–86. Nevertheless, four nests that were used 1984–86 were still active during the seasons of 1995–97. Although it is unknown if they were used by the same birds, this might have been the case. F. G. Stiles and I, during our previous work in the area in 1984–86, banded a pair of adults on 29 April 1986 at a cave in which later the same year they nested. On 12 July 1995, at the same site, I recaptured one of the birds banded there in 1986 (G-93, re-banded B-21). The band was worn on one side but readable. The same bird was recaptured in 1996 and 1997 at the same site, and in May 1996 the G-93 band was gone, but B-21 was in good shape, indicating that plastic bands last c.10 years. Thus the same birds can use the same nest for at least 13 years, providing an indication of their longevity. All members of this subfamily are suspected to be very long-lived species. For example, for Black Swift *Cypseloides niger* Lowther & Collins (2002) reported max. age as 16 years and one month, and for the same species Marín (1997) reported re-use of the same nest for >21 years, although it was not certain if the same birds were involved.

**Eggs and incubation.**—All clutches observed were of two eggs, as in other colonies of White-collared and the larger White-naped Swift *Streptoprocne semicollaris*, with the exception that Biancalana (2014) found a nest with three nestlings of *S. zonaris* in south-east Brazil. In the intermediate-sized Biscutate Swift, nests with 3–4 eggs have been recorded (Andrade *et al.* 1985, Pichorim 2002), but all of those cases of nests with more than two

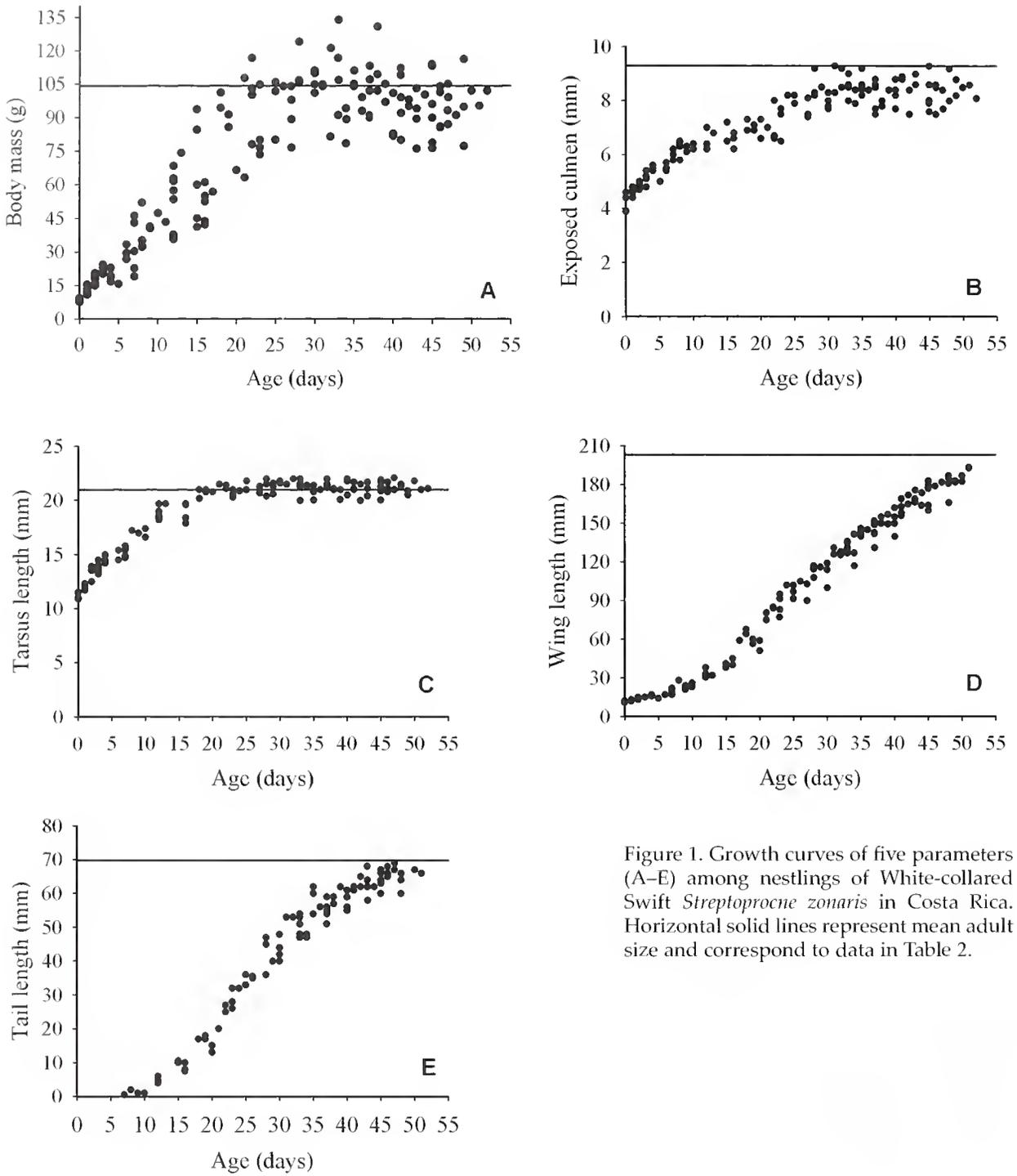


Figure 1. Growth curves of five parameters (A–E) among nestlings of White-collared Swift *Streptoprocne zonaris* in Costa Rica. Horizontal solid lines represent mean adult size and correspond to data in Table 2.

eggs might reflect intraspecific parasitism, as clutch size appears to be naturally two eggs and because the birds in those cases were nesting in a more congested space. The issue warrants genetic study of nests containing more than two nestlings, to prove or disprove this hypothesis.

Eggs were dull white but become dirty (due to mud) as incubation proceeds. Mean fresh egg mass was 9.85 g (9.4% of adult mass) and egg shapes were sub-elliptical (39%), long sub-elliptical (35%), short sub-elliptical (17%) and short oval (8%) ( $n = 23$ ). For egg measurements and mass, see Table 1. I was only able to determine the precise incubation period at three nests, and the mean was 26 days (25–27 days). Previously, Marín & Stiles (1992), in a comparative study of several Cypseloidine species, estimated the incubation

period at *c.*30–35 days, in the absence of actual data. This was based on body and egg size relative to the smaller species (i.e., larger species, larger egg, thus longer incubation period). However, Marín & Stiles (1992) were incorrect in this assumption. In this respect, among the Cypseloidine swifts there appears to be some emerging trends. More tropical species have a longer incubation period than more temperate representatives. For example, in the tropical population of *S. zonaris* (present work) the incubation period was 26 days, vs. 22 days for a subtropical population in Argentina (Passeggi 2011). In a one-egg species, Black Swift has both tropical and temperate populations with the same trend, 29 vs. 24 days (Marín 1999). Secondly, two-egg species (*Streptoprocne*) have a relatively shorter incubation period than one-egg species (*Cypseloides*). For example, two similar-sized species lay two- and one-egg clutches respectively, Chestnut-collared Swift *Streptoprocne rutila* (25 days) and Spot-fronted Swift *Cypseloides cherriei* (29 days: Marín 2008).

For the subtropical population of Biscutate Swift, a two-egg species that is only marginally larger than White-collared, Pichorim (2002) found that the mean incubation period was 24 (22–28) days, i.e. well within the range for two-egg species. Biscutate Swift also has more tropical populations and it would be most interesting to discover their incubation period and to see if it follows the same trend.

The incubation pattern observed for White-collared Swift using the data from the temperature data-loggers indicated an irregular schedule. Data from three nests and 26 days of useful data indicated that the adults incubated a mean 65% of daylight hours. The birds left the eggs uncovered for long periods of time, with a gap sometimes of several hours (1–8 hours) in the morning and a short gap of 45–60 minutes during late afternoon. However, on some occasions they incubated nearly the entire day. This pattern was also observed in the smaller Chestnut-collared Swift in the same study area (Marín 2008).

**Nestling development.**—I followed the development of 33 nestlings, but I was only able to obtain full data from hatching (day zero) to fledging for five nestlings. Partial data (2–9 data points) were gathered for 28 nestlings of known age (Fig. 1A–E). The species had a high mortality rate during the early stages (see below), making it difficult to gather complete datasets.

Soon after hatching, eggshell remains were not removed by the adults but remained in the nests or beside them, until they were dissolved by the high humidity at the site. On hatching nestlings were naked, with eyes closed, skin was pink-flesh, with the skin between the culmen and forehead bright pink, while the distal part of the culmen was blackish with a well-defined egg tooth. Feather papillae were barely visible as subcutaneous dashes. The feet were pinkish and claws greyish tipped black; at hatching they were 45.4 % of adult size.

TABLE 1  
Dimensions and mass of White-collared Swift *Streptoprocne zonaris* eggs (*n* = 23) at the study site in Costa Rica.

Feature	Mean	SD	SE	Range
Length (mm)	34.9	1.59	0.33	32.4–38.6
Width (mm)	23.3	0.49	0.10	22.2–24.3
Mass <sup>a</sup> (g)	9.9	0.95	0.30	8.6–11.5

<sup>a</sup> Mass from fresh eggs; sample size *n* = 10.

TABLE 2  
Measurements of adult White-collared Swifts *Streptoprocne zonaris* at the study site in Costa Rica.

Feature	Mean	SD	SE	Range	n
Mass (g)	104.8	7.6	0.7	87–129	109
Exposed culmen (mm)	9.3	0.4	0.03	8.5–10.4	99
Tarsus length (mm)	21.1	0.9	0.1	19.0–23.2	96
Wing length (mm)	203.4	6.3	0.6	186–218	104
Tail length (mm)	69.9	6.1	0.6	48–85	100
Wingspan (mm)	515.2	11.1	1.4	487–541	58
Tail fork (mm)	12.6	5.8	0.7	0–29	62



Figure 2. A potential additional predator of young swifts, a crab in the family Pseudothelphusidae, which was observed on 4 June 1996 carrying a moribund nestling from a nest placed near water level (Manuel Marín)

On hatching (day zero) nestlings had a mean mass of 8.75 g ( $n = 6$ ; range 7.7–9.4 g, or 8.3% of adult size; for adult size see Table 2). Body mass increased fast, healthy nestlings reached adult mass by days 21–22 (Fig. 1A). On average, max. body mass reached by nestlings was 110.9 g (105.9% adult size) by 33 days. The max. body mass reached by any nestling was 133.7 g, or 127.6% of adult mass, at age 33 days. The growth constant was  $k = 0.225$  and  $T_{(10-90)}$  period was 19.5 days. During the  $T_{(10-90)}$  period the fastest-growing birds increased mass at a rate of 4.1 g per day, or 3.19% of adult mass per day. Within the Cypseloidine, the growth trend is that the largest species are fastest and the smallest are slowest, in direct contrast to most avian groups (Gill 1990, Marín & Stiles 1992, Marín 1997, 1999).

On hatching the exposed culmen was 4.3 mm (41.1% of adult size) and reached adult size at age 31–32 days (Fig. 1B). Tarsus length at hatching was 11.22 mm (51.25% adult size), being the most advanced feature on hatching, and acquired adult size by 20–21 days (Fig. 1C). On hatching wing length was 11.5 mm (5.6% adult size) and reached adult size post-fledging. The max. wing length of any nestling was 193.5 mm at age 51 days (95.1% adult size; Fig. 1D). The tail feathers started to emerge by days 7–8 and in some nestlings reached near-adult size at the time of fledging (Fig. 1E). Semi-plumes began to appear by age 7–8 days and by 11–12 days the greyish semi-plumes covered the entire body, except the face, chin, belly and distal part of the wing. At age 23–27 days body feathers began to replace the semi-plumes. From 27–28 days the collar was well defined, and feathers on the forehead, breast and lower belly (not undertail-coverts) were very finely white-edged, with some variation, as several birds ready to fledge had broad white-edged feathers on the lower belly, but most had finely white-fringed feathers. Primaries, secondaries and rectrices become broadly white-tipped and very finely white-edged. Eyes were fully open by days 12–13. For other growth parameters see Table 3. Nestlings departed the nest on average by age 47 (43–51) days, in broad agreement with other findings, i.e. 40–48 days in north-central

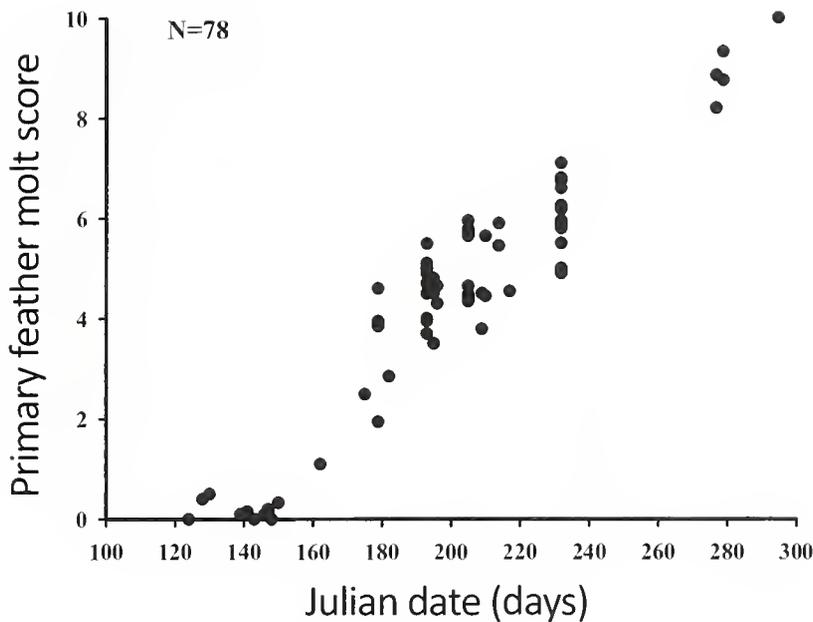


Figure 3. Primary moult score by Julian date in the central Costa Rican population of White-collared Swift *Streptoprocne zonaris*. Julian day 100 = 9 April; day 150 = 29 May; day 200 = 18 July; day 250 = 6 September; day 300 = 26 October. For determination of moult scores see Methods.

Argentina (Passeggi 2011) and 41–51 days in southern Brazil (Biancalana 2014). In terms of nestling development, there appears to be little difference between White-collared and Biscutate Swifts (Pichorim 2002).

**Mortality.**—Most mortality occurred at the egg or early nestling stage. During 1995–97 I followed the fate of 32 nests: of 64 eggs, only 49 nestlings (76.5%) hatched. Egg rolling or eggs falling from the nest was the major cause, with a total of ten eggs lost in such circumstances, two were added, two were flooded due to an increase in river water levels, and one loss was due to unknown causes. Egg rolling occurred more frequently when 2–3 nests were close together and was observed more often during the early or mid-incubation stages. It possibly is indicative of disputes for nest sites or mates. If birds lost their eggs there was never any re-nesting attempt. Of 49 nestlings that hatched, only 21 fledged (57%) and among the 28 fatalities 50% died before age five days. Overall nesting success was 32.8%. The study period (1995–97) was thus characterised by very low nesting success compared to that found in the same area during 1984–86, cf. Marín & Stiles (1992). However, most mortality was during the early stages of life and was weather-related. The 1996 season was extremely wet, with some 655 mm of rain in the area during May, whereas the 45-year mean for the same month and area is 288 mm (Instituto Meteorológico Nacional, Costa Rica, Rancho Redondo weather station). Similarly, during 1997, heavy rainfall occurred in June, >40% above average for the area. These unusually wet years produced substantial flooding, destroying many nests and probably

TABLE 3  
Major developmental events in White-collared Swift *Streptoprocne zonaris* nestlings in Costa Rica.

Event	Age (days)
Semi-plumes emerge	3–4
Semi-plumes sprouting	7–8
Full coat of semi-plumes	11–12
Eyes start to open	7–9
Egg tooth disappears	13–21
White collar defined	21–23
Pin feathers on primaries emerge	12–16
Pin feathers on primaries break sheaths	15–16
Inner primaries fully grown	34–37
All secondaries fully grown	40
Pin feathers on rectrices emerge	8–9
Pin feathers on rectrices break sheaths	11–13
Active when handled	8–9
Fledge	43–51

limited food provisioning for the young at the most critical stage or the very early stages before reaching homeothermy. This was reflected in the large mortality and starving early-stage nestlings. Seventeen nestlings were found dead, principally due to starvation and mainly during 1996. Of the 17, eight were found dead outside their nests, six were drowned due to rising water levels, and five disappeared without trace, all of them from low (10–40 cm above ground level) nests. On 4 June 1996, I found a crab (*Pseudothelphusidae*; Fig. 2) carrying a moribund nestling from one of the nests near water level, which might explain the disappearance of some or many other nestlings. On 8 and 11 July 1996, along the river I found two moribund but recently fledged young just below a large waterfall. There was an inaccessible large cave behind this waterfall, with a large but unknown number of nesting birds. On 8–9 July 1996, there were heavy rains in the area (55–60 mm during the morning) and the river was overflowing, but there was no route by which water could have entered the cave, thus it is probable that on leaving their nests, the birds miscalculated and hit the water ‘curtain’ covering the cave entrance. Whitacre (1989) found that at some Mexican colonies rolling and falling of eggs and young was the major cause of mortality.

**Primary moult.**—Swifts are highly dependent on their flight feathers and, like most bird species, must moult their primary feathers, with this replacement occurring once per year and sequentially, progressing from the innermost to outermost feather. Both wings are moulted symmetrically. Adult White-collared Swifts began to moult the inner primaries between mid April and late May (Fig. 3), coinciding with egg laying. At the study site, there was only very slight inter-year variation in primary feather moult. For example, a bird banded on 12 July 1995 had a primary moult score of 2.95, while on 14 July 1996 the same bird had a score of 3.5, and another individual on the same dates had scores of 3.7 and 3.5, respectively. I have several such examples, making it reasonable to combine the annual data. However, the different breeding populations are well synchronised, even between years. Wing moult started with the inner primaries and coincided with late incubation or hatching of the nestlings. For example, several adults captured at their nests in mid–late May had the innermost primary new in sheath, with a moult score of 0.1–0.2, and the same birds when recaptured three months later, in late August, had moult scores of 5.9–6.6. Several individuals captured in early October had scores of 8.2–9.3. A single example from late October had a score of 10, or 100%. Thus, breeders completed primary moult by late October to mid November, after *c.*6 months. However, non-breeders started their primary feather moult 1.5–2.0 months earlier, and in some cases perhaps even before thus. For example, at a site in Bijagua, northern Costa Rica, where there is a large waterfall used only as a nocturnal roost and shelter during large storms, no nest was found in either 1984–86 or 1995–97. Birds captured there between mid and late July in different years had a mean moult score of 7.75 (SD = 1.1, *n* = 20). Thus, non-breeders had finished their wing moult earlier, around August–September (*cf.* Fig. 3). For swifts in general, moult is a long process occupying 5–6 months, being similar in duration across the family in many different species, e.g., House Swift *Apus affinis* (Zhitong 1982), Chestnut-collared Swift (Marín & Stiles 1992), White-throated Swift *Aeronautes saxatilis* (Marín 2003) and several *Chaetura* spp. in central and South America (MM unpubl.). However, for future moult studies it is important to be aware that non-breeders follow a slightly different moulting schedule to breeders, *c.*1.5–2.0 months earlier.

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- Address:* Museum of Natural Science and Dept. of Biological Sciences 119 Foster Hall, Louisiana State University, Baton Rouge, LA 70803, USA, e-mail: mma95@hotmail.com. Current address: Casilla 15 Melipilla, Chile.

## A further specimen of the extinct Jamaica Petrel *Pterodroma caribbaea* (Carte, 1866)

by Bernard Zonfrillo

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**SUMMARY.**—Of the three or four extinct marine bird species in the North Atlantic, Jamaica Petrel *Pterodroma caribbaea* is arguably the least known. The number of known specimens—26—is around one third of those for Great Auk *Pinguinus impennis* and around half that of Labrador Duck *Camptorhynchus labradorius*. The petrel first became known anecdotally in the c.1780s and the first recorded specimens, collected in 1829 and the 1840s, were forwarded from Jamaica to England, but no taxonomic description was published until 1866, when Alexander Carte named the species *Pterodroma caribbaea*. However, two earlier birds sent to England were seemingly ‘lost’. No Jamaica Petrel has been seen alive since 1879. I located what is probably one of the first-ever specimens and discuss why no description of it was published.

The earliest mention of what was surely Jamaica Petrel *Pterodroma caribbaea* was by Browne (1789), a bird he referred to as the ‘Larger Dark Peterill’. Dr E. N. Bancroft (1829) subsequently suggested that, what was probably this species, be called ‘*Procellaria jamaicensis*’ without description—and therefore a *nomen nudum*. Bancroft had collected one or two skins but could find no description of a similar species in any of the books in his possession, so he sent one to the editor of the *Zoological Journal* in 1829. Bancroft, in his letter, provided some information as to how the bird was hunted on Jamaica’s highest point, Blue Mountain Peak, on 17 March 1829 by a terrier dog, and was apologetic regarding the sorry state of the specimen. He stated that the species ‘... burrows only in crevices on the tops of our highest mountains, scarcely accessible’. There is no record of where Bancroft’s specimen ended up, other than with the editor of the journal. Known specimens, all collected in the Cinchona area of Jamaica’s Blue Mountains, number 26 individuals (Imber 1991). However Gosse (1847), who never saw the species alive but thought it was probably an alcid, reported that the bird was known locally as ‘Blue Mountain Duck’. Specimens were apparently collected from Jamaica’s Blue Mountains during Gosse’s time, but Jamaica Petrel was not formally described until nearly 20 years later, by Carte (1866). Gosse (1847) and Carte (1866), quoting Richard Hill, recorded that William Thomas March knew of two individuals collected in Jamaica. The first obtained by Mr George Atkinson of Newcastle-upon-Tyne and the second by Sir Henry Barkly. Promised a description of the bird by Atkinson, Gosse (1847) noted that this never subsequently transpired. A further pair was collected by W. T. March and forwarded to Dublin, where described by Carte (1866). These specimens, syntypes, are now in the National Museum of Ireland, Dublin. The delay in publishing the description of this new species was partially due to the first two collected specimens becoming apparently ‘lost’ or untraceable, and one of the recipients, George Atkinson, dying before a description could be prepared. In Carte’s description, mention of the first specimen being sent to Atkinson, shortly before the latter’s death, suggested to me that the skin mentioned by Gosse was perhaps still extant in the Newcastle area, where Atkinson was long resident.

Most specimens (22) were obtained by Kew botanist William Nock during his time at Cinchona in Jamaica. Specimens attributed to others as 'collected' were probably those transported by couriers from Jamaica to England. None was ever taken at sea, or from any other island. Knox & Walters (1994) erroneously stated that 'only about 7 specimens were ever collected', whereas Bourne (1965) had seen nine skins and knew of six others acquired by Edward Newton and 'dispersed' to various museums around the world. Prof. A. Newton noted in a register of birds from Jamaica that William Nock had collected all 22 birds at Cinchona, in November–December 1879 (Benson 1972). Two mounted Nock specimens are at the Institute of Jamaica in Kingston (pers. obs.). They were listed by Imber (1991) within his total of 26 known specimens, 22 taken by Nock, two—the syntypes—from W. T. March and one each that came via J. Gould and J. Taylor now at the Natural History Museum, Tring (NHMUK). The latter two, not personally collected by either Gould or Taylor, being donations, perhaps came from March, or perhaps Bancroft? Knox & Walters (1994) specifically mentioned the 'extremely delicate' state of one of the NHMUK skins and that it was collected 'prior to 1875'. This may fit the terrier-chewed description by Bancroft. Presumably Sir Edward Newton also obtained his six specimens from William Nock, who clearly knew where the birds bred, having spent seven years at Cinchona, cultivating trees for medicinal purposes.

Cinchona, at c.2,000 m above sea level, is not easy to reach and its tracks and paths are frequently washed away due to heavy rainfall and hurricanes (pers. obs.). Cinchona lies north of Kingston in the parish of St. Andrew, at the head of the Green River. During the petrel's winter breeding period of November–February, strong convection up-draughts can build after nightfall, probably making this area ideal for flying or certainly fledging in an otherwise unremarkable part of the forested Blue Mountains (pers. obs.). Temperatures can be low for Jamaica at 10+°C, but ideal for rearing a down-covered chick in a burrow, where daytime temperatures usually exceed 30°C. Nearby Blue Mountain Peak, where Bancroft claimed his 1829 specimens were collected, has not been thoroughly searched. However, that name was given well before Cinchona was established as a botanical garden (in 1868) and the Cinchona area may have been the epicentre of the petrel colony on that ridge, Bancroft using Blue Mountain Peak as the closest named geographical feature.

Despite several searches on land in Jamaica over the decades (Scott 1891, Diamond 1971 in van Halewyn & Norton 1984), including by the author (1990s and 2001), no certain examples of this petrel have been encountered since 1879, when the last birds were taken by Nock at Cinchona. The species is now generally believed to be extinct. Recent (1997 and 2009) searches at sea off south-east and northern Jamaica, respectively, also drew a blank (BZ pers. obs.; [www.birdscaribbean.org/wp-content/uploads/2015/BCPEWG/Shirihai\\_Jamaica\\_AtSea\\_Nov09.pdf](http://www.birdscaribbean.org/wp-content/uploads/2015/BCPEWG/Shirihai_Jamaica_AtSea_Nov09.pdf)). However, much suitable habitat in Jamaica remains to be searched and knowing the history of other *Pterodroma* spp., both in the Americas and elsewhere, searching for the Jamaica Petrel should not cease.

### **The Hancock Museum (Newcastle) specimen**

Through correspondence with Dr R. Stobbart at the now re-named Great North Museum (formerly Hancock Museum) in Newcastle-upon-Tyne, I established that a petrel, reg. no. B106.48, in the skin collection, appeared to be a 'dark-phase Black-capped Petrel *Pterodroma hasitata*'. Subsequently, during a visit to the museum, I was able to confirm its identification as *P. caribbaea*. Attached to the bird was an apparently contemporaneous tag with the words 'W. J. Trevelyan' and 'Trinidad', both written in ink, but without additional data.

There are no records of *P. caribbaea* from Trinidad, although its former occurrence at sea anywhere in the Caribbean or even Atlantic was by no means impossible. However,



Figure 1. The Hancock Museum specimen of Jamaica *Pterodroma caribbaea*, dorsal (left) and ventral images (Bernard Zonfrillo)

Trinidad has neither breeding petrels, nor records of any other *Pterodroma* species, and has many predators (French 1973). Trevelyan was a notable sea captain and certainly brought back other natural history material from the Caribbean to the Newcastle area, but other bird skins, also labelled as being from the Caribbean, clearly originate from the Indian subcontinent. Friends of Captain Trevelyan, particularly William Kelaart and his brother, both Ceylon-born medics, frequently sent natural history specimens to him from Ceylon and later Trinidad. It seems probable that in visiting various ports, Trevelyan assembled material from different islands and, if labels were lost in transit or became detached from their specimens, he replaced them with one based on the last port of call, or was simply confused as to the petrel's origin. Consequently, the specimen probably received its label when being forwarded to George Atkinson or might equally have been placed on the specimen long after reaching Newcastle. It was donated to the Hancock Museum one year after his death by George's brother, Richard Atkinson, in 1848 (R. Stobbart *in litt.* 2001). To further confuse matters, the Hancock Museum has a note stating that a 'package of bird skins from Trinidad' apparently including the Jamaica Petrel specimen, was donated by

Walter Calverly Trevelyan Bt., in 1863, i.e. 15 years after Richard Atkinson had already donated the petrel in question. It may have involved another unknown specimen or more probably never existed? Somehow, the bird first mentioned by Carte, eventually got from Jamaica to Trevelyan to Richard Atkinson, and finally to the Hancock Museum where it has remained. George Atkinson knew from correspondence that Gosse had enquired about a description of the bird taken in Jamaica, and Atkinson initially promised that it would be prepared, but was clearly too ill to produce it before his death.

John Hancock, the Newcastle museum founder, sent many letters to Trevelyan but none mentioned bird specimens (R. Stobart *in litt.* 2001) and Trevelyan, principally a sea captain, would probably have been unaware of the species' status or that it was new to science.

From published records, 26 specimens are known to exist in collections worldwide, just two of them in Jamaica. The few museums sent a specimen received just one or at most two (Benson 1972). These seabirds are far scarcer in collections than, for example, prized Great Auks *Pinguinus impeunis*, and the fact that a specimen—the first to be collected no less—was documented as sent to Newcastle-upon-Tyne must surely point to this being the bird in question and its locality of collection as being Jamaica and not Trinidad. The specimen stated by W. T. March to have been obtained by Sir Henry Barkly has, as yet, not been located, but might possibly also still exist, perhaps under the guise of *P. hasitata* or some other petrel. A search should also be made for this last bird, since 25 of the 26 have now been located. No egg was ever collected.

### *Pterodroma hasitata* and *P. caribbaea*

I was able to trace the first 'undescribed' *P. caribbaea* specimen to the former Hancock Museum, Newcastle-upon-Tyne. Any specimen of *P. hasitata* would also be unusual in a European museum collection, but the Newcastle bird is an obvious *P. caribbaea* (Fig. 1). The so-called 'phases of *P. hasitata* were 'lumped' with Jamaica Petrel by Bond (1936), in a footnote to *P. hasitata*, probably based on little more than the single specimen in the American Museum of Natural History, New York. Darker specimens of *P. hasitata* are usually characterised by lacking the dorsal neck-ring, which is also a feature of some Great Shearwaters *Puffinus gravis*, where the dorsal and crown colours merge (pers. obs.). The neck-ring on *P. hasitata*, when present, is very obvious at sea and is a major identification feature, along with the species' gleaming white underparts and rump (Douglas & Zonfrillo 1997). The rump of *P. caribbaea* is dull lead-grey. The rest of the plumage is sepia. In Carte's notes (1866) he mentioned W. T. March's notion that Richard Hill's recognition of the petrel was based on a description of the Diablotin (Black-capped Petrel) from Dominica, a bird he strangely claimed was 'uncommonly ugly'.

Much has been made of historical and anecdotal occurrences of the Jamaica Petrel away from Jamaica. Bent (1964) stated that the name Diablotin was also applied to Audubon's Shearwater *Puffinus lherminieri*, to add to the confusion. Père Labat (1792) gave an account of the *Pterodroma* in Guadeloupe and Dominica. His notes from 1696 represent a mix of fact and fiction, stating that the Diablotin 'produces two chicks' and that their down is 'yellow', neither of which statements is true. He remarked that the plumage of adults was 'black', which some authors, even today, have taken to indicate that the species involved was Jamaica Petrel. However, along with the fact that virtually all downy young *Pterodroma* are grey or brown and solitary, Jamaica Petrel is also brown, not black, and has an obvious silvery rump patch. Other all-dark species such as Trindade Petrel *P. arminjoniana* or Kermadec Petrel *P. neglecta*, perhaps even the usually coastal Bulwer's Petrel *Bulweria bulwerii*, could have been involved, given their all-brown plumage. Therefore, Labat's comments should not be taken as credible until such time as bones or specimens are verified

from these islands, as to date every specimen, photograph and sighting from Guadeloupe and Dominica has been of typical *P. hasitata*. Bent (1964) also questioned the veracity of these *P. caribbaea* comments but included the species as possibly breeding alongside Diablotins.

The importance of finding what probably was originally destined to be the type specimen of *P. caribbaea* adds to the location of known material of this species. While far from extinct, *P. hasitata* should not have been confused with this distinctive petrel. Unfamiliarity with both species, either as specimens or in the field, combined with attaching new labels to birds long after their death, and incorrect dates of collection has led to the confusion surrounding an extinct species that even when alive was probably always very rare and extremely restricted in its range within Jamaica.

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Address: Graham Kerr (Zoology) Building, Univ. of Glasgow, Glasgow G12 8QQ, Scotland, e-mail: Bernard.Zonfrillo@glasgow.ac.uk

## First record of Yellow-billed Cuckoo *Coccyzus americanus* on Tristan da Cunha, South Atlantic Ocean

by Alexander L. Bond & Trevor Glass

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Tristan da Cunha lies 2,800 km from South Africa, and >3,000 km from the coast of Brazil in the South Atlantic Ocean. It is the most remote inhabited island in the world, with St. Helena, the nearest island, >2,400 km away. Its remoteness and history of human habitation has resulted in a low diversity of terrestrial breeding birds and, because the island is not sited on any flyway, migrants are rare (Wace & Holdgate 1976, Ryan 2007). Nevertheless, there are occasional records of vagrant landbirds, mostly from the Americas. Barn Swallow *Hirundo rustica* (including *H. r. erythrogastrer*) is perhaps the commonest, with at least five records (Hagen 1952, Elliott 1953, Richardson 1984). Cattle Egrets *Bubulcus ibis* have been common in more recent years (Ryan 2007). There are also single records of Eastern Kingbird *Tyrannus tyrannus*, Willow Warbler *Phylloscopus trochilus* (Ryan 2007, 2008) and Common Nighthawk *Chordeiles minor* (Ryan 1989).

On 19 November 2015, C. Repetto, an island resident, found a weak, unfamiliar bird in her garden, and brought it to us for identification, whereupon we immediately recognised it as a Yellow-billed Cuckoo *Coccyzus americanus* (Fig. 1). The bird was dead when examined, and very emaciated, weighing 34 g, whereas typical mass is 55–70 g (Hughes 2015). Sex could not be reliably determined. The bird had replaced its two inner rectrices, while the rest were very worn; the primaries and secondaries were freshly grown, as were the wing-coverts. Measurements: total head length 50.9 mm, exposed culmen 24.7 mm, bill depth at nares 7.8 mm, tarsus 24.9 mm, straightened



Figure 1. Yellow-billed Cuckoo *Coccyzus americanus*, Tristan da Cunha, 19 November 2015, showing the right side (top), spread wing (dorsal view; middle) and spread tail (dorsal view; bottom) (Alexander L. Bond)

flattened wing 146 mm and tail 140 mm. Some geographic variation in linear measurements exists among breeding populations (Banks 1988, Hughes 2015), but the Tristan da Cunha specimen's morphometrics do not appear to match those from any one region. The specimen has been deposited at the Natural History Museum, Tring (NHMUK 2016.3.1).

Yellow-billed Cuckoo is a long-distance Neotropical migrant, breeding in eastern North America, and wintering in South America, mostly east of the Andes south to Argentina (Meyer de Schauensee 1982) and Uruguay (Rappole *et al.* 1983), between October and May. There are numerous records in the Western Palearctic, mostly in September–December (Cramp 1985), from Norway (Skipnes & Folvik 1998) to France (Reeber *et al.* 2008) and Iberia (de Juana & Comité Ibérico de Rarezas de la SEO 1996). In Africa, there is a single record from Marrakech, Morocco, in October 1977 (Thévenot *et al.* 2003). There are also records from the Azores every 5–10 years, including a large influx involving several birds in 1965 (Bannerman & Bannerman 1966, Clark 2006). There are no records for sub-Saharan Africa (Dowsett & Forbes-Watson 1993, Fry *et al.* 2002, Sinclair & Ryan 2003), Ascension Island or St. Helena (Rowlands *et al.* 1998, McCulloch 2004).

The cuckoo at Tristan could have been a ship-assisted vagrant, as >700 vessels pass through the Tristan da Cunha EEZ (i.e. waters 200 nautical miles around the islands) annually, but prevailing winds on the islands are north-west, which could easily bring vagrants from South America. The bird arrived the day following a large frontal system moved west to east. This record represents the first for this genus in the Southern Hemisphere outside South America, and the sixth vagrant landbird species recorded on Tristan da Cunha.

There are few other records of vagrant *Coccyzus* spp.; most are island residents or are much less migratory (Payne 2005). The exception is Black-billed Cuckoo *C. erythrophthalmus*, another long-distance Neotropical migrant, breeding in the northern USA and southern Canada, and wintering south to Colombia, Venezuela and Peru (Hughes 2001). There are many fewer European records of this species than of Yellow-billed Cuckoo (Cramp 1985), including just one from the Azores (Hartert & Ogilvie-Grant 1905).

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*Addresses:* Alexander L. Bond, RSPB Centre for Conservation Science, Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK, e-mail: alex.bond@rspb.org.uk. Trevor Glass, Conservation Dept., Government of Tristan da Cunha, Edinburgh of the Seven Seas, Tristan da Cunha, TDCU 1ZZ, South Atlantic Ocean.

## Description of the nest and parental care of Spotted Tanager *Tangara punctata*

by Tomaz Nascimento de Melo & Renata da Silva Xavier

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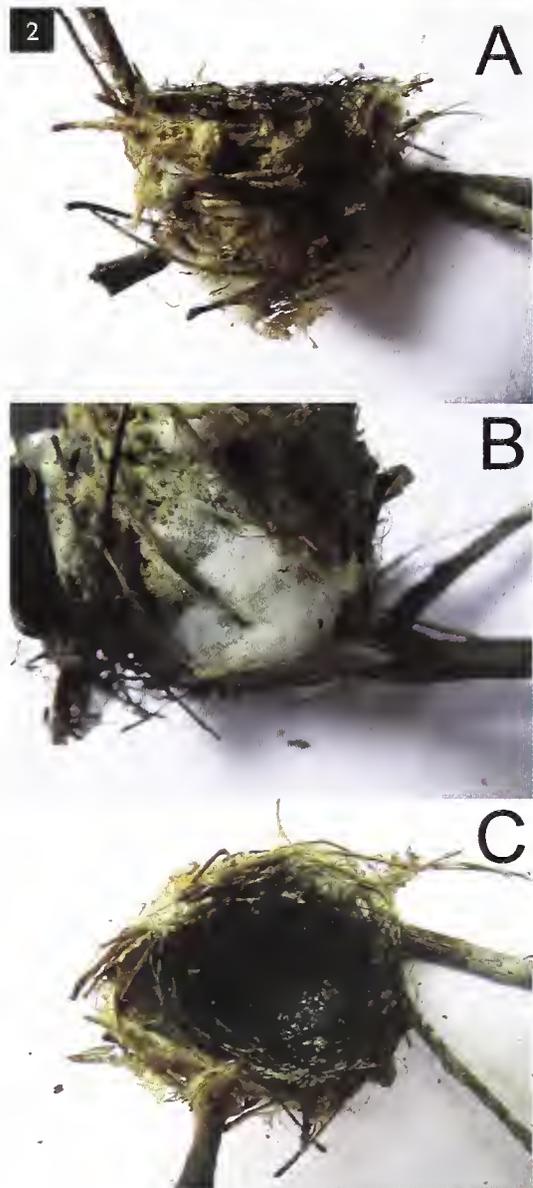
Spotted Tanager *Tangara punctata* is a small, mainly green and black-spotted thraupid found in Venezuela, the Guianas, Ecuador, Peru, Bolivia and much of Amazonian Brazil (Isler & Isler 1987, Hilty 2011, Pansacula & Burns 2012). Five subspecies are recognised, with *T. p. punctata* in Amazonia and the others in the Andes (Hilty 2011, Pansacula & Burns 2012). Besides differences in plumage and habitat, a molecular study revealed significant genetic differentiation between populations from Amazonia and the Andes (Burns & Naoki 2004), suggesting that more than one species might be recognised within *T. punctata* (Pansacula & Burns 2012). In Amazonia, the species occurs in *terra firme* forest and savanna. It feeds on fruits and arthropods, mainly in the canopy, but can descend lower (Isler & Isler 1987, Hilty 2011).

Isler & Isler (1987) reported that, for most tanagers, little is known concerning basic aspects of their reproductive behaviour. For c.15 of the 49 species of *Tangara*, no information on breeding biology is available and even for the other species available data are incomplete or based on observations made in captivity (Hilty 2011). According to Pansacula & Burns (2012) many aspects of the biology of *T. punctata* are little known, and its reproductive biology wholly unknown. Here, we present the first description of a *T. punctata* nest, with notes on the egg and parental care.



Figure 1. Spotted Tanager *Tangara punctata* nest in the canopy of a *Protium heptaphyllum* tree, Museu da Amazônia, Manaus, Amazonas, Brazil, February 2016 (Tomaz Nascimento de Melo)

Figure 2. Side view of the Spotted Tanager *Tangara punctata* nest (A), detail of the *Ceiba pentandra* seed down used in its construction (B) and view of the incubation chamber (C) (Tomaz Nascimento de Melo)



Data were collected at the Museu da Amazônia (MUSA; 03°00'S, 59°56'W), on the north-east edge of the city of Manaus, Amazonas, Brazil. The MUSA covers 200 ha within the Adolfo Ducke Forest Reserve, a 10,000-ha fragment of *terra firme* forest administered by the Instituto Nacional de Pesquisas da Amazônia (INPA). The fragment's southern boundary, where the MUSA is located, is subject to anthropogenic pressure, including fires and garbage dumping by local residents. The climate is classified as tropical humid, with relative humidity of 75–86% and annual rainfall of 1,750–2,500 mm. The wet season is between November and May, with peak rains in March–April. The dry season is in June–October; September is the hottest and driest month. Mean annual temperature is 26°C, fluctuating up to 8°C during the day (Baccaro *et al.* 2008).

Photographic documentation was obtained using a GoPro Hero 4 camera attached to a 4 m-stick, supported by a branch close to the nest, and a Canon SX50 HS camera, with 50× zoom. Observations were made from the tower, using



Figure 3. Adult Spotted Tanager *Tangara punctata* with nestling, Museu da Amazônia, Manaus, Amazonas, Brazil, February 2016 (Renata da Silva Xavier)

binoculars, at a distance of c.5 m from a platform 2 m above the nest. Once the breeding attempt had finished, the nest was subsequently collected.

On 13 February 2016, while conducting observations from a 28 m-platform of the canopy tower at the MUSA, an adult *T. punctata* was observed at a nest on a 28 m-high *Protium heptaphyllum* Burseraceae (Fig. 1). The nest was well concealed by the tree's leaves, and was 26 m above ground, c.5 m from the tower and 50 cm from the tree's outermost branches. The nest tree is located at the edge of the clearing surrounding the tower and 500 m from the fragment edge.

The low cup / fork nest (*sensu* Simon & Pacheco 2005) was attached at its sides to three thin branches of the tree, but with no support below it. The external part of the nest was covered by dry leaves and thin dry rachises (Fig. 2A), bound by fibres of *Ceiba pentandra* (Malvaceae) seed down, which were also used to attach the nest to the substrate (Fig. 2B). The incubation chamber was covered by thin black rootlets (Fig. 2C). The nest had an external diameter of 69 × 67 mm and internal diameter of 44 × 50 mm. Nest height was 60 mm and the incubation chamber was 34 mm deep. It held a single nestling, eyes still closed, covered in grey down with a white bill, and one egg, white spotted brown, which was observed just once, in winds that moved the leaves concealing the nest.

On 14–15 February 2016, nest activity was monitored between 07.00 and 10.00 h, for a total of six hours; it was not possible to monitor activity in the subsequent days. Both adults provisioned the fledgling, however one only remained <1 minute in the nest tree, whereas the other brooded the nestling after feeding it (Fig. 3), staying in the nest 3–25 minutes (mean = 10.7 minutes, SD = 6.7, *n* = 9), during which time the bird constantly rearranged the nest interior using its bill. Adults were observed bringing food to the nestling 12 times, usually together, but twice just one of the adults fed the young. When arriving in the vicinity of the nest, the adults gave short calls and quickly headed to it. The young was not

observed vocalising. The nestling was fed small, unidentified fruits and arthropods; twice it consumed small caterpillars. On two occasions, one of the adults transferred food to the other, which was already at the nest, to feed the nestling. Consumption of faecal sacs by the adults was observed twice, but they were never seen to carry faecal sacs away from the nest.

Variations have been reported in materials used for nestbuilding among the species of *Tangara*, even between different nests of the same species. The *T. punctata* nest we observed was much like most nests described for the genus, except the globular nest of Green-naped Tanager *T. fucosa*, being cup-shaped and saddled between branches (or sited directly onto the substrate), well concealed by vegetation (Skutch 1954, 1981, Isler & Isler 1987, Gonzaga & Castiglioni 2005, Sheldon & Greeney 2007, Greeney *et al.* 2008, 2011, Kirwan 2011, Sheldon *et al.* 2014). Use of moss as the principal or secondary material has been reported in nests of several *Tangara* species (Skutch 1954, 1981, Isler & Isler 1987, Sheldon & Greeney 2007, Greeney *et al.* 2011, Sheldon *et al.* 2014), but was not found in that of *T. punctata*. A predominance of rachises in the outer layer and dark roots in the nest's lining has also been reported in the nest of Speckled Tanager *T. guttata chrysoplirys* (Skutch 1954), which species also does not use moss in the construction. These two species are considered to be very close relatives (Burns & Naoki 2004) and, in this case, choice of material may indicate shared behaviour, rather than simple availability of materials (Gonzaga & Castiglioni 2005). *Ceiba pentandra* seed down was used to bind the other materials and attach the nest to the substrate in place of cobwebs, which are commonly used by congenics.

Our observations of parental care partially correspond to those of other *Tangara*. Although some studies have reported pairs of adults being helped by others to feed the nestlings (Skutch 1954, Skutch 1961, Snow & Collins 1962, Long & Heath 1994, Sick 1997), we only ever observed two individuals bringing food to the nest simultaneously, as also reported by Sheldon & Greeney (2007) for Beryl-spangled Tanager *T. nigroviridis*. However, the number of adults feeding the young can vary in the same species (Skutch 1961), so more observations are required to determine what is normal in this respect for *T. punctata*. As in many other species of *Tangara*, during our observations both adults visited the nest simultaneously to feed the young (Skutch 1954, Sheldon & Greeney 2007, Sheldon *et al.* 2014), although this behaviour was not observed by Kirwan (2011) for Green-and-gold Tanager *T. schrankii*. Skutch (1954) reported that simultaneous visits reflect the behaviour of *Tangara* pairs that always keep together while foraging.

According to Skutch (1954) and Sheldon *et al.* (2014), in other species of *Tangara* brooding is more frequent during the first days of life, when the nestlings still lack down. During our brief observations, it was possible to observe that the nestling was not feathered, explaining the mean c.11 minutes of brooding observed following each feed, similar to the observations of Sheldon *et al.* (2014) for Flame-faced Tanager *T. parzudakii* during the first days of life. Brooding period, however, appears to vary between species, with short durations reported by Sheldon & Greeney (2007) for *T. nigroviridis*, even when nestlings are very small.

Consumption of faecal sacs by the adults, observed in our study, corresponds to behaviour described by Skutch (1981) and Long & Heath (1994) for several other *Tangara*. Skutch (1981) reported that during the first days of life, consumption of faecal sacs is more frequent, but as nestlings grow the adults start to carry faecal sacs away from the nest. However, Sheldon & Greeney (2007) did not find any relationship between the nestlings' age and consumption of faecal sacs by adults. Our observations also contrast with those by Gelis *et al.* (2006), who witnessed Golden Tanagers *T. arthus* removing faecal sacs from the nest when the young were very small, and Sheldon *et al.* (2014), who recorded such behaviour as typical in *T. parzudakii*.

Although differences exist between nest materials used by different species, the materials and characteristics of the *T. punctata* nest we found are unlike most other *Tangara* species' nests (Skutch 1954, 1981, Isler & Isler 1987, Sick 1997, Gonzaga & Castiglioni 2005, Sheldon & Greeney 2007, Greeney *et al.* 2008, Gussoni & Develey 2011, Hilty 2011, Kirwan 2011, Sheldon *et al.* 2014). The data presented here represent the first published information concerning the breeding biology of *T. punctata*. Nest descriptions for other species might prove interesting for understanding relationships among the genus *Tangara*.

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- Addresses:* Tomaz Nascimento de Melo, Museu da Amazônia (MUSA), Av. Margarita, s/n°, Cidade de Deus, Manaus, Amazonas, Brazil, e-mail: tomaznmelo@hotmail.com. Renata da Silva Xavier, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. André Araújo, 2.936, Petrópolis, Manaus, Amazonas, Brazil, e-mail: renatadasilvaxavier@yahoo.com.br

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