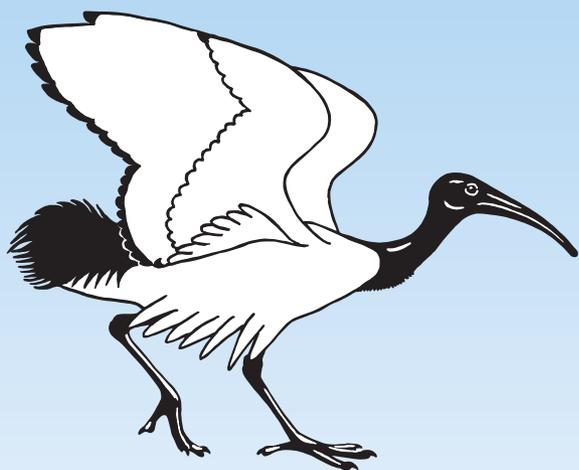


Bulletin of the British Ornithologists' Club



Volume 134 No. 3
September 2014

FORTHCOMING MEETINGS

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

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

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

The cash bar opens at **6.00 pm** and those who wish to eat after the meeting can place an order. **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.

Tuesday 23 September 2014—6.30 pm—Dr Andrew Gosler—Ornithology to ethno-ornithology

Abstract: Why are we ornithologists? Because we are fascinated by birds, yes, but why are humans so captivated by the ecology, evolution and behaviour of another vertebrate group that a UK Government Chief Scientist should complain that a disproportionate amount was spent on bird research to the detriment of other taxa? Whatever the answer to this, the fact that humans everywhere are enthralled by birds should point the way to how we might engage, re-engage or differently engage people in all countries with nature, and so focus resources most effectively for its conservation. Ethno-ornithology is the study of human relationships and associations with birds, be they benign or harmful for the birds themselves. This talk expands on these issues and describes how the speaker's own lifelong engagement with birds led to an interest in the very issue of human interest in birds itself.

Biography: Andy Gosler is University Research Lecturer in Ornithology and Conservation at Oxford University, where he holds a joint position between the Edward Grey Institute of Field Ornithology and the Institute of Human Sciences. His research interests span bird ecology and evolution, through ethno-ornithology to conservation. He is a former Editor of *Ibis*, a recipient of medals from the BTO and BOU and is the originator and Director of EWA: the Ethno-ornithology World Archive.

Saturday 22 November 2014—Asian birds, joint meeting with Oriental Bird Club and Natural History Museum

A one-day meeting in the Flett Theatre, Natural History Museum, South Kensington, London SW7 5BD. 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 will comprise:

Can the Spoon-billed Sandpiper be saved?—Dr Debbie Pain

AVentures: new species and rediscoveries of Asian birds?—Dr Pamela Rasmussen

Sumatra: the island that just keeps on giving (but sparingly!). A personal account—John Gregory

Survival of Asia's large frugivorous birds inside and outside protected areas—Dr Stuart Marsden

Warblers and larks: unexpected relationships and cryptic species—Dr Per Alström

Allan Octavian Hume: the 'Pope' of south Asian ornithology—Dr Robert Prŷs-Jones

Access to NHM is possible from 10.00 am, when coffee/tea will be available adjacent to the Flett Theatre. The meeting will begin at 10.30 am, with a break for lunch around 12.50 pm. Many food outlets are available both within NHM and nearby in South Kensington. Following the OBC AGM at 2.00 pm, the afternoon session will begin at 2.30 pm and, including a half-hour break for coffee/tea, finish by 5.30 pm. NHM closes at 6.00 pm. For additional up-to-date details, please check the BOC website: <http://www.boc-online.org>

Tuesday 10 March 2015—6.30 pm—Dr Clemency Fisher—A jigsaw puzzle with many pieces missing: reconstructing the 19th-century bird collection of John Gilbert

Full programme details will be made available in the September Bulletin and on the BOC website: <http://www.boc-online.org>

Further Tuesday evening meetings in 2015 are scheduled for **19 May** (including AGM) and **22 September**. In addition, a one-day joint meeting with the Ornithological Society of the Middle East and the Natural History Museum is currently being planned for a Saturday in November.

The Chairman: Chris Storey, 22 Richmond Park Road, London SW14 8JT UK. Tel. +44 (0)208 8764728. E-mail: 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 20 May 2014 with Chris Storey in the Chair. Thirteen members were present.

1. **Apologies for absence** were received from David Fisher and Clive Mann.

2. **Minutes of AGM 2013.** The Minutes of the 2013 AGM held on 21 May 2013 which had been published (*Bull. Brit. Orn. Cl.* 133:165–166 and the BOC website) were approved and signed by the Chairman.

3. **Chairman's Review, Bulletin Editor's Report, Trustees' Report and Accounts for 2013.** Copies of the document were available at the meeting. The Chairman began by thanking Helen Baker for all that she had done for the Club during her time in the Chair: it was considerable and the Club was much in her debt. He added that, with her usual generosity, Helen had agreed to help with the running of the website. The Chairman also thanked the Committee members, and Guy Kirwan, Eng-Li Green and Steve Dudley for all their support and work during the past year. He added that David Montier was retiring from his position of *Hon. Treasurer* and that Richard Malin, a new member of the Club recently co-opted onto the Committee, had agreed to put his name forward for election to that position. The forthcoming June Bulletin would include an announcement of a Special General Meeting on 23 September, prior to the evening meeting that day, at which the election of Richard Malin to the role of *Hon. Treasurer* would be proposed. The Chairman concluded by remarking that the Committee had begun to reappraise its activities. The Club faced a declining membership, a substantial reduction in numbers attending evening meetings and had assumed sole responsibility for the Checklist series following the BOU's unilateral decision to withdraw from joint publication of it and associated works, although BOU would continue to handle sales of existing joint works and future Checklists published by the Club. The Committee intended to ensure the BOC's funds were best used to further the Club's aims consistent with its charitable status and current realities, and that the Club was run in as effective and cost-efficient manner as possible.

The *Hon. Secretary* expressed regret at the disappointing audiences, averaging *c.*20, attending the four diverse and uniformly excellent evening meetings, held in February (Ascension Island birds), May (White-shouldered Ibis *Pseudibis davisoni* in Cambodia), September (Malagasy region birds) and November (avian land-use in Cyprus). Unless attendances improve in 2014, the Committee would need to consider discontinuing the long tradition of dinner meetings. By contrast, the joint one-day meeting, with the African Bird Club and the Natural History Museum, held at the NHM on Saturday 6 April, attracted an audience well in excess of 100, building on the success of previous joint ventures.

The four issues of the Bulletin for vol. 133 (2013) comprised 352 pages, a recent record, including 28 papers of broad geographical scope though with a continuing emphasis on the Neotropical region. Taxonomic issues continued to figure importantly, and two new subspecies were described, of Subalpine Warbler *Sylvia cantillans* and Upper Magdalena Tapaculo *Scytalopus rodriguezii*. The interval between receipt and publication for accepted papers has continued to be reduced under the present *Hon. Editor* and now averages only a little over seven months, with the free inclusion of colour illustrations where justified clearly attractive to authors. With the withdrawal of the BOU from involvement in Checklist production, a meeting of an *ad hoc* Sub-committee of the Club took place in December to consider the future of Club involvement in Checklists and other Occasional Publications. This made recommendations for consideration by the Committee in 2014.

The *Hon. Treasurer* introduced the Accounts for the year ended 31 December 2013. He referred first to the Investments in the Balance Sheet, which showed an increase over the year of £33,514. Of that figure £32,328 was due to an increase in the market value of the unit trusts held in the Herbert Stevens Trust Fund, the balance being distributions reinvested. Members' subscriptions had declined by £460 and investment income by almost £1,000, mainly because a two-year fixed term deposit had matured early in the year and could only be replaced at a much lower rate. Bulletin costs had increased to £16,024, partially explained by there being more pages in 2013 than in 2012. A grant of £500 had been made to the Museum Curators' Conference to support a delegate from St Petersburg. With total income of £23,994 and expenditure of £30,147, there was a

deficit for the year of £6,153. However with total assets of £414,680, the Club remains in a healthy position. The *Hon. Treasurer* proposed and the Meeting accepted the adoption of the Report and Accounts.

4. Election of Officers. Robert Prŷs-Jones and David Montier were confirmed as continuing in office as *Hon. Secretary* and *Hon. Treasurer*, respectively. Note: subsequently it was noted that the resolution was redundant since under the Club's new rules their re-election in 2013 was for a term of four years, ending in 2017 unless terminated earlier.

5. Any Other Business. There was none.

The 977th meeting of the Club was held on Tuesday 20 May 2014 in the upstairs room of the Barley Mow, 104 Horseferry Road, Westminster, London SW1P 2EE. Twenty members and eight non-members were present. Members attending were: Miss H. BAKER, Mr K. BETTON, Cdr. M. B. CASEMENT, RN, Mr S. CHAPMAN, Mr R. CHARLES, Prof. R. CHEKE, Mr K. HERON JONES, Mr G. M. KIRWAN (*Speaker*), Mr R. LANGLEY, Mr R. MALIN, Mr D. MONTIER, Mr R. PRICE, Dr R. PRŶS-JONES, Mr A. RANDALL, Mr N. REDMAN, Dr P. RUDGE, Mr P. SELLAR, Mr S. A. H. STATHAM, Mr C. W. R. STOREY (*Chairman*) and Mr M. WALTON.

Non-members attending were: Mrs J. HERON JONES, Mr K. HYATT, Mrs J. McDONALD, Mrs M. MONTIER, Mr A. PEAL, Mrs H. PRICE, Mr W. PRICE and Mr A. SIMMONS.

Guy Kirwan spoke on *Cuban birds at home and abroad, in the field and museum*. His talk commenced with brief résumés of Cuban geography, climate, peoples and life. Thereafter, he went on to discuss the development of ornithology in Cuba, starting with three important figures from the 19th century: Felipe Poey y Aloy, the so-called 'father of Cuban natural history', commemorated in a museum named for him and a journal *Poeyana*; Juan Lembeye Lartaud, a Frenchman, remembered in the scientific name of the Cuban Gnatcatcher *Poliophtila lembeyei*; and, of course, the German, Johannes (Juan) Gundlach, whose staggering contributions to Cuban natural history, but especially ornithology, are immortalised in the names, both scientific and vernacular, of numerous taxa. Between 1900 and the 1960s, Cuban ornithology remained vibrant, with important contributions from visiting and resident ornithologists, including from the Americans Thomas Barbour, Charles Ramsden and James Bond, but also from many Cubans, with those of José Hernández Bauzá, Joaquín Fernández de la Vara, Gastón Villalba, Stephen Bruner and Abelardo Moreno y Bonilla being especially outstanding. Modern-day Cuba presents many challenges to ornithological research, not least because of the embargo, and was particularly problematic during the so-called 'Special Period' following the collapse of the Soviet Union and of Russian financial support of the Castro regime. Nevertheless, the last couple of decades have witnessed considerable work on waterbirds, especially from the team of ornithologists based at La Havana University, and on taxonomy, avian palaeontology and ecology from staff at the National Museum of Natural History in Havana, while personnel from the Instituto de Ecología y Sistemática, also in Havana, have pursued a wide range of research interests.

Guy's talk then turned to the habitats and birds of Cuba, with special emphasis on the endemics, of which 27 taxa are currently recognised by one or more authority at species level; given Cuba's much larger size this is perhaps surprisingly fewer than either for Jamaica or Hispaniola. Many of these endemics are treated as threatened by IUCN / BirdLife International. More remarkably, at least seven and possibly nine genera are currently considered endemic to the country, namely *Cyanolimnas* (Zapata Rail *C. ceveiai*), *Starnoenas* (Blue-headed Quail-Dove *S. cyanocephala*), *Margarobryas* (Bare-legged Owl *M. lawrencii*), *Xiphidiopicus* (Cuban Green Woodpecker *X. percussus*), *Ferminia* (Zapata Wren *F. ceveiai*), *Teretistris* (Yellow-headed Warbler *T. fernandinae* and Oriente Warbler *T. fornsi*) and *Torreornis* (Zapata Sparrow *T. inexpectata*), with *Priotelus* (sometimes restricted to Cuban Trogon *P. temnurus*) and *Ptiloxena* (Cuban Blackbird *P. atrovioleacea*) potentially also confined to archipelago. Nevertheless, it should be emphasised that genetic work, to better establish relationships between these taxa and perceived closest relatives, is much needed for virtually all of these birds.

Finally, Guy outlined the field and (especially) museum work being undertaken by his co-authors and himself in preparing a new, detailed checklist to Cuban birds (to be published by BOC), as well as providing some brief thoughts on the perennial question of prospects for the Ivory-billed Woodpecker *Campephilus principalis bairdii* in Cuba.

Dr James Francis Monk, DM (1915–2014)

James died peacefully at home in Goring-on-Thames on 8 May in his 99th year. His memorial service on 27 May at nearby Streatley parish church was packed with his many friends and admirers. The congregation was greeted by the soft sounds of a dawn chorus, and readings and hymns, chosen by James himself, while the eulogies gave appropriate tribute to his lifelong passion for birds.

Born in India, where his father was on the staff of St. Stephens College through the Cambridge Mission to Delhi, but aged four he was sent to England to be brought up by an aunt in Cheltenham, then to Twyford preparatory school where his interest in birds was first ignited. Subsequently, as a student at Winchester College (1924–29), he was encouraged to follow the example of his illustrious predecessor Edward Grey,

later Viscount Grey of Falloden (1876–80), in whose memory the college nature reserve is named. James studied medicine at Trinity College, Oxford, where he came to know many influential and well-known ornithologists, who were later to have a major influence on his subsequent ornithological career, leading to his membership of the BOU, and the BOC, which he joined in 1946.

Having achieved his final medical qualification in 1941, James was drafted into the Royal Army Medical Corps and in 1943 was sent to North Africa where, during breaks from tending casualties, he birdwatched in the desert. The opportunity to witness the spring migration through Tunisia stimulated his interest in trans-Saharan migration. After the war, he returned to pursue a medical career and his love of ornithology, and met his future wife, Diana, at his mother's house in Oxford; their courtship included visits to watch birds at local sewage farms. James entered full-time General Practice in Goring-on-Thames in 1947, remaining until his retirement as senior partner in 1981. His earlier research on malaria gained him a degree (Oxford) in 1950.

James married Diana in February 1948, and they remained in Goring for the next 66 years. Returning from their honeymoon, the discovery of a pair of Wrynecks *Jynx torquilla* in the garden led to James undertaking a national review for the British Trust for Ornithology of the status in Britain of this increasingly rare species (*Bird Study* 10: 112–132, 1963), while his analysis of the breeding biology of Greenfinch *Chloris chloris* was distinguished for being the first paper published in *Bird Study* (1: 1–14, 1954).

His special interest in landbird migration resulted in two papers: Elliott, H. F. & Monk J. F., 1952, Land-bird migration over the Suez route to East Africa, *Ibis* 94: 526–530; and Moreau R. E. & Monk J. F., 1957, Autumn migration in southwest Portugal, *Ibis* 99: 500–508. It was at this point that I first made contact with James. Our early careers were remarkably similar, and although my Winchester College tutors groomed me for a medical career, I followed my family tradition and joined the Royal Navy, pursuing my lifelong interest in birds via the Royal Naval Birdwatching Society. So began lengthy correspondence with both James and Reg Moreau, who encouraged me in my own studies on this subject in the Mediterranean. Following advice from both David Lack and Bill Bourne, I made a series of recordings of radar echoes from an aircraft carrier in the Mediterranean during 1961–63, which resulted in a paper in *Ibis*. It was only thanks to James, who took infinite trouble to edit my amateur drafts that it finally appeared in print, and he also authorised the inclusion of photographs, which were rather a novelty at the time. Many other authors were similarly grateful for his care and editorial advice.

When Reg Moreau died in 1970, James undertook to finish his nearly completed final work: Moreau, R. E. & Monk, J. F. (1972) *The Palearctic-African bird migration systems*. Academic Press, London.

In 1975, it was almost entirely via James' initiative that the BOU launched a series to cover parts of the world for which up-to-date and comprehensive avian checklists were unavailable, and for 13 years James organised and edited these. This series continues to this day, but responsibility for publication has recently transferred solely to the Club.

Over a period of 32 years, James held every important office in the BOU, except Hon. Treasurer, serving as Assistant Editor of *Ibis* 1956–60, Editor 1960–66, Hon. Secretary (1967–72), Vice-President 1978–82 and President 1983–87. He was a Life Member of the BOC, where his record was equally impressive, as Vice-Chairman 1965–68, Chairman 1968–71, Editor *Bull. BOC* 1976–91 and he continued on BOC Committee 1991–94. In 1992 he edited the Bulletin's Centenary Supplement 112A *Avian systematics and taxonomy*. The Club was especially indebted to James, who donated proceeds from the sale of his personal library, amounting to over £3,600, to establish a fund to help finance BOC publications. His contribution to ornithology and publications was described, in the citation for his award of the BOU Medal in 1988 (*Ibis* 130: 471–472), as 'unique in this century', but remarkably he earned this accolade whilst a GP in a very busy practice. How he managed to achieve this using only a typewriter, before the advent of computers, remains a mystery to all who knew him.

His family recall their father was often preoccupied with his papers, working late at night and at weekends. This prompted his younger daughter to put a notice on his study door reading 'Ibis going on in here. Please knock before going in. Thank you.'

James was famed for his approachability and generosity with his time among all who worked closely with him. He was wise and very shrewd with his advice. As an impecunious student at Oxford he came to know Richard Meinertzhagen and even tutored members of his family. Tom Gladwin commented that, although he didn't understand his concern at the time, James advised 'care' in analysing Meinertzhagen material.

As editor, he took infinite care to make papers accessible to a wide readership, and his own writings appealed to a wide circle of amateur birdwatchers. In the early 1990s he wrote regularly for the monthly *Goring Gap News*, and his texts were subsequently published as *Birds for all seasons, chronicles from the Thames Valley* (1997). His daughter Catherine read a delightful extract from one of these at his memorial service.

James was first and foremost a conscientious fieldworker but, throughout his long and eventful career, he was also passionate about his family, his garden and his dogs. His final years were marred by deteriorating eyesight and mobility problems, but he remained alert to the end, and enjoyed exchanging bird anecdotes with visitors. He never complained, and was lovingly supported by family and friends; the service collection was for the Royal National Institute of Blind People (Talking Books) from which he had benefitted so much in his latter years of blindness.

Michael Casement

Colour aberrations in extinct and endangered birds

by Julian P. Hume & Hein van Grouw

Received 20 December 2013

SUMMARY.—Several groups of birds have suffered high extinction rates, especially rails, pigeons, parrots and passerines. Some island species that disappeared in the early 19th century, e.g. Lord Howe Gallinule *Porphyrio albus*, Rodrigues Parakeet *Psittacula exsul* and Mascarene Parrot *Mascarinus mascarinus*, are known from only a few skins and illustrations, whereas the Huia *Heteralocha acutirostris* of New Zealand is known from hundreds of specimens. Furthermore, two North American species—Passenger Pigeon *Ectopistes migratorius* and Carolina Parakeet *Conuropsis carolinensis*—which became extinct in the early 20th century, are also represented by hundreds of specimens. Other supposedly extinct bird species are enigmatic. Confusion exists concerning the unique specimens of Sharpe's Rail *Gallirallus sharpei* and Townsend's Bunting *Spiza townsendi*, paintings of a parrot from the West Indies and an aberrant white Huia, as well as aberrant specimens of the Critically Endangered Kakapo *Strigops habroptilus*. Much has been written concerning these birds and why they became extinct, or have become extremely rare, but few data are available concerning colour aberrations in certain specimens; the literature is also riddled with incorrect terminology. This paper addresses this shortfall and describes the various colour aberrations in these extinct and endangered birds and why they have occurred.

The Rallidae (rails and coots), Columbidae (pigeons and doves), Psittacidae (parrots and macaws) and Passeriformes (passerines) are all widely distributed, occurring on every continent except Antarctica. All have suffered extremely high extinction rates (Hume & Walters 2012), especially those genera endemic to oceanic islands. This is primarily due to severe anthropogenic factors, especially over-hunting, deforestation and introduction of exotic species. Many of these extinct taxa are known from very few specimens, particularly those that disappeared in the 19th century. These include Lord Howe Gallinule *Porphyrio albus* (ex. c.1844), Rodrigues Parakeet *Psittacula exsul* (ex. c.1875) and Mascarene Parrot *Mascarinus mascarinus* (ex. c.1800) (Hume 2007, Hume & Walters 2012), all of which are represented by just two known skins. In contrast, Huia *Heteralocha acutirostris* (ex. 1907) of New Zealand is known from hundreds of specimens (Fuller 2000) and the Critically Endangered Kakapo *Strigops habroptilus* by >1,000; both were particularly sought after during the 19th century (Butler 1989, Hume & Walters 2012). Carolina Parakeet *Conuropsis carolinensis* (ex. 1918) and Passenger Pigeon *Ectopistes migratorius* (ex. 1914), of the continental USA, are known from at least 720 skins (Luther 1996) and 1,532 skins (Hahn 1963), respectively. Much has been written about these birds and why they became extinct (Rothschild 1907, Greenway 1958, 1967, Fuller 1987, 2000, Butcher 1992, Hume 2007, Hume & Walters 2012), but little documentation exists for specimens exhibiting unusual colour aberrations. The unique specimens of Sharpe's Rail *Gallirallus sharpei*, obtained in 1865 and of unknown provenance but considered an extinct species (Olson 1986), and Townsend's Bunting *Spiza townsendi*, collected once in 1834 and also considered extinct (Paynter 1970), are discussed. Some aberrant-coloured skins of Kakapo, illustrations of an enigmatic *Amazona* parrot from the West Indies, and a white Huia are also described.

This paper addresses the probable reasons why these colour aberrations occurred, and elucidates some of the erroneous misconceptions associated with these birds. In particular, the much-used term ‘partial albinism’ is an incorrect terminology that cannot be used to describe any avian taxon exhibiting partial white feathering (van Grouw 2006, 2012, 2013).

Rallidae

LORD HOWE GALLINULE (SWAMPHEN) *Porphyrio albus* (White, 1790)

Endemic to Lord Howe, a small, remote island between Australia and New Zealand in the Tasman Sea, c.600 km east of Australia, *P. albus* was considered common when discovered in 1788 (Hutton 1991), but soon fell victim to over-hunting and introduced mammalian predators, becoming extinct between 1832 and 1844 (Hindwood 1940). The population was derived from Purple Gallinule *P. porphyrio*, but differed in its white plumage and bill, wing and leg proportions (Forbes 1901, Ripley 1977); thus Lord Howe Gallinule is given specific status. Two specimens, as well as several contemporary illustrations and subfossil remains, are available (Forbes 1901, Iredale 1910, Fuller 2000, Holdaway & Anderson 2001). Neither skin has accurate provenance data.

The first illustration was probably by Arthur Bowes Smyth, surgeon on one of the First Fleet vessels, the *Lady Penrhyn*, which arrived at Lord Howe on 16 May 1788 (Hutton 1991). The drawing depicts one white and two pied gallinules, and Smyth described the birds as ‘some white, some blue and white, others all blue’. Other contemporary images demonstrate that the species was variably coloured, with some completely white, others white with blue speckling, some entirely blue. Phillip (1789) described the adult female



Figure 1. Watercolour of live Lord Howe Gallinules *Porphyrio albus* showing the various stages of progressive greying discussed in the text. Fig. 1a (left) shows a pair exhibiting the same colour aberrations as the extant specimens; illustration by George Raper c.1790 (from Hindwood 1940). Fig. 1b (above) shows the three colour stages described by White (1790); illustration by Thomas Watling c.1792 (from Fuller 2000).

White Gallinule (*Porphyrio albus albus*)

Painting no. 22 (c.1790, artist unknown) in a collection of original drawings in the Alexander Turnbull Library, Wellington, New Zealand.
By courtesy of the Trustees.



Figure 2. Comparison of the two extant specimens of Lord Howe Gallinules *Porphyrio albus*, both of which exhibit progressive greying, with a normal-coloured Purple Gallinule *P. porphyria*: Fig. 2a (top) holotype NMW 50761; Fig. 2b (above left) WML D3213; Fig. 2c (above right) artist's impression of the Liverpool specimen (Julian P. Hume); Fig. 2d (left) Eastern Purple Gallinule *P. p. melanotus* BMNH 1887.5.2.66 dorsal and ventral views (Hein van Grouw). Note that the holotype is completely white.

as all white, but was informed that the male had some blue on the wings. White (1790), followed by Latham (1824) and Gray (1862), stated that young were all black, turning bluish grey, then pure white with maturity (Fig. 1b). White's (1790) statement that juveniles were normal-coloured before developing white feathers (= feathers without melanin) at maturity, strongly suggests that the species exhibited the aberration progressive greying, which can be defined as 'the progressive loss of pigment cells with age' (van Grouw 2013). From the onset of this condition, the bird gains an increasing number of white feathers with every moult. In the early stages, they are usually spread randomly over the bird, but eventually the entire plumage is white. Progressive greying may or may not be inheritable; some forms are related to age, while in others the progressive loss of pigment cells is due to inheritable disorders such as vitiligo (van Grouw 2013). Progressive greying is common in birds, especially in the Corvidae, Passeridae and Turdidae (van Grouw 2012). The aberration affects only the melanin, not the carotenoid pigments (reds and yellows), therefore Lord Howe Gallinule's bill and legs retained normal coloration.

The widespread Australasian subspecies of Purple Gallinule, *P. p. melanotus* (Fig. 2d), still occurs on Lord Howe and some exhibit blue and white feathering (Mayr 1941, Ripley 1977), but it appears that these birds had disappeared entirely by 1977. Mayr (1941) considered the survival of blue individuals was due to them being less conspicuous, after the original population of white birds had disappeared; however, Hindwood (1965) thought that blue birds occasionally arrived from Australia and interbred with the resident white population. Unsurprisingly, the differences in coloration resulted in a wealth of confusing taxonomic literature (Rowley 1875, Forbes 1901, Rothschild 1907, Mathews 1928), exacerbated by confusion over provenance (Hume & Walters 2012). This has led to doubts concerning the specific status of the Lord Howe birds. Regardless of this, what is certain is that a population of probably flightless, white or partially white gallinules was formerly resident on Lord Howe.

NMW (Naturhistorisches Museum Wien) 50.761, type (Fig. 2a). This specimen was obtained from the sale of the Leverian collection in 1806, and labelled '*Fulica albus*, Norfolk Island' (Pelzeln 1873) in error. It is considered the type, as White (1790) mentioned that the bird on which his drawing was based was deposited in the Leverian collection (Pelzeln 1873). The skin, which was originally mounted, is in good condition, and the natural red coloration of the bill and shield is visible. Although faded, the legs are pale orange-brown, and thus were probably reddish in life. The specimen is all white, with no trace of yellowish sheen or any purple feathering (*contra* Rothschild 1907: 144). The remiges and rectrices are soft, and the remiges almost completely covered by the uppertail-coverts. Wing length is shorter than in the Liverpool specimen (Greenway 1967).

WML (Liverpool World Museum) D3213 (Fig. 2b–c). A mount, this specimen was originally obtained by Sir Joseph Banks, but the collection date is unknown. It must have been collected post-1778, when the island was first discovered (Hutton 1991). The skin went to the Bullock collection, was purchased at auction by Lord Stanley in 1819, then bequeathed to Liverpool by the 13th Lord Derby and finally donated to the museum c.1850 (Forbes 1901). It is generally in good condition, considering its age, but with extensive feather loss on the head and neck. General coloration is white with yellowish reflections on the neck and breast. Purplish-blue speckling occurs on the top of the head, cheeks and neck, and is more concentrated on the head, especially near the dorsal surface of the shield. There are several purplish-blue feathers on the back, scapulars and lesser coverts, and some of the lateral rectrices are purplish brown. The remiges and rectrices are soft, and the primaries shorter than in *P. porphyrio* (Forbes 1901, Greenway 1967). The bill, shield, iris, legs and

feet were bright red or yellow in life (Philip 1789, White 1790), but the bill and feet in the Liverpool skin have been painted red.

Rothschild (1907) correctly suggested that *P. albus* was not albinistic, but that the population was in the evolutionary process of becoming pure white. Our analysis of museum skins confirms that albinism was not present in the population (*contra* Taylor & van Perlo 1998, Fuller 1987, 2000, Hume & Walters 2012), and that white coloration in the two extant specimens is caused by a presumably inheritable form of progressive greying. The Liverpool bird had not yet reached the final stage of this condition, hence the retained normal-coloured feathers, whereas the Vienna specimen was in the final stage and therefore all white. The individuals that occurred on Lord Howe until 1977 exhibiting white and blue coloration were probably a local population of *P. p. melanotus*, which also carried the gene for progressive greying. They too are now extinct.

SHARPE'S RAIL *Gallirallus sharpei* (Büttikofer, 1893)

Several rails are known from unique skins or illustrations, and the enigmatic Sharpe's Rail *Gallirallus sharpei*, first described in 1893 (Büttikofer 1893), is one such. It is considered to be closely related to Buff-banded Rail *Gallirallus philippensis* (Olson 1986), an extremely widespread species found on many islands and archipelagos in the South Pacific, New Guinea, New Caledonia and New Zealand, as well as Australia and Indonesia (Ripley 1977, Taylor & van Perlo 1998). Buff-banded Rail has been treated as at least 21 subspecies, most of which are not threatened, but Macquarie Island Rail *G. p. macquariensis* became extinct c.1870 due to the introduction of feral cats and Wekas *G. australis* (Hume & Walters 2012). The type of *G. sharpei* was received at the Rijksmuseum van Natuurlijke Historie, Leiden (now Naturalis), in 1865 from the Amsterdam natural history dealer, G. A. Frank (Büttikofer 1893, Olson 1986). The original range is unknown, but H. Schlegel thought that the bird was a juvenile of the South American Spotted Rail *Pardirallus maculatus* (Büttikofer 1893), an error that initiated great confusion over its true provenance (R. B. Sharpe *in* Büttikofer 1893). In 1893, J. Büttikofer, Schlegel's successor and probably biased by the latter's provenance allocation (Olson 1986), described it as a distinct species from South America in honour of Sharpe, who had brought it to his attention (Büttikofer 1893). O. Bangs (*in* Peters 1934) placed the rail in *Hypotaenidia* and, as it was never recorded again, this prompted Peters to suggest that it might be an extinct species. *Hypotaenidia* has been applied to bar-winged or buff-banded rails of the genus *Gallirallus* (Olson 1986), and Olson concluded that Sharpe's Rail, which was similar in many aspects of size and morphology to volant *G. philippensis*, should be placed there too.

On many occasions, unique bird skins have been ignored by modern ornithologists, especially those collected on islands during the 18th and 19th centuries, which has commonly resulted in their relegation to dubious status. Based on the available evidence, Olson (1986) thought that, as the bird differed significantly in plumage pattern and coloration, it probably represented an extinct species, and speculated that the skin was procured from Java, Sumatra or Borneo. Unusually among island rails, which are often characterised by flightlessness (Olson 1973, Livezey 2003), Sharpe's Rail exhibited no reduction in wing length (Olson 1986).

RMNH (Rijksmuseum van Natuurlijke Historie, Leiden) 87485 (Fig. 3). Sharpe's Rail is a mid-sized, dark-coloured bird, upperparts brownish black, paler and more brownish on upperwing; white-spotted mantle, scapulars, upperwing-coverts, undertail-coverts and tail; remiges dull brown, strongly barred white; sides of head, chin, throat and neck grey; rest of underparts brownish black; flanks irregularly marked with small white spots; bill, legs and



Figure 3. Sharpe's Rail *Gallirallus sharpei* RMNH 87485 (left) exhibiting category 3 melanism compared with a normal-coloured Buff-banded Rail *G. philippensis* RMNH 185133 (right) (© Steven van der Mije / Naturalis)

feet reddish. Sharpe's Rail lacks the chestnut-coloured nape and ocular stripe, ochraceous pectoral band and pale superciliary of Buff-banded Rail (Fig. 3).

The dark and spotted appearance of Sharpe's Rail vaguely resembles that of Spotted and Buff-banded Rails, therefore it is not obviously an aberrant specimen. The plumage appears 'natural', and thereby convinced previous authors that it differed from any known species. But the 'natural look' is an important distinguishing feature of melanism, as this aberration does not cause a qualitative and / or quantitative loss of pigment.

In general the appearance of a melanistic bird is dark, predominantly blackish, but this is not always the case. There are at least three ways in which melanism can affect plumage (van Grouw 2013): (1) normally dark markings become bolder and noticeably 'overrun' their usual boundaries (the rest of the plumage is often somewhat darker too); (2) all plumage becomes darker, appearing dark brown or black; and (3) normal pattern and / or pigment distribution is changed, but plumage is not necessarily darker.

Melanism can therefore be defined as 'an abnormal deposit of melanin in skin and / or feathers', which means that melanism is not necessarily an increase of pigment, but may be the result of a changed distribution or 'abnormal deposit' of the same amount of melanin (van Grouw 2013).

The possibility that *G. sharpei* represents a colour aberration was not considered until mtDNA revealed that the specimen can be referred to *G. philippensis* (Naturalis unpubl. data). Therefore the unique specimen of Sharpe's Rail is not an extinct species (van Grouw 2010), but is in fact an outstanding example of category 3 melanism of Buff-banded Rail.

Columbidae

PASSENGER PIGEON *Ectopistes migratorius* (Linnaeus, 1766)

Probably once the most abundant bird species on Earth, its extinction is one of the most damning acts of human greed and thoughtlessness: it defies belief that a species so abundant could be exterminated so quickly. Its range was inextricably linked to the eastern deciduous forests of North America and Canada, from the Great Plains east to the Atlantic, north to southernmost Canada, and south to Virginia and northern Mississippi. In winter they migrated to the south-eastern USA, the Caribbean slope of central Mexico, and even Cuba (Schorger 1955, Gibbs *et al.* 2001). Early accounts describe the immense numbers of individuals that congregated during the nesting season and especially on migration, although such concentrations were irregular (Hume & Walters 2012). The decline began in the early 1800s, and coincided with an increase in deforestation and commercial exploitation, particularly following the development of new railroads and telegraph systems after the American Civil War. Wherever the pigeon concentrated in numbers, it was subject to wanton slaughter; they were in huge demand for meat and the feather trade (Butcher 1992). By the end of the century the species was almost extinct. The last recorded wild specimen was shot on 24 March 1900 (Fuller 2000). A few were kept in private aviaries, but they proved poor breeders; the last, a captive female called Martha, outlived the rest by four years. She died on 1 September 1914 in Cincinnati Zoo (Shufeldt 1915).



Figure 4. Passenger Pigeon *Ectopistes migratorius* BMNH 1939.12.9.4071 exhibiting the brown aberration (left) lateral view; (second from right) dorsal view; compared with normal-coloured bird BMNH 1918.12.3.3 (Hein van Grouw / © Natural History Museum, Tring).

Passenger Pigeon is known from at least 1,532 skins and 16 skeletons (Hahn 1963). It was a large dove with long wings and a long graduated tail, and adults were sexually dichromatic. Males had the head bluish grey; display area at back of neck iridescent bronze, green or purple depending on the light; back tinged slate-grey with olive-brown; lower back and rump greyish blue and greyish brown on uppertail-coverts; two central rectrices brownish grey, rest white; wing-coverts brownish grey with irregular subterminal spots; primaries and secondaries darker greyish brown; secondaries edged white; throat and breast rich pinkish rufous, becoming paler on lower breast to white on undertail-coverts; bill black, iris carmine-red, bare orbital ring purplish red, legs and feet red. Female similar but overall duller, greyish-brown head, neck and back; reduced iridescent markings; underparts buff-brown, less rufous and tail shorter; legs and feet paler red, iris orange-red, and orbital ring greyish blue.

BMNH (Natural History Museum, Tring) 1939.12.9.4071 (Fig. 4). This aberrant specimen, an adult female, has no provenance other than it formed part of the Rothschild collection at Tring. Rothschild had a great interest in colour aberrations and this specimen is probably the only aberrant-coloured Passenger Pigeon in existence. It differs from normal-coloured birds in being washed brown on the upperparts, wing-coverts, secondaries and tail where grey normally occurs; the primaries, lower breast and belly are white; the black subterminal spots brown; the top of head, lower back and uppertail-coverts pale grey, but the neck iridescence is unaffected. The aberration is caused by the mutation brown, 'an inheritable qualitative reduction of eumelanin due to incomplete synthesis (oxidation) of eumelanin' (van Grouw 2013). This mutation is the most common in wild birds, and the probable reason is that the gene for brown is sex-linked. In birds, males have two Z-chromosomes, whereas females have a Z and W (Bellott & Page 2009), thus in sex-linked mutations the gene is located on the Z-chromosome alone. This explains why only brown females occur in the wild, as females need only one gene to express the recessive brown mutation. In contrast, to produce a brown male, a heterozygous father and brown mother are essential; the likelihood of this occurring under natural conditions is extremely remote. The bill and feet are usually slightly paler in brown (not discernible in this specimen), but eye colour remains the same (van Grouw 2012). The result of this aberration is that the black eumelanin pigment becomes brown, but the reddish or yellowish-brown phaeomelanin is unaffected. The white coloration is due to further bleaching by exposure to natural light, whereby old feathers can be much paler than fresh ones (van Grouw 2012, 2013). The original un-faded brown coloration is clearly visible in this individual on the inner webs of the flight feathers, which have not been exposed to light.

Psittacidae

RODRIGUES PARAKEET *Psittacula exsul* (Newton, 1872)

Known from two specimens, the last collected in 1875 (Newton & Newton 1876). Their coloration appears to differ from normal-coloured wild birds, which has resulted in much confusion. Rodrigues Parakeet was first mentioned by the Huguenot, François Leguat, in 1692–93 (Leguat 1708), and then by the Réunionnais mariner, Julien Tafforet (1725–26), who also observed other parrots (our translation from the original manuscript):

'The Parrots are of three kinds and in quantity. The largest [*Necropsittacus rodericanus*] are larger than a pigeon and have a very long tail, the head big as well as the beak; most are from the southern islets to the south of island where they eat a small black seed that produces a small shrub whose leaves have the scent of lemon, and come to the mainland to drink water; others remain on the mainland, where they find these

small shrubs. The second species [σ *Psittacula exsul*] is slightly smaller, and much more beautiful, because it has its plumage green like the previous, a little blue, and a little red above the wings as well as their beaks, the third species [♀ *P. exsul*] is small, all green and the beak black.'

The parrots were extremely abundant, but Tafforet noted that they generally occurred on offshore islets (probably due to the presence of rats on Rodrigues itself: Hume 2007), only visiting the main island for water. The astronomer Pingré, who was on Rodrigues to observe the transit of Venus in 1761 (Alby & Serviabile 1993), noted that both parrots had become rare, *Necropsittacus* especially; this was the last time the latter species was mentioned. Over the next century, slash-and-burn agriculture and free-roaming livestock turned the island into a wasteland (Cheke & Hume 2008). Remarkably, the parakeet survived; it was not until 1871 that the first specimen, an adult female, was collected and the species formally described (Newton 1872). A second transit expedition to the island took place in 1874, which included several naturalists, and the first natural history survey was undertaken (North-Coombes 1971). The Revd. H. H. Slater wrote a manuscript describing the surviving birds on Rodrigues, but only small extracts were published (Günther & Newton 1879, Slater 1879, Hume *et al.* 2014). The parakeet was by now extremely rare, and Slater remarked on the single specimen he saw during his three-month stay at the Plaine Corail, south-west Rodrigues. The following is taken verbatim from his field notes (Slater 1874):

Palaeornis exsul. I saw one specimen of this bird as I was going from my camp to a distant cavern: unfortunately I had not my gun with me or I could easily have shot it as



Figure 5. The two extant specimens of Rodrigues Parakeet *Psittacula exsul* exhibiting the parblue aberration. Male UMZC18/Psi/67/h/I (right) lateral and dorsal views; holotype female UMZC18/Psi/67/h/I (left) lateral and dorsal views (Julian P. Hume).

it came within thirty feet of me: I believed it to be a male at the time, and it is probably the one procured since by Mr Caldwell; I never had time to hunt for it subsequently. I was informed by a native (Quibus minime credendum pot [who cannot be trusted]) that he had seen two specimens at the N. end of the Island, but I had never time to visit that region.

Assistant Colonial Secretary, William James Caldwell (1875), who arrived on Rodrigues 12 May 1875, saw several parakeets during his stay, but was unable to obtain a specimen himself. However, he did receive a male from a local resident and ship's pilot, William Vandorous, who had killed and sexed the bird on 14 August 1875 (Newton & Newton 1876); it was probably that seen by Slater. This was the last time the parakeet was recorded.

CUMZ (University Museum of Zoology, Cambridge) 18/Psi/67/h/I ♀ holotype (Fig. 5). Newton (1872) and Newton & Newton (1876) described the female in fresh plumage as overall dull greyish glaucous, darker above, with a blue or green sheen depending on the light; primaries deep greenish blue, secondaries slightly darker; rump and belly verditer-blue, becoming greener on vent; black collar from nostrils to sides of head; bill black, iris black with yellow ring, legs and feet greyish black. Originally preserved in alcohol, the specimen was removed from solution when it was described (Newton 1872).

CUMZ (University Museum of Zoology, Cambridge) 18/Psi/67/h/I ♂ (Fig. 5). Differs in being larger and in having the top of head clearer glaucous, less grey; black stripe more distinct, extending upwards from nostrils to nape of neck and almost meeting there; primaries with dull black patch on inner web near tip; central secondaries dusky black; maxilla deep crimson, becoming horn at tip, mandible dark reddish brown (Newton & Newton 1876). The feathers exhibit more wear than the female, and thus are less well preserved.

The unusual coloration of *P. exsul* has caused much debate, so it is important to establish a general overview of parrot coloration. The predominant greens of most parrots are not true colours as they are not formed by green pigments; instead, the green is produced by two different pigments (eumelanin and psittacin) in combination with feather structure. As in all birds, melanin, or more precisely, eumelanin, is one of the pigments that determines colours in parrots. Eumelanin is normally black or dark brown, but depending on the way the microscopic pigment granules are arranged (i.e. their density) in the feather cells, it appears black (dark brown) or as different shades of grey. The eumelanin granules in the deeper cells of the feather barbs, together with their special structure, distort the light as it passes through, making the feathers appear blue. Thus, blue is a structural colour and not a pigment. The second pigment, psittacin, is unique to parrots. Yellow is the commonest colour of psittacin, but the related colours red, orange and pink can also be produced by it. Psittacin, when present, is distributed in the cortex, the outermost layer of a feather barb, and combined with the structural blue coloration, creates the bright shades of green characteristic of most parrot species (Martin 2002).

The inheritable absence of psittacin, which causes blue feathers instead of green, is probably the commonest mutation in parrots and is, for obvious reasons, called blue. In all parrot species inheritance is recessive and not sex-linked (Martin 2002). For a recessive mutation to appear, a bird must inherit a gene for the mutation, in this case blue, from both parents. The coloration caused by blue mutations varies in shade, depending on the normal colours (wild type) in the relevant species. For example, in *Psittacula* the blue coloration will be evenly distributed and intense, as is the original green of these species. In contrast, an uneven distribution and intensity of green can result in an uneven distribution of blue (see Kakapo).

The allele responsible for the total absence of psittacin in parrots is often referred to as true blue, but several other alleles produce reduced quantities of psittacin (Martin 2002). Due to the 'diluted' psittacin exhibited by such mutations, overall colour will lie somewhere between green and blue, an aberration known as parblue. Newton & Newton (1876) described *P. exsul* as being greyish glaucous, with green or blue reflections depending on the angle of light. This suggests that the cause of the colour aberration was due to a parblue mutation rather than true blue.

MASCARENE PARROT *Mascarinus mascarinus* (Linnaeus, 1771)

Endemic to Réunion, the youngest of the Mascarene Islands (Cheke & Hume 2008), this species disappeared before anything was recorded of its ecology. A few captive birds arrived in Paris during the late 18th century, by which time it was probably already extinct in the wild. The last individual, a specimen in King Maximilian of Bavaria's menagerie, reportedly died in 1834 (Hahn 1834, Milne-Edwards & Oustalet 1893, Hachisuka 1953, Greenway 1958, 1967, Fuller 1987, 2000, Forshaw 1989); however, this is extremely unlikely and the species was almost certainly extinct by c.1800 (Hume 2007). The specimen described by Hahn was not preserved, but two exist, the holotype in Paris (MNHN 211; Fig. 6a,c) and another in Vienna (NMW 50.688) (Fig. 6b–c). The latter has frequently been described as 'partially albinistic' (Pelzeln 1873, Fuller 2000, Hume & Walters 2012) or as a 'variety' of Mascarene Parrot (Latham 1781), as the skin has some white feathering (Fig. 6c). Latham (1781: 265) gave the first detailed description of the specimen:

'In the Leverian Museum is one of these [*Mascarinus*], with the mask in front. The ground colour of the plumage the same as in the above [as Brisson (1760), see below], but irregularly sprinkled with white feathers throughout; the tail, part white, part brown, but not regular; some of the quills and tail feathers being wholly white, while the opposites, which should have answered them, were white and brown: it is a particular and beautiful *lusus naturae*.'

Both skins are now faded, and in the 1790s, the wings and tail of the Paris specimen were severely damaged due to sulphuric acid fumigation in an attempt to eliminate pests (Milne-Edwards & Oustalet 1893). Most depictions of Mascarene Parrot are biased by the faded coloration of the specimens and early descriptions and illustrations, which depict the bird with a purplish head, black mask, pale brown body with darker wings and tail, and white bases to the lateral rectrices (see Hume 2007). However, birds described in life differed significantly, with Dubois (1674: 172) in 1671–72 providing the best description: 'Parrots a little bigger than pigeons, with plumage the colour of squirrel fur [blackish brown: see Mourer-Chauviré *et al.* 1999], a black hood on the head, the beak very large and the colour of fire.'

Brisson (1760: 315) gave the following description of a fresh skin: 'head and neck ash-grey; back, wings, rump and underparts very dark ash-grey; tail dark ash-grey, with lateral feathers white at base; bare skin around eye region, bill, bare skin around upper bill and iris bright red; legs and feet pale flesh; claws grey-brown' (translation from Hume 2007). Little of the original coloration is discernible in the two extant skins (Fig. 6); only the black mask and red bill are clearly visible.

MNHN (Muséum National d'Histoire Naturelle, Paris) 211 (Fig. 6a). No details exist as to this specimen's provenance, but probably it was one of the live individuals that resided in Paris in the late 1700s (Hume 2007). Overall coloration uniform pale brown, with slightly darker primaries and secondaries; first two primaries with white bases; underparts



Figure 6. The two extant specimens of Mascarene Parrot *Mascarinus mascarinus*: Fig. 6a (top left) holotype MNHN 211 (Julian P. Hume); Fig. 6b (top right) NMW 50.688, dorsal and lateral views (Julian P. Hume); Fig. 6c (below) illustration of both specimens, drawn to scale (Julian P. Hume). The greyish-blue head of the Paris holotype (centre left and centre) is not discernible in the Vienna specimen, and the tail has been reconstructed. The irregular white feathering in the Vienna skin is due to poor diet in captivity.

paler; head brown with black mask; tail dark brown with white bases to lateral feathers; bill bright red; legs greyish brown.

NMW (Naturhistorisches Museum Wien) 50.688 (Fig. 6b). The Vienna specimen was purchased from the sale of the Leverian collection in 1806 (Pelzeln 1873, Schifter 1994). Nothing else is known about it. Overall uniform brown, greyer on the head and neck, with individual white feathers on mantle, back, rump and underparts; primaries pure white (one side has been clipped), secondaries white with dark brown tips; head brown with black mask; tail has white and dark brown feathers; legs and feet reddish brown.

The pale brown coloration is clearly an artefact of fading due to light exposure, from grey to brown (Hume 2007, van Grouw 2013), which has occurred in other ancient skins that were predominantly grey or black in life, but are now brown, e.g. a Captain James Cook specimen of Hawaii 'O'o *Moho nobilis*, and Townsend's Bunting *Spiza townsendi* (pers. obs., this paper). The red bill and black mask are unaffected. The Vienna skin exhibits random white feathering on the body, with white primaries and asymmetrical white tail feathers, which is almost certainly a result of food deficiency. It is more than likely that the bird was a long-term captive (H. Schifter pers. comm.), perhaps being another of those birds alive in Paris during the 1770s (Hume 2007). The clipped primaries further suggest that it was caged. The dietary requirements of parrots were doubtless poorly known in the 18th century, and almost certainly inadequate for maintaining a healthy bird. This specimen of *Mascarinus* was probably therefore unable to extract sufficient quantities of the amino acid tyrosine from its food, which is necessary for normal melanin synthesis. In consequence, white feathers appeared in the plumage. In nearly all other parrots, the affected feathers would be yellow (or orange / red) instead of white because psittacin would still have been present. However, vasa parrots *Coracopsis* sp. and Mascarene Parrot are the only species that naturally lack psittacin in their plumage (HvG unpubl.).

The affinities of *Mascarinus* are obscure and not satisfactorily resolved. Based on coloration and skeletal morphology, it has been considered related to south-east Asian Psittaculini (Hume 2007), whereas molecular evidence places it with Lesser Vasa Parrot *Coracopsis nigra* (Kundu *et al.* 2012); however, the latter result has been questioned (Joseph *et al.* 2012, Safford & Hawkins 2013). Whether the lack of psittacin in both genera represents convergent evolution or supports a close relationship remain unclear.

CAROLINA PARAKEET *Conuropsis carolinensis* (Linnaeus, 1758)

Formerly present over much of the eastern USA, from Florida and southern Virginia west to eastern Texas, Oklahoma, Kansas and Nebraska. It has been divided into two subspecies, Eastern Carolina Parakeet *C. c. carolinensis* and Western Carolina Parakeet *C. c. ludovicianus*, separated by the Appalachians (Snyder & Russell 2002). Considered common when described in the late 1700s, but as early as 1831 the species was rapidly declining as a result of persecution due to its habit of damaging fruiting crops. The birds disappeared in advance of European settlement of the west and, as the species became rarer, there was an increase in collecting for aviculture. By the end of the 19th century, Carolina Parakeet was almost extinct, and the last confirmed report from the wild was in Florida on 18 April 1904 (McKinley 1985). Several parakeets were kept in captivity, but breeding success was low and mortality high. The last bird died in Cincinnati Zoo on 21 February 1918 (Hume & Walters 2012), apparently in the same enclosure in which the last Passenger Pigeon had expired just four years earlier.

Carolina Parakeet is known from at least 720 skins and 16 skeletons (Hahn 1963, Luther 1996) and c.50 eggs, but not all of the latter are considered authentic (McKinley 1977). The nominate subspecies was generally green with a bluish tint, paler on the underparts;



Figure 7a (left). Carolina Parakeet *Conuropsis carolinensis* NMW 50.795 showing the red suffusion aberration; Fig. 7b (right) normal-coloured bird BMNH 1896.12.1.57, dorsal, ventral and lateral views (Julian P. Hume / © Natural History Museum, Tring). This condition is due to long-term confinement and poor diet

forehead, lores, bare skin around eye and upper cheeks orange; rest of head and upper part of neck, bend of wing, carpal edge and thighs yellow; outer webs of primaries yellow at base; tail green; bill yellowish horn; iris pale brown, legs and feet pinkish-brown. The western race differed in being greener, with less bluish tint, having less yellow on wings and being generally paler. As far as we are aware, there has not previously been any description of colour aberrations in the species.

NMW (Naturhistorisches Museum Wien) 50.795 (Fig. 7a). Purchased from the Leverian sale in 1806, it appears that it may have been a captive individual (data from label). It differs dramatically from normal-coloured specimens (Fig. 7b), the green of the mantle and back being replaced by brownish orange and the underparts with yellow, with more orange in the central breast. The wing-coverts are green, richly suffused orange, whereas the primaries and tail are unaffected, being the usual green. The yellow of the head is also replaced by orange, but the bill, legs and feet are normal. A second captive specimen (NHMW 50.682) exhibits similar coloration and was also purchased from the Leverian sale.

The aberrant coloration exhibited by these birds is caused by an increase and abnormal distribution of red / orange psittacin, a condition known in parrots as red suffusion (Martin 2002). In very rare cases, the increase of red pigment is due to inheritable factors (mutations), but usually it is ill health and / or food deficiency that are the cause (A. K. Jones pers. comm.). Protein deficiency and liver diseases are widely recognised as causing persistent reddish feathering, and lack of direct sunlight, presumably resulting in a lack of vitamin D, may also be a contributory factor. Given that the Vienna specimen was in captivity prior to 1806, when little was known about natural diet, the red suffusion was probably the result of poor physical condition and / or food deficiency.

GEORGE EDWARDS' PARROT *Amazona* sp. (Fig. 8a)

In 1764, George Edwards, the celebrated 18th-century naturalist, painter and author, produced a watercolour of an unknown parrot (see Fuller 2000: 209; Fig. 8a). The painting



bears the inscription: 'A very uncommon parrot from Jamaica. Drawn from Nature the size of life by G. Edwards, July 1764.' On the back in Edwards' own hand is a more detailed description, repeated here verbatim:

'The insides of the wings and under Side of the tail is of a Durlis [meaning unknown] yellow, the colours of the upper sides casting faintly through them. This bird was lent to me by Dr. Alexander Russel and is preserved in his collection. It was shot in Jamaica and brought Dried to England. The people on Jamaica did not remember Ever to have Seen one of this species of Parrots before.

Geo. Edwards, July, 1764.

Some of the fethers have their tipps red and Others have them yellow. The fethers on the under sides, Back and rump have yellow with fine transverse lines of red.'



Figure 8a (top). Watercolour dated July 1764 by George Edwards of an *Amazona* parrot, probably *A. collaria*, exhibiting the opaline aberration; the skin was taken on Jamaica and brought to England, but its whereabouts are unknown (© Errol Fuller). Fig. 8b (below). The two extant Jamaican *Amazona* parrots, Yellow-billed Amazon *A. collaria* BMNH 1891.4.1.32, far left dorsal, and second from right ventral views; Black-billed Amazon *A. agilis* BMNH 1845.4.29.3, second from left dorsal, and second from right ventral views, alongside a Cuban Amazon *A. leucocephala* BMNH1890.6.1.158, third from left dorsal, and far right ventral views (Hein van Grouw / © Natural History Museum, Tring).

TABLE 1

Measurements of Jamaican *Amazona* parrots compared with Edwards' Parrot painting. All specimens held at Natural History Museum, Tring. TL = Total length; WL = Wing length; HL = Head length (head and bill); BD = Bill depth. {n = number of specimens}; (M = mean); Range = smallest to largest; [SD = Standard deviation]. Edwards' Parrot falls within low range of *A. agilis* in all measurements except head length and bill depth, which are too large compared with other measurements, suggesting that the painting was not accurately drawn to scale.

Species	TL {n} (M) Range [SD]	WL {n} (M) Range [SD]	HL {n} (M) Range [SD]	BD {n} (M) Range [SD]
<i>Amazona collaria</i>	{8} (256.2) 225–280 [20.48]	{8} (178.7) 175–190 [5.82]	{8} (58.5) 53–70 [6.04]	{8}(27.1) 26.0–28.0 [0.99]
<i>Amazona agilis</i>	{6} (238.3) 225–245 [8.16]	{6}(166.0) 155–175 [7.79]	{6}(56.6) 55–60 [2.58]	{6} (24.0) 23.0–25.0 [0.89]
Edwards' Parrot	{1} (243)	{1}(165.0)	{1}(62.0)	{1} (25.0)

Because of the uniqueness of this specimen and the fact that it is associated with one of the West Indian Islands, where so many parrot species have become extinct (Rothschild 1907, Greenway 1967, Fuller 1987, 2000, Hume & Walters 2012, Wiley & Kirwan 2013), George Edwards' parrot has been discussed as a possibly extinct species (Shuker 1999, Fuller 2000). It bears a strong resemblance to an *Amazona* parrot, a widespread genus in Middle and South America as well as the West Indies (Forshaw 1989, Juniper & Parr 1998). Furthermore, two extant *Amazona* are native to Jamaica, Yellow-billed Amazon *A. collaria*, with a mean 25.62 cm in total length ($n = 8$), and Black-billed Amazon *A. agilis*, mean 23.83 cm ($n = 6$) (Table 1). The supposed life-size rendition of Edwards' Parrot measures c.24.3 cm long (from top of head to tail tip), is intermediate between *A. agilis* and *A. collaria*, and fractionally larger than *A. agilis*. However, wing length is shorter, while combined head and bill length is much larger than either species; bill depth is intermediate between the two. This suggests that Edwards' 'life-size' rendition is not accurate, and that any measurements from the illustration must be viewed with great caution.

Yellow-billed Amazon (Fig. 8b) is predominantly apple-green, with blue on the head merging into green, throat and lower cheeks pinkish, greater wing-coverts, alula and outer webs of flight feathers blue, uppertail green with yellow tips and red basally. Black-billed Amazon (Fig. 8b) is mainly green, with red primary-coverts, blue primaries, darker blue secondaries, and green uppertail with outer tail feathers red at base of inner webs. Edwards' depiction has predominantly red coloration, but more importantly it shows the blue in the primaries as being unaffected. Edwards' Parrot may have exhibited an inheritable form of red suffusion, but more probably the colour was caused by a mutation known as opaline (see Kakapo). This gene markedly reduces the distribution of melanin, especially in the body plumage, and increases the spread of psittacin; this pigment is strongly emphasised in species with red, orange or pink psittacin (Martin 2002). Normally, Yellow-billed Amazon has reddish-pink psittacin in its plumage, therefore we suggest that Edwards' Parrot was not an extinct species, but an opaline aberration of Yellow-billed Amazon, with increased deposits of psittacin. It is less likely to be an aberrant Black-billed Amazon due to the lack of red psittacin in the normal plumage coloration (wild type) and the black bill (Fig. 8b). Although not from Jamaica, if there is any doubt concerning the collection locality, Cuban Amazon *A. leucocephala* (Fig. 8b) might also be considered as another strong candidate for Edwards's Parrot. This species has even more reddish-pink psittacin in its plumage than *A. collaria*.

Strigopidae

KAKAPO *Strigops habroptilus* Gray, 1845

Formerly occurred on North Island, South Island and Stewart Island, and prior to human occupation of the islands had one of the widest distributions of any New Zealand bird (Gibbs 2007). It is the only known flightless parrot, which made it extremely vulnerable to human disturbance. Kakapo began to decline following Polynesian settlement and this accelerated with the arrival of European settlers. The introduction of mammalian predators, especially rats, mustelids, domestic cats and dogs (Sutherland 2002), rapidly eliminated it from most areas, and the demand for museum skins in the late 19th century, when thousands were collected (Butler 1989), reduced the species to a few remote localities. The last report on North Island was in 1927, three males were recorded on South Island in 1987, but have not been recorded since, and the last record on Stewart Island was in 1997, when a female was transferred to predator-free Codfish Island (Powlesland *et al.* 2006). Due to intense conservation management, around 126 individuals survive on four offshore islets (BirdLife International 2013), but the future of the Kakapo is far from secure.

A nocturnal, cryptic species, its plumage provides perfect camouflage in its natural habitat of mossy, damp forest. The upperparts are olive-yellow and moss-green barred or mottled black or dark brownish grey; underparts pale greenish yellow streaked brown, forehead yellowish brown; and face, neck, belly and undertail-coverts more yellowish, streaked pale green and finely mottled brownish grey. Nevertheless, there is much individual variation. The bill is pearly grey with an ivory tip, iris dark brown, and legs and feet greyish-brown. However, at least two wild-caught yellow specimens of Kakapo exist.

CMNZ (Canterbury Museum, New Zealand) Av2059 (Fig. 9a). This specimen was captured by the Bradshaw brothers in 1898 near Cromarty, Fiordland, which is in Kisbee Bay in Preservation Inlet (Galbreath 1989). Walter Buller, the New Zealand ornithologist and dealer, kept it alive on a diet of potatoes before it became part of his collection (Butler 1989). It was also illustrated in an originally unpublished painting entitled 'Two Kakapos' by J. G. Keulemans (Fig. 9c; Galbreath 1989). Buller (1905) recorded that the entire plumage was vivid canary yellow, fading to pale yellow on the cheeks and throat; the bill was white and the legs and feet flesh-coloured. It is very clear from Buller's account that he considered it to be one of his most precious specimens.

The yellow coloration is almost certainly due to the mutation *ino*, which can be described as 'a strong qualitative reduction of melanin' (van Grouw 2013). Among parrot breeders, this mutation is known as *lutino*, because of the predominant yellow colour. In *ino* mutations, melanin synthesis scarcely occurs, which results in the yellow psittacin becoming clearly visible. Because *ino* is a recessive and sex-linked mutation (van Grouw 2013), a wild-caught *ino* Kakapo is likely to be female (see Passenger Pigeon).

AM (Auckland War Memorial Museum) LB8526 (Fig. 9b). A second aberrant specimen, a relaxed mount, was collected by G. Mueller, a surveyor and engineer, in Jackson Bay, South Westland, prior to 1888 (Buller 1888: 178). Although superficially similar to the *ino* Kakapo described above (Fig. 9a), it differs in having natural green tips to the feathering (unaffected melanin deposits) in parts of its plumage, especially on the head, mantle and wings. This aberration vaguely resembles certain forms of recessive leucism in parrots (Martin 2002), but the overall appearance strongly suggests opaline (see Edwards' Parrot), a condition that alters pigment distribution. In this specimen, the presence of unaffected melanin only in the feather tips (especially on head and mantle), the absence of melanin (barring) in the tail and outer webs of the flight feathers, and because the melanin in the inner webs is unaffected, further supports an opaline aberration. Because this mutation is



Figure 9. Three colour aberrations exhibited by Kakapo *Strigops habroptilus*: Fig. 9a (top left). Ino aberration CMNZ Av2059, dorsal, lateral and ventral views (© Paul Scofield / Canterbury Museum, New Zealand); Fig. 9b (top right) opaline aberration AM LB8526, dorsal, lateral and ventral views (© Jason Frogatt / Auckland War Memorial Museum); Fig. 9c (centre left) originally unpublished painting of CMNZ Av2059 by John Gerrard Keulemans entitled 'Two Kakapos' (from Galbreath 1989); Fig. 9d (centre right) parblue aberration BMNH 1853.6.9.1 type of *S. greyi*, dorsal, lateral and ventral views (© Natural History Museum, Tring); Fig. 9e (bottom left) mounted bird in the collection of Errol Fuller (Julian P. Hume); Fig. 9f (bottom right) normal-coloured Kakapo BMNH 1927.12.18.1 (Hein van Grouw / © Natural History Museum, Tring) .

proven to be recessive and sex-linked in all parrots (Martin 2002), and if our opaline determination is correct, the AM specimen is probably female.

BMNH (Natural History Museum, Tring) 1853.6.9.1 (Fig. 9d). The reduction of melanin resulting in yellow is not the only colour aberration exhibited in Kakapo,

as similar reduction of psittacin produces individuals with predominantly blue plumage. One notable specimen (BMNH 1853.6.9.1) is the holotype of *S. greyii* (Fig. 9d), which has an intense blue hue to the upperparts and some on the underparts, and was originally considered to be a different species (Gray 1862). A second specimen, owned by E. Fuller, is extensively marked with turquoise-blue (Fig. 9e). In BMNH 1853.6.9.1, the tail and flight feathers are particularly worn, which strongly suggests that it was kept in captivity. In both specimens, the upperparts exhibit the more extensive and stronger blue hue. Although the BMNH specimen was seemingly a captive, the absence of psittacin is almost certainly not due to confinement. Reduction in intensity of yellow psittacin due to poor physical health (mostly liver diseases) or a chronically deficient diet is extremely rare in parrots (A. K. Jones *in litt.* 2013), so it is more likely that the Tring specimen was caught because it was an unusual coloration and subsequently kept in captivity. We believe, therefore, that both of the above-mentioned specimens exhibited the parblue aberration (see Rodrigues Parakeet).

Because this mutation can be extremely variable depending on the wild type, the phenotype can exhibit blue coloration that is unevenly distributed. In the case of a parblue Kakapo, the olive and moss-green upperparts in a normal-coloured bird (Fig. 9f) are more likely to exhibit stronger blue than the more yellowish-green underparts.

Callaeidae

HUIA *Heteralocha acutirostris* (Gould, 1837)

The largest member of the New Zealand endemic family, the Callaeidae (wattlebirds), and confined to North Island, Huia exhibited extreme sexual dimorphism in the bill, the male's being relatively short and slightly decurved, and the female's much longer and heavily curved. The sexes evolved different foraging techniques; males used their strong, short bill for chiseling at hard substrates such as decaying wood to extract insect larvae, whereas females used their long, thin bill for probing crevices (Buller 1873). The fossil record reveals that it was originally widespread on North Island (Worthy & Holdaway 2002), but by the time Europeans arrived the species was largely restricted to the south of the island. Huia declined rapidly as human settlement proceeded (Buller 1905) and widespread destruction of undisturbed, old-growth forest appears to have been a major factor in its demise (Morris & Smith 1995). As it became rarer, large numbers were taken for the feather trade and museums; by the late 19th century, Huia was effectively extinct (Hume & Walters 2012). A few were recorded between 1890 and 1907, with the last confirmed sighting on 28 December 1907 (Myers 1923) despite claims that it survived until at least the 1960s.

Huia is known from hundreds of skins (Fuller 2000); a unique egg and subfossil remains are at the Museum of New Zealand, Wellington. General coloration was black with green gloss; terminal tail band white; facial wattles orange; bill ivory; iris brown, legs and feet black. The sexes were similar; the juvenile duller, with a brownish wash. A specimen illustrated by Keulemans *c.*1900, London, for Buller (1905) entitled 'Three Huia', but never published, depicts a pure white individual (Keulemans & Coldewey 1982) (Fig. 10). Buller was told that the specimen was for sale, but when he inquired about it, the owner had already sold the bird (Buller 1905); its whereabouts are now unknown.

Although the painting by Keulemans was probably made from a mounted specimen and therefore the dark eye is not reliable; it is unlikely that the individual exhibited true albinism. Albinism, from the Latin *Albus* (= white), is defined as a 'total lack of melanins in feathers, eyes and skin' (van Grouw 2013). The complete lack of melanin is due to the hereditary absence of the enzyme tyrosinase in the pigment cells, as this enzyme is necessary for initiating melanin synthesis; melanin cannot be created without it (Fox &



Figure 10. Unpublished illustration by John Gerard Keulemans of a female ino Huia *Heteralocha acutirostris* (far right) (© Te Papa 1993-0029-6). We have been unable to locate this specimen.

Vevers 1960). In almost all cases, this results in a completely colourless bird, whereas the red or pinkish hue present in the eyes and skin is caused by blood being visible through the colourless tissue. Albinos rarely occur in the wild, although the mutation is not uncommon in birds. Their scarcity is due to the absence of melanin in the eye, which makes them extremely light-sensitive and susceptible to damage from sunlight, and they also have a poor depth of vision. Therefore, it is not primarily the white plumage that makes albinos vulnerable in the wild, but their poor eyesight; most succumb to starvation and predation soon after fledging (van Grouw 2013).

The bird illustrated by Keulemans (Fig. 10) appears to be adult, which almost certainly eliminates albinism as a cause. It is more likely that progressive greying, leucism or ino was involved. In progressive greying, the bird would have moulted several times before becoming entirely white, but an aberrant pied Huia would surely have been a target for collectors; it is unlikely that such a bird went unnoticed, especially as it survived to adulthood. Leucism, which is a congenital and heritable absence of pigment cells from all of the skin areas where they would normally provide the growing feather with pigment, is very rare in wild birds (van Grouw 2012, 2013), and thus probably can be ruled out. As ino is not uncommon in wild birds, and individuals can be all white, it is the most likely explanation for the aberration. The fresh plumage of an ino may show some very pale coloration, but it is the strong bleaching effect of natural light that rapidly turns the bird almost pure white. Furthermore, although the eyes of an ino are also reddish due to the reduction of melanin, they do not suffer the poor eyesight of an albino. As ino birds survive comparatively well in the wild and the mutation is not uncommon, we believe that Keulemans illustrated a Huia exhibiting this condition.

Although we cannot be absolutely certain about the colour aberration of this Huia without a specimen, the fact that the illustrated bird is a female strongly supports the recessive and sex-linked mutation characteristic of an ino (van Grouw 2012, 2103).

Cardinalidae

TOWNSEND'S BUNTING *Spiza townsendi* (Audubon, 1834)

The unique type (Fig. 11a) was collected by J. K. Townsend on 11 May 1833, at New Garden, Chester County, Pennsylvania, and described the following year (Audubon 1834). There has been much debate as to its status, it being variously considered an extinct species (e.g. Paynter 1970, AOU 1983), a colour variant of Dickcissel *S. americana* (Parkes 1985) or a hybrid female *S. americana* × male Blue Grosbeak *Passerina caerulea* (E. Coues in Sharpe 1888). The type (USNM 10282) is in poor condition, with the original coloration now barely discernible; the specimen has foxed, producing an overall wash of pale brownish beige (Fig. 11b).

Audubon (1834; Fig. 11c) described the fresh plumage as having the upperparts, head, neck, sides and upper breast slate-blue; back and upperwings tinged yellowish brown, streaked black on interscapular area; eyestripe, chin, throat, central line on underparts and edge of wing white; black-spotted line from lower corner of mandible down side of throat, connecting with crescent of streaks on upper edge of slate-blue breast. Adult male Dickcissel (Fig. 11d) has olive-grey crown and cheeks, brown mantle streaked black on back, wings darker, rusty patch on shoulder, and superciliary stripe and underparts yellow, becoming buff on belly, with a black throat patch. Variable dark streaking occurs on the flanks and sometimes the belly. Females (Fig. 11d) have a brown crown and cheeks, with black-streaked flanks. Juvenile males (Fig. 11d) are browner, and the throat patch is black-speckled. Juvenile females are duller and browner, and have black or brown speckling on upper breast.

Parkes (1985) suggested that Townsend's Bunting was a female colour variant of Dickcissel that lacked normal carotenoid pigments, resulting in the complete absence of yellow. Holt (2002–03) questioned this conclusion, as Townsend explicitly stated that the specimen was male, but considered that it was an aberrant first-year male Dickcissel. Our comparison of adult males, females and juvenile Dickcissels with the unique skin and original illustration of Townsend's Bunting (Audubon 1834) suggests that the situation is far more complex. For example, the lack of yellow due to diet or a single genetic change would result in the bird lacking all yellow pigments, leaving the melanins unaffected (Martin 2002).

If Townsend's Bunting was a female Dickcissel as suggested by Parkes (1985), the diagnostic brown crown and cheeks should still be present. Townsend stated that it was a male, so it should have exhibited the black throat patch, unless juvenile. Finally, Holt's (2002–03) suggestion that the specimen was a juvenile male is supported by the lack of a full black throat patch, but juvenile males are brown above, not grey. In the Townsend's Bunting specimen, there is black speckling (eumelanin) concentrated on the sides of the upper breast, no dark streaking on the flanks, and the upperparts are grey. This coloration and pattern is not found in any plumage of Dickcissel.

At this stage, we cannot determine if the specimen of Townsend's Bunting is the result of hybridisation, a colour aberration, or caused by some other genetic change. That it might be an extinct species is highly unlikely, but it cannot be ruled out. No molecular work has been undertaken on the skin, but mtDNA analysis may be the only way to resolve this conundrum.



Figure 11. Townsend's Bunting *Spiza townsendi*: Fig. 11a (top) holotype, USNM 10282, male (Julian P. Hume); Fig. 11b (above left) illustration showing the specimen today (above), and how it would have looked when described by Audubon in 1834 (below) (Julian P. Hume); Fig. 11c (above right) from Audubon (1834); Fig. 11d (left) Dickcissel *S. americana*, from left to right in lateral view, adult male BMNH 1899.2.1.4108, juvenile male BMNH 1885.13.14.147, and adult female BMNH 1899.2.1.4126 (Hein van Grouw / © Natural History Museum, Tring). The cause of this probable colour aberration is unclear.

Discussion

Colour aberrations are not uncommon in birds (van Grouw 2006, 2013), so it is unsurprising that they occur in extinct and threatened species. However, few of these extinct bird colour aberrations had been analysed, despite the specimens themselves being apparently well known. The factors involved in producing unusual coloration can be complex, and it appears that in some species discussed here, illness and poor diet in captivity resulted in aberrant plumage. There may also be a bias in collecting from wild populations, e.g. the parblue aberration of *Psittacula exsul*, white *Porphyrio albus* or parblue and yellow specimens of *Strigops habroptilus*, as it is more likely that an unusual-coloured example was collected rather than normal-coloured birds. However, despite >1,500 skins of Passenger Pigeon, >700 skins of Carolina Parakeet, and hundreds of Huias having been collected, we have only located single colour aberrations of Passenger Pigeon and Huia, and two Carolina Parakeets, none previously described in the literature. During the 19th century, the demand for unusual colour varieties of birds was extremely high and examples

TABLE 2

Causes and effects of colour aberrations of extinct and endangered birds discussed in the text. *Conditions caused by physical factors and not by true genetic aberrations.

Colour aberration	Cause	Effect	Species exhibiting mutation
Progressive Greying	Partial or total lack of melanins in feathers due to progressive loss of pigment cells in some or all of the skin areas with age.	All-white plumage or all-white feathers mixed with normal-coloured feathers. Bill and feet can be normal-coloured or pink. Always normal-coloured eyes.	Lord Howe Gallinule <i>Porphyrio albus</i>
Melanism	Abnormal deposit of melanin in skin and / or feathers.	Normal pattern and / or pigment distribution is changed, but plumage is not necessarily darker.	Sharpe's Rail <i>Gallirallus sharpei</i>
Brown	Qualitative reduction of eumelanin due to incomplete synthesis (oxidation) of eumelanin.	Black becomes brown.	Passenger Pigeon <i>Ectopistes migratorius</i>
Red Suffusion*	Poor physical condition in captivity.	Reddish-orange psittacin randomly spread through the plumage.	Carolina Parakeet <i>Conuropsis carolinensis</i>
Pigment loss*	Due to food deficiency, lacks sufficient quantities of tyrosine in diet, resulting in disturbed melanin synthesis.	Random white feathering intermixed with normal-colours; bill and feet normal-coloured.	Mascarene Parrot <i>Mascarinus mascarinus</i>
Opaline ⁽¹⁾	Reduced melanin distribution, especially in the body plumage, and an enhanced spread of psittacin, notably red psittacin.	A predominant reddish coloration with minimal dark (melanin) plumage markings.	Edwards' Parrot <i>Amazona cf. collaria</i>
Opaline ⁽²⁾	Reduced melanin distribution, especially in the body plumage.	Predominant yellow coloration with minimal dark (melanin) plumage markings.	Kakapo <i>Strigops habroptilus</i>
Ino ⁽¹⁾	Strong qualitative reduction of melanin.	Yellow psittacin (lutino) clearly visible	Kakapo <i>Strigops habroptilus</i>
Parblue ⁽¹⁾	Quantitative reduction of psittacin.	Coloration between green and blue.	Kakapo <i>Strigops habroptilus</i>
Parblue ⁽²⁾	As above.	Coloration between green and blue.	Rodrigues Parakeet <i>Psittacula exsul</i>
Ino ⁽²⁾	As above	Pale, cream-coloured feathering that is rapidly bleached to white by exposure to light. Paler bare parts, reddish eyes.	Huia <i>Heteralocha acutirostris</i>
Undetermined	Lack of lipochrome pigments? Hybridisation?	Loss of yellow pigmentation	Townsend's Bunting <i>Spiza townsendi</i>

of extinct or endangered species were particularly sought after; a yellow Kakapo owned by Buller was considered to be one of his most prized possessions.

In ornithology in general, colour aberrations are poorly understood, which has been further exacerbated by incorrect terminology (van Grouw 2006, 2012, 2013). For example, almost all birds that exhibit any white feathering are termed 'partially albinistic', and this is often applied to extinct birds too, e.g. the Vienna Mascarene Parrot. The inherent condition of true albinism cannot, by definition, be partial. Either true albinism is present, whereby the individual lacks the enzyme tyrosinase, or white feathering can be explained by other factors, e.g. leucism, ino, progressive greying and poor diet (van Grouw 2006, 2012, 2013). Studies of extant birds that exhibit unusual coloration can assist understanding of why similar aberrations occurred in extinct species, and can sometimes provide new information about the bird's ecology or a specimen's history. In these cases in particular, it is important to understand the processes involved and to use correct terminology (Table 2). The aim of this study is to highlight extinct or endangered bird species that exhibit colour aberrations and we would welcome hearing from curators with additional specimens of interest. It is probable that many more examples exist than those discussed here.

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The Critically Endangered Mascarene Petrel *Pseudobulweria aterrima*: identification and behaviour at sea, historical discovery of breeding sites, and breeding ecology on Réunion, Indian Ocean

by Hadoram Shirihai, Tony Pym, María San Román & Vincent Bretagnolle

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SUMMARY.—Results from pelagic expeditions to study Mascarene Petrel *Pseudobulweria aterrima* off Réunion, Indian Ocean, in December 2012, are presented. At-sea identification features, flight characters and feeding behaviour are described, as well as comparisons with confusion taxa. Adult plumage, the least known, is described in detail. Photographs, believed to be the first of this species taken at sea, are presented. One shows a female with an egg inside her body, providing evidence of return from pre-laying exodus and adding to understanding of the breeding cycle. Thirty-three individuals were recorded during three days at sea. Nine presumed breeding burrows, at six different sites, were found on Réunion in 1997–99 and the background to this significant discovery is included, together with an updated population estimate for this elusive species.

The Critically Endangered Mascarene Petrel *Pseudobulweria aterrima* is one of the least known of the world's Procellariiformes (e.g. Brooke 2004, Gangloff *et al.* 2012). Recent molecular work (Bretagnolle *et al.* 1998, Gangloff *et al.* 2012) confirmed *P. aterrima* as a distinct species within the genus *Pseudobulweria*, which comprises four extant species, including the Critically Endangered Fiji Petrel *P. macgillivrayi*, Critically Endangered Beck's Petrel *P. becki*, and Near Threatened Tahiti Petrel *P. rostrata*. The genus is sister to *Puffinus* and *Calonectris* shearwaters, which in turn are most closely related to *Bulweria* and *Procellaria*. It is not closely related to *Pterodroma* petrels as was expected (Imber 1985, Gangloff *et al.* 2012).

Bonaparte described Mascarene Petrel in 1856 as *Procellaria aterrima*, naming it for its black plumage (Jouanin 1970). As a breeder it is endemic to Réunion. A sub-fossil mandible of unknown age was discovered on Rodrigues, Mauritius, 836 km east of Réunion (Bourne 1968) and a roadkill was found in Black Gorges National Park, Mauritius in 2002 (Tatayah *et al.* 2011).

Ten specimens were collected on Réunion in the 19th century (1825–1890, of which just four still exist), but the species was then 'lost' for 80 years until two more were collected, in 1970 and 1973 (Bourne 1965, Jouanin 1970, 1987, Attié *et al.* 1997). Attié *et al.* (1997) listed 31 birds seen at sea between 1978 and 1995 though only ten were considered 'certain' and none was photographed. In 1995 another bird, freshly dead after being hit by a vehicle, was found (Attié *et al.* 1997).

In 1997, VB discovered a colony of *P. aterrima* on Réunion. Attié *et al.* (1997) estimated the total population at <1,000 individuals (range 181–1694 from statistical modelling using at-sea records) and the breeding population to be 250 pairs (range 45–400; assuming that breeders constitute c.25% of total population). French conservation and biological institutes have been involved with various protection measures, e.g. searching for breeding sites and, importantly, rescue and release, where possible, of birds disoriented and grounded by artificial lights (Le Corre *et al.* 1999, 2002, 2003, Riethmuller *et al.* 2012). This has resulted in



Figure 1. Adult Mascarene Petrel *Pseudobulweria aterrima*, off Réunion, December 2012; note unique jizz of heavy bill, well-projecting neck and head, long posterior body, graduated tail, and long slender almost even-width wings with rounded tips (Hadoram Shirihai, © Tubenoses Project)



Figure 2. Adult Mascarene Petrel *Pseudobulweria aterrima*, off Réunion, December 2012; note characteristic head shape, deep bill and tapering posterior body (Hadoram Shirihai, © Tubenoses Project)

25 being rescued in 1996–2010 (Riethmuller *et al.* 2012) with another three in 2011 (Kohler *et al.* 2012). Despite the existence of specimens, and that live birds have been grounded, it is only relatively recently that the species' morphometrics have been detailed (Attié *et al.* 1997, Riethmuller *et al.* 2012).

Following our success in studying Beck's Petrel in the Bismarck Sea, Papua New Guinea (Shirihai 2008), and Fiji Petrel off Gau, Fiji, western Polynesia (Shirihai *et al.* 2009), we decided to apply proven techniques off Réunion, to locate Mascarene Petrel. HS, TP & MSR have field experience with all four *Pseudobulweria* and their confusion species, which makes us uniquely placed to comment on the at-sea identification of Mascarene Petrel, and the difficulty in separating it from other dark petrels.

Riethmuller *et al.* (2012) stated that 18 adults, 12 juveniles and six birds of indeterminate age were collected or grounded in 1834–2010, although photographs of 4–6 different grounded birds available to us were all fledged juveniles. The physical appearance of adults / immatures is least known, therefore we describe these plumages and provide guidance for ageing. Because Mascarene Petrel is generally an 'almost nondescript all-dark petrel', aspects of its shape and proportions, flight modes and behaviour, e.g. foraging techniques, are of major importance for identification.

Our observations confirm that structurally and behaviourally Mascarene Petrel belongs within the genus *Pseudobulweria* and that it shares several features with its congeners; the smaller-sized dark-plumaged *P. macgillivrayi*, the almost similarly sized but white-bellied *P. becki*, and the distinctly larger and white-bellied *P. rostrata* (Fig. 3). Measurements of the four *Pseudobulweria* appear in Table 1.



Figure 3. Specimens of the four extant *Pseudobulweria* petrels, from largest to smallest: Tahiti *P. rostrata* (left), Beck's *P. becki*, Mascarene *P. aterrima* and Fiji Petrels *P. macgillivrayi*; for information concerning the Beck's specimen see Shirihihi (2008), for the Mascarene specimen see Bourne (1965) and the Fiji Petrel specimen see Shirihihi et al. (2009) (Hadoram Shirihihi, © Natural History Museum, Tring)

TABLE 1

Measurements of the four species of *Pseudobulweria*. *P. aterrima* specimens were measured by VB, live bird measurements (') from Riethmuller et al. (2012). All measurements of other species by VB. Wing length = chord, culmen = tip to feathers, bill depth at hook. Specimens at AMNH (New York), UMZC (Cambridge), RMNH (Leiden), MHNR (Réunion), MNHN (Paris), AMS (Sydney), NMNZ (Wellington), BMNH (Tring), FM (Suva). Museum acronyms explained in Acknowledgements.

Sample sizes given in first column, and shown in other columns only where different.							
<i>P. aterrima</i>		Wing length	Tarsus	Culmen	Bill depth	Tail	Mass
Adult	Specimens	238.4 ± 8.4 (8)	39.6 ± 2.15	28.1 ± 2.0	11.4 ± 1.0 (6)	100.4 ± 6.0	222 ± 14.1 (2)
	Live birds ¹	245.6 ± 8.3 (14)	39.7 ± 1.13	27.7 ± 1.27	10.7 ± 0.8 (13)	106.4 ± 7.7	221.5 ± 28.1 (13)
Fledglings	Live birds ¹	243.7 ± 10.5 (15)	39.9 ± 1.10	27.6 ± 1.17	10.3 ± 0.54 (14)	106.7 ± 9.4 (6)	213.3 ± 29.4
<i>P. becki</i>	Specimens	244.7 ± 5.7 (3)	37.9 ± 1.42	26.8 ± 2.02	10.4 ± 2.31	100.3 ± 0.58	-
<i>P. macgillivrayi</i> (adults and one fledgling)	Specimens and live birds	215.8 ± 9.43 (4)	36.4 ± 0.51 (3)	25.7 ± 1.14	10.2 ± 1.81 (3)	87.5 ± 5.06	131.5 ± 16.26 (2)
<i>P. rostrata</i> (adults)	Specimens	294.8 ± 7.08 (43)	48.0 ± 1.98	35.9 ± 1.34	14.4 ± 0.67	119.6 ± 4.64	374.2 ± 23.3 (6)

TABLE 2
Summary results of pelagic field work, off Réunion, Indian Ocean, 17, 18, 22 December 2012.

	17 Dec 2012	18 Dec 2012	22 Dec 2012
Mascarene Petrels seen	2	14	17
Period chumming	2 hours	3.5 hours	3.25 hours
Location	21°34.005'S, 55°24.960'E 15 nm from St Pierre	21°42.586'S, 55°21.648'E 25 nm from St. Pierre	21°42.586'S, 55°21.648'E 25 nm from St. Pierre
Sea conditions	Beaufort 2 / 3 light to gentle breeze creating wavelets	Beaufort 2–4 light to moderate breeze creating small waves	Beaufort 4 / 5 moderate to fresh breeze creating moderate waves
Other species seen	See Table 4		

Methodology

The same approach to our previous expeditions, searching for Beck's Petrel in 2007 and Fiji Petrel in 2009, was followed. Finding Mascarene at sea, like these petrels, was not by chance but was fully researched in advance. From our experience working with the other *Pseudobulweria* (HS, TP, MSR; see Shirihai 2008, Shirihai *et al.* 2009), and Zino's Petrel *Pterodroma madeira* in Madeira (Shirihai 2009), we had developed a tested method for deciding on sea positions to deploy the chum, to attract petrels close to the boat.

Timing.—Expedition dates were 17 December 2012 to 1 January 2013. Three days were spent at sea, 17, 18 and 22 December 2012, though more were originally allowed. We concur that the species breeds during the austral summer on Réunion (<http://birdlife.org/datazone/speciesfactsheet.php?id=3878>; Le Corre 1999, Le Corre *et al.* 1999, 2002, Riethmuller *et al.* 2012) with an incubation period during October to January (but see Breeding ecology).

Chumming.—Our objective was to observe the birds attracted, and gather data on identification and behaviour of Mascarene Petrel. Large frozen blocks of chum were used, prepared on Réunion ahead of our arrival and kept in cold storage. Each block weighed *c.* 25 kg, the maximum manageable size, and comprised 70% grained or cut fish offal with oil, and 30% fresh water; this was frozen then cut using a mechanical ice saw. We had refined and perfected the mix on previous expeditions, where it was found that floating blocks are highly attractive to tubenoses. Frozen blocks allow the offal to float longer, permitting petrels to take the food before it sinks, whilst creating a pungent and constant oil slick, the aroma being pushed downwind to petrels some miles away. One or two blocks were dropped overboard at hourly intervals.

Study area.—The tropical Indian Ocean island of Réunion (21°08'S, 55°32'E) lies 675 km east of Madagascar and 170 km south-west of Mauritius, the nearest island (Fig. 4). An overseas department of France, it has a population of >837,000 people, the vast majority in the coastal lowlands. The island is 63 km long and 45 km wide. It is mainly mountainous, dominated by two volcanos, one active, and four calderas. These forested highlands have many canyons and cliff faces where Barau's Petrels *Pterodroma baraui* and Tropical Shearwaters *Puffinus bailloni* breed, and Mascarene Petrels have long been suspected of doing so, with calling birds confirmed. In Creole villages, like Grand Bassin, the legend of the *Timise*, an imaginary black flying creature that emits chilling nocturnal screams, is now known to relate to Mascarene Petrels (VB pers. obs.; Riethmuller *et al.* 2012).

Information on breeding locations was known to VB, while Riethmuller *et al.* (2012) showed historical locations of grounded birds. Also, we considered the location of Réunion in relation to neighbouring islands and the direction of prevailing winds. The latter are

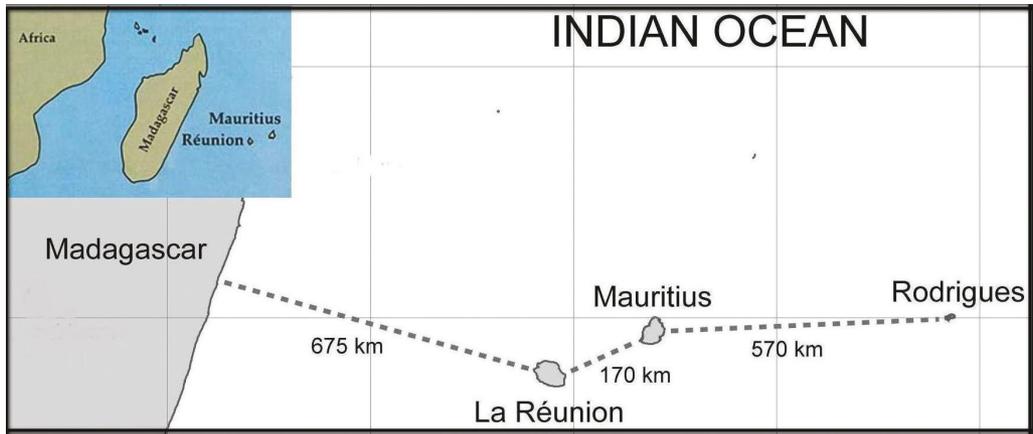


Figure 4. Geographic position of Réunion, Indian Ocean.



Figure 5. Study area: at-sea GPS positions where Mascarene Petrels *Pseudobulweria aterrima* were recorded by us (red). Most were heading towards land as dusk approached. Position 1: two on 17 December 2012. Position 2: 14 birds on 18 December 2012 and 17 on 22 December 2012. Approximate locations of calling birds marked purple. The vast majority of birds grounded (21 of 30; 70% of those in 1970–2010) were in the area shaded yellow (see Riethmuller *et al.* 2012). Satellite images courtesy of Google Inc. All rights reserved © 2013 DigitalGlobe.

TABLE 3

Mean wingspan, body lengths and weights of tubenose species frequenting Réunion waters; in declining order from heaviest in mass. Data from Attié *et al.* (1997), Brooke (2004) and Onley & Scofield (2007).

	Wingspan (cm)	Body length (cm)	Weight (g)
Great-winged Petrel <i>Pterodroma macroptera</i>	97	39	587
Wedge-tailed Shearwater <i>Ardenna pacifica</i>	98	45	415
Barau's Petrel <i>Pterodroma baraui</i>	96	38	400
Trindade Petrel <i>Pterodroma arminjoniana</i>	99	38	393
Mascarene Petrel <i>Pseudobulweria aterrima</i>	88	35	222
Tropical Shearwater <i>Puffinus bailloni</i>	69	31	217
Jouanin's Petrel <i>Bulweria fallax</i>	79	31	173
Bulwer's Petrel <i>Bulweria bulwerii</i>	67	27	100

relevant to seabird flight dynamics, and was coincidentally the same as in Fiji. We deduced that birds would arrive from the south or south-west aided by the south-easterly wind. Records at sea, in Attié *et al.* (1997), appeared to largely confirm this. We concentrated effort south-southwest of the island, and chummed 15 nautical miles (21°34.005'S, 55°24.960'E) and 25 nm (21°42.586'S, 55°21.648'E) from the fishing port of St. Pierre (Fig. 5).

Vessel.—Our base was at Grand Bois in southern Réunion, close to St. Pierre from where we travelled to the survey area in a privately chartered 10-m sports-fishing boat.

Camera equipment and GPS.—Canon EOS-1DX camera body, and 300 mm / F2.8 and 500 mm / F4 lenses. We used a mobile GPS, Garmin Colorado 300 with a marine chart programme, to waymark positions, travel between locations, and log sightings.

Data collection.—Usually the boat drifted just off the chum 'slick', permitting birds to move freely along the slick and to feed undisturbed, while affording us the best angle for observing birds already attracted and incoming. We counted birds and noted activity during sessions of 30–60 minutes. For each species the estimated number of birds during the session and the maximum number seen at one time were recorded. For consistency, the same observer made all counts. These counts were relevant to commoner species found in these waters, especially Barau's Petrel, Wedge-tailed Shearwater *Ardenna pacifica* and Tropical Shearwaters and, most importantly, can be directly compared to the numbers of Mascarene Petrel in any period. At the end of each day we agreed conservative totals. This method is the same as that used in Papua New Guinea, Fiji, Vanuatu, Madeira and Cape Verde (Shirihai 2008, Shirihai *et al.* 2009, 2010, Shirihai & Bretagnolle 2010, Bretagnolle & Shirihai 2011) where counts during chumming were used to monitor numbers of rarer species vs. commoner ones. Each Mascarene Petrel seen was afforded a number (with individual description, behavioural notes and photographic record) used in the analyses below. The three observers (HS, TP, MSR) had appropriate field skills to identify the region's seabirds, and had studied tubenoses at sea over many years, but for any record of rare species, including Mascarene Petrel, the record had to be unanimously considered certain.

Thirty-three Mascarene Petrels were observed, 12 of them photographed. All other petrels seen during the expedition are recorded in Table 4.

TABLE 4
 Petrel species seen during field work off Réunion, Indian Ocean. For scientific names see Table 3.

	17 Dec 2012	18 Dec 2012	22 Dec 2012
Great-winged Petrel			1
Barau's Petrel	>100	300	120
Mascarene Petrel	2	14	17
Wedge-tailed Shearwater	>100	40	50
Tropical Shearwater	>200	50	30
Bulwer's Petrel	1	12	20
Jouanin's Petrel	1	1	1
Wilson's Storm Petrel		1	1
Matsudaira's Storm Petrel		1	

Results

Mascarene Petrel sightings.—Times are local (GMT + four hours). See Table 4 for all species and their numbers. **17 December**—Two together [MP#1, MP#2: photographed] at 19.10–19.15 h, at 21°34.005'S, 55°24.960'E (c.15 nm from St. Pierre). Despite sea conditions being very calm with little wind, i.e. usually unsuitable for viewing gadfly petrels, many were seen (Tables 2, 4). No tubenose showed interest in the well-laid chum trail until, late in the day, a lone Jouanin's Petrel *Bulweria fallax*, followed by a single Bulwer's Petrel *B. bulwerii*, visited the slick, then two Mascarene Petrels. **18 December**—Fourteen during 3.5 hours of chumming, with one remaining for 40 minutes. It was the only species to take any floating morsels. Approaches to the chum; singles at 15.47–15.53 h [MP#3: photographed], 16.11–16.51 h [MP#4: photographed], 17.10–17.15 h [MP#5], 17.21–17.24 h [MP#6], 17.30–17.35 h [MP#7], 17.45 h [MP#8]; then an influx from 18.14 h with singles at 18.14–18.21 h [MP#9: photographed], 18.30 h [MP#10], 18.37 h [MP#11], 18.44 h [MP#12: photographed], two at 18.48–18.53 h [MP#13: photographed, MP#14], two at 19.06–19.15 h [MP#15, MP#16: photographed]. All were at 21°42.586'S, 55°21.648'E (c.25 nm from St. Pierre). **22 December**—Total of 17 individuals came to the chum: two at 16.10–16.58 h [MP#17: photographed, MP#18; both together for first ten minutes, but MP#17 stayed on and off for 48 minutes], one at 17.10–17.15 h [MP#19: photographed], one at 17.20–17.36 h [MP#20], three at 17.52–18.02 h [MP#21–23], one at 18.08–18.18 h [MP#24: photographed]; then an influx from 18.39 h, with three at 18.39–18.44 h [MP#25–27, all visiting briefly then continuing in direction of the island], singles at 18.48 h [MP#28: photographed], 18.50 h [MP#29], 18.55–18.58 h [MP#30: photographed], 19.02–19.06 h [MP#31: photographed], and two at 19.08–19.25 h [MP#32–33]. We discounted five further sightings as possibly the same. All were at 21°42.586'S, 55°21.648'E (c.25 nm from St. Pierre). Summary in Table 2.

Description and at-sea recognition

A full description of Mascarene Petrel follows, based on the 33 birds studied. Our observations confirm that in structure and behaviour *P. aterrima* is a typical *Pseudobulweria*, and given reasonable views can be reliably identified at sea but that it is extremely similar, almost identical, in plumage to Great-winged Petrel *Pterodroma macroptera*.

Size.—We observed Mascarene Petrel directly alongside Barau's Petrels, Wedge-tailed and Tropical Shearwaters (which three species breed on Réunion and are the most frequent offshore), and Bulwer's Petrels, as well as twice with Jouanin's Petrels and once Great-winged Petrel. These observations confirm that Mascarene Petrel is medium-sized



Figures 6–8. Bill structure of Mascarene Petrel *Pseudobulweria aterrima* (left and centre; adults, off Réunion, December 2012) and Great-winged Petrel *Pterodroma macroptera* (right; off Durban, South Africa, November 2013), showing Mascarene’s well-developed latericorn (6a), mandibular unguis (6b), and the large protuberance of the maxillary unguis (6c). Here, extreme variations of the hook tip; on the left lacking, centre maximum, but still shorter and less pointed than in *Pterodroma* (Hadoram Shirihai, © Tubenoses Project)

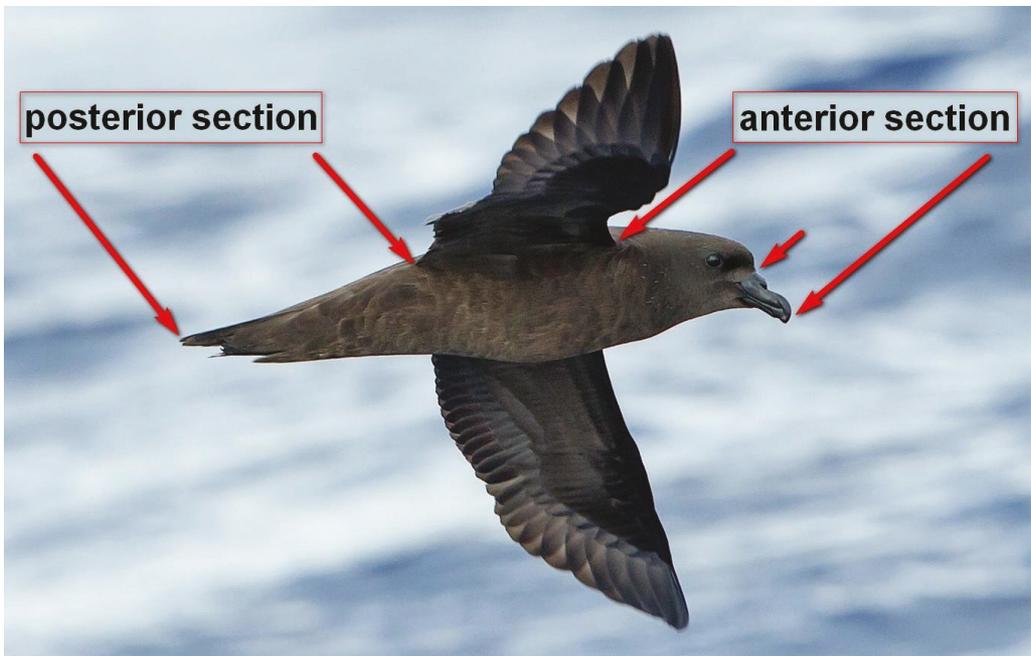


Figure 9. Adult Mascarene Petrel *Pseudobulweria aterrima*, off Réunion, December 2012; diagram describing body structure and proportions—see text (Hadoram Shirihai, © Tubenoses Project)

and somewhat smaller, at least in wingspan, than Barau’s Petrel, Great-winged Petrel and Wedge-tailed Shearwater, by 7–15%, and in overall length is smaller than the first two by 5–10%, and by as much as *c.*20% from the third. However, it is larger and heavier than Tropical Shearwater and Jouanin’s Petrel, by 10–15% in wingspan and 5–10% in overall length. It is much larger than Bulwer’s Petrel, by *c.*20% in wingspan and 15% in length. Total length is *c.*350 mm (Riethmuller *et al.* 2012) and wingspan 880 mm. Perceived size and bulk at sea are corroborated by weights in Table 3 (full measurements appear in Table 1).

Proportions.—Typical *Pseudobulweria* with large bill, well-protruding head and neck, and proportionately long wings, but also a very long posterior section (rear section of body with tail, behind trailing edge of wing; Fig. 9).

Head and bill.—Head in profile rather square, with an almost 90° slope to the forehead, flattish crown, and a noticeable bulge at the apex of the forehead (e.g. Fig. 1). The size and arrangement of the bill plates result in a highly compressed stocky bill, distinctly different from the bill structure of *Pterodroma* (Figs. 6–8). The well-developed latericorn covers 40–50% of the bill volume in profile (in *Pterodroma* 30–40%). Both unguis are well developed, with the maxillary unguis being massive, covering c.30% of the bill in profile, extending from the base of the naricorn and appearing as a huge rounded lump. The hook tip is very short and rounded, lacking the sharp point of most tubenoses. We found the ‘square’, robust bill visible even at distance, and when close the shape and relative size differs from that of Great-winged Petrel (*cf.* Separation from Great-winged Petrel). However, there is some variation and juveniles, probably also immatures, show a slightly slimmer bill, less thickset, with the hook slightly longer and sharper (*cf.* Bare parts).

Wings.—Proportionately narrow, clearly less pointed than Great-winged Petrel, with the ‘hand’ (= primaries) shorter and a more rounded contour to the trailing edge. The ‘arm’ (= secondaries) appears disproportionately narrower and longer, and comprises c.65% of wing breadth (e.g. Figs. 1, 10, 12, 14). Mascarene Petrel has a characteristic narrow wing of relatively even width. The full-stretched wing has the outermost primary (p1) equal to, or falling short of, p3 and perhaps as short as p4, which produces a short rounded ‘hand’. The spread wings in lateral view can appear rounded, but beware a foreshortening effect. When gliding, and the wings become bowed and partially folded, the outermost primary is longest. This deceptive change in wing formula has also been documented for North Atlantic *Pterodroma* (Shirihai et al. 2010).

Body structure.—Unique, noticeably in length of posterior section (e.g. Figs. 9, 10, 12), affording *P. aterrima* a distinctive overall shape in flight and providing a key identification aid. The species’ long posterior section tapers strongly to a very pointed tail; it is at least 50% longer than the head and neck area, and at least 20% longer than the anterior section, i.e. complete neck, head and bill forward of the leading edge of the wing (e.g. Figs. 2, 9, 12). The undertail-coverts almost reach the tail tip; only the tips of the longest rectrices project, further enhancing the elongated posterior section (e.g. Figs. 1, 2, 9, 12).

In profile, the anterior body of Mascarene Petrel comprises a long neck, rather thick at its base, narrowing towards the head, the central body section with a deep and rounded belly, and the posterior body which is well defined, much slimmer, tapers and is perceptibly long, consequently appearing slightly disproportionate (Fig. 9).

The feet were observed on several occasions, prior to landing and when taking off from the water. They do not project beyond the tail, ending far from the tip. The pointed tail is constantly held folded, or partially so, in flight but on landing or take-off it is spread. It is highly graduated and wedge-shaped, not rounded or square-ended as some field guides illustrate (*cf.* Past records of Mascarene Petrel at sea).

Within *Pseudobulweria* Mascarene Petrel is closest in size and proportions to Beck’s but its square head profile, bill structure and long slim rear body are similar to the smaller Fiji Petrel.

Jizz and flight.—All-dark plumage, long rear body, well-projecting neck and head with heavy bill, plus long, slender, almost even-width wings with rounded tips give Mascarene Petrel a characteristic jizz (e.g. Figs. 1, 2, 9, 12). Like other Procellariiformes, flight modes vary markedly with wind speed, direction and behaviour when birds are actively foraging or in transit.

Réunion experiences little wind in November–February, the optimum months to search for Mascarene Petrel offshore; mean wind speed being 18 kph, Beaufort Force 3, gentle breeze (www.wunderground.com, mean over five-year period). During our three days at



Figures 10–13. Adult Mascarene Petrels *Pseudobulweria aterrima*, off Réunion, December 2012: top two images (10, 12) show characteristic shape with well-projecting neck and head, heavy bill, long and slender almost even-width wings with rounded tips, and long posterior body; bottom two (11, 13) show how brown plumage can look almost black in poor light (Hadoram Shirihai, © Tubenoses Project)

sea, we experienced light to fresh winds, Beaufort Force 1–5, i.e. typical conditions. The following describes the usual flight modes of the species off Réunion.

Flight is typical of *Pseudobulweria*: effortless on long wings, sometimes partially bowed, often fully stretched and extended. When gliding into wind the wings are held rather stiff and straight. Not an energetic flyer, wingbeats were neither deep nor fast but supple. In Beaufort Force 4, moderate breeze, flight was deliberate with only a few shallow flaps and some zigzagging advances over a generally straight course. When excited at the chum, more erratic changes of direction were observed, with swift increases in flapping and pouncing glides. In c.35 kph (Beaufort Force 5–6) winds, several birds performed higher arcs, even if characteristically brief; these began as a gradual ascent to c.7 m above the surface, then a moderate or steep descent to quickly return to the ocean. Actions less agile than most *Pterodroma*. Indeed, Mascarene Petrel never performed the graceful, rapid flight with reluctant flapping, or the high, long and steep arcs and dynamic soaring of *Pterodroma*. Seen head-on, or directly from behind, the wings were held slightly below body level forming a shallow arc. We concluded that Mascarene Petrel generally flies rather low, patrolling the surface, and is readily lost to view between waves before suddenly reappearing.

Plumage.—A uniformly dark brown petrel, but at close range and in different lights, contrasting shades between certain feather tracts and subtle coloration patterns evident. The description below details the finest close views and also how the plumage is perceived at distance. Individual variation will be apparent.

In close views, or good photographs, under overcast conditions the head, neck and body show the following contrasting shades: head and neck dark brown, while from about the breast, or level with the wing's leading edge, to the undertail-coverts the body quite abruptly becomes medium brown; there is also a darker patch on the upper flanks, just below the wing. Head and neck are not only darker but more uniformly so, whilst the body from breast downwards is slightly paler and can appear unevenly blotched due to exposed dark feather bases forming diffuse asymmetric barring. In certain lights and angles, some close-up photographs show rusty, even purple-brown, hues (Figs. 1, 15, 20). The degree of such rusty shades and barring can be subtle and varies individually. Furthermore, in photographs, an exceptional pattern of delicate straw-yellow markings on the neck is apparent, tiny spots that become narrow lanceolate shaft-streaks on the lower neck / breast from where they become very faint; the streaks are reminiscent of *Catharacta* skuas although they are fewer, very much smaller and much less noticeable (Figs. 14, 18). Though only visible in very close views, most birds do seem to have them, if varying in number.

The head has a quite well-marked dark loreal mark, from in front of the eye to the side of the forehead, visible in lateral and head-on views, and on some birds further enhanced by pale patches at the base of the forehead-sides. Some also show a rather large dark area around the eye, but it is very ill-defined and paler than the lores, albeit adding to the overall darkness of the head and neck (e.g. Figs. 2, 13, 15).

The upperparts and upperwing lack any distinct pattern being fundamentally concolorous dark brown (Figs. 10, 15). However, in certain lights the lower back, rump to uppertail, lower scapulars / humerals, marginal-coverts, sometimes the exposed secondaries, and perhaps several outer primaries, are darker brown. The bulk of the remaining coverts are slightly paler due to exposed feather bases. No paler carpal bar or any M pattern on the open wings except, at most, a very faint suggestion of this. From above the pale outer webs of the remiges and narrow whitish primary shafts can be visible, especially when the wing is outstretched (Fig. 15).

The underwing is generally dark, with four consistent, clear patterns and contrasting shades, some important for field identification. Firstly, the median and lesser underwing-



Figures 14–15. Adult Mascarene Petrel *Pseudobulweria aterrima*, off Réunion, December 2012; note structure and jizz, darker shades on head and leading and trailing edges to wings, delicate straw-yellow markings on neck, and diffuse asymmetric barring on body (Hadoram Shirihai, © Tubenoses Project)

coverts are almost as dark brown as the head, and are generally darker than the greater coverts and exposed undersides to the remiges, which are more greyish brown. Secondly, a 'marginal' stripe on the fore coverts and carpal area, covering the lesser, inner median and greater primary-coverts, is blackish brown, forming quite a distinctive forewing band. This recalls the pattern on other *Pseudobulweria*, especially Fiji Petrel, but does not project onto the secondary coverts (i.e. there is no ulnar bar) unlike on many gadfly petrels. Thirdly, the tips to the underside of the secondaries are similarly blackish forming a well-defined trailing edge. Fourthly, the five outermost primaries, especially the 2–3 outermost, are also darker brown, forming a rather diffuse dark wingtip. At certain angles this can appear almost black. The darker tracts, described above, form a 'frame' to the underwing (e.g. Figs. 2, 12–14, 16, 18, 22), which is more, or less, pronounced depending on light, angle and distance.

The tail from below just protrudes beyond the undertail-coverts; from above and below, it is dark brown, concolorous with the uppertail-coverts and rump, or perhaps subtly darker, and shows no pattern.

In bright light the brown of the body and upperwing can appear brighter and richer, and if the underwing catches the light the greyer basal remiges and greater coverts appear paler. At certain angles the feathers on the upperparts and upperwing can appear darker,

exaggerating the contrast with the pale outer webs and primary shafts, whilst in direct sunlight the contrast is reduced. In poor light, such as dawn and dusk, the overall brown plumage appears blacker (Figs. 11, 13).

At distance the head and neck usually appear a shade darker than the rest of the body, the underwing looks almost uniformly dark and the complex dark frame to the underwing is invisible, although the relatively darker fore coverts of the underwing and, to a degree, the paler underwing panel is occasionally visible at 300–500 m.

Bare parts.—The bill is essentially black in grounded juveniles, whilst in adults it is more greyish black, or matt black in shade or harsh light. At sea, bills appeared scratched and bleached, a feature known to indicate adults. The bills of adults appear more robust than those of grounded juveniles, though the measured difference in depth is very slight (10.7 mm for adults vs. 10.3 mm for fledglings; Table 1). Conversely, the tip of the maxillary unguis in juveniles is slightly longer and more pointed, but is still valuable in separation from Great-winged Petrel (see below). Irides blackish. Tarsi striking, pale pinkish flesh with a variable pale bluish tinge (= bluish pink) mostly on the webs. Their colour contrasts strongly with that of the body and feet (Fig. 35). The latter are mostly dark brownish black from the outer side of the base of the tarsi over the outer toes. On the middle and inner toes black covers c.70%, with the base of the webs pink; base of middle toe bluish pink and base of inner toe purer blue. The overall coloration of the tarsi and feet is virtually identical to that of Fiji Petrel (Shirihai *et al.* 2009).

Ageing and moult.—All photographs of grounded petrels examined by us were of juveniles. These had fresh plumage, being evenly feathered, with plumage overall plainer and blacker, less brownish than the adults / immatures documented at sea. Adults / immatures showed, to varying degrees, mixed-generation feathers on the body with fresher darker feathers and older paler browner ones, although most remiges and rectrices were of the same generation. Two birds had 2–3 newer inner primaries, which were fresher and darker, and 1–2 outer secondaries, forming moult limits. None of the 33 petrels seen or photographed had moult gaps in the wings or tail. Overall, the remiges and coverts were still rather fresh and we can assume that adults undertake a complete post-breeding moult, presumably sometime in May–October.

Separation from similar species

To reliably identify Mascarene Petrel at sea, or review any photograph considered to be this species, it is necessary to critically assess size, proportions and some of the subtle colour patterns while taking into consideration the effects of light. Previous experience with other species is beneficial, especially the confusion species discussed here. The sea around Réunion, and the Indian Ocean as a whole, supports other all-dark petrels and shearwaters, and we stress that any claimed Mascarene Petrel away from Réunion waters will be difficult to prove unless well photographed. Most confusion taxa described below are illustrated in Pl. 1–2.

Separation from Great-winged Petrel.—Of greatest concern is *Pterodroma (m.) macroptera* to which the following refers, and not the larger Grey-faced Petrel *P. (m.) gouldi*. This Southern Ocean species breeds in the austral winter. In the non-breeding season it occurs mainly at 25–50°S, but does reach further north with records off Réunion. It is most likely to occur in October–February though Attié *et al.* (1997) mentioned records in July–September. Great-winged Petrel is easily misidentified as Mascarene; they have similar all-dark plumage and even the substantial size difference could be misjudged. Mascarene is 15–20% shorter winged (244 mm vs. c.300 mm). Wingspan is c.880 mm in Mascarene and c.970 mm in Great-winged Petrel. Overall length is c.350 mm and c.390 mm, respectively. Body mass



Figures 16–17. Comparison, at distance, between Mascarene Petrel *Pseudobulweria aterrima* (left: off Réunion, December 2012) and Great-winged Petrel *Pterodroma macroptera* (off Crozet Islands, March 2004): note slim outline, length of posterior body and ratio anterior : posterior in Mascarene Petrel, which shows more neck and lacks deep-chested structure of Great-winged; however, on occasion, the species can possess quite similar profiles (Hadoram Shirihai, © Tubenoses Project)



Figures 18–19. Mascarene Petrel *Pseudobulweria aterrima* (left: off Réunion, December 2012) and Great-winged Petrel *Pterodroma macroptera* (off Crozet Islands, March 2004) in gliding flight, showing typical shapes, with Mascarene's even-width, more slender wings and rounder wingtips; note fine straw-yellow spotting / streaking on neck-sides that may be distinctive of Mascarene (Hadoram Shirihai, © Tubenoses Project)

for Mascarene is max. 270 g, whereas Great-winged is usually considerably more than 500 g. Our experience with both species infers that correct evaluation of these size differences, although substantial, is only possible when other species are directly alongside. Extensive previous experience with Great-winged should greatly assist in this process. Mascarene is a less energetic flyer, especially when flying low in light winds, when it can appear heavier and larger than it really is, and conversely Great-winged, being a 'livelier' *Pterodroma*, can in strong winds ostensibly appear smaller and slimmer. Separation is best based on structural differences.

Compared to Great-winged (Figs. 16–23; Pl. 1), the posterior section of Mascarene is longer, more slender, tapering and pointed. Wing shape is narrow and of even width.



Figures 20–21. Comparative close views of Mascarene Petrel *Pseudobulweria aterrima* (left: off Réunion, December 2012) and Great-winged Petrel *Pterodroma macroptera* (off Durban, South Africa, November 2013): on first appearance, practically identical, but note proportions before (anterior section) and after (posterior section) the wing; head shape and bill structure are key features, while the outer primary of this Great-winged is still short and growing (at end of post-nuptial moult) resulting in a rounder wingtip, closer to Mascarene Petrel (Hadoram Shirihai, © Tubenoses Project)



Figures 22–23. Comparative close views when arcing of Mascarene Petrel *Pseudobulweria aterrima* (left: off Réunion, December 2012) and Great-winged Petrel *Pterodroma macroptera* (off Durban, South Africa, November 2013): it is unlikely that observers claiming Mascarene Petrel in the past appreciated the close similarity between the two species (Hadoram Shirihai, © Tubenoses Project)

Great-winged is altogether more stout and thickset with a large rounder head, relatively shorter bull-necked appearance in flight, deep full chest, stockier belly, and broader rear. The latter is due to a shorter projection of the posterior body, which is broad and less tapering. The wing of Great-winged has a longer, more pointed ‘hand’ and a considerably wider ‘arm’. The line of the central body smoothly and gradually becomes the rear, yet in Mascarene there appears to be a noticeable step between the two sections.

Mascarene Petrel is languid in flight, flying relatively low above the water, recalling a shearwater rather than a *Pterodroma* and lacking the dashing aerial manoeuvres of that genus. However, in the non-breeding season, away from Réunion and where storms may occur, the flight could differ. Mascarene displays what we describe crudely as a ‘crucifix’ outline, whereas the overall outline of Great-winged is more ‘anchor-shaped’ with the wings swept back and a squarer tail.

In close views of Mascarene, the more square-shaped head, with its vertical forehead, is very different to the rounder shape of Great-winged and the diagnostic bill structure can be seen; the distal end of the naricorn slopes at 45–50° from the latericorn, less acute than in Great-winged Petrel, and the nasal tubes differ in shape.

Mascarene and Great-winged Petrels have identical plumage; even the delicate patterns and subtly shaded areas appear to overlap. We could not detect any consistent or clear-cut plumage feature that separates them. Mascarene tends to show a better-developed dark ‘frame’ to the underwing, including the ‘forewing band’, but weaker patterning on the upperwing. Many Great-winged in moult, or when fresh, have a bluish-grey cast to the greater and median coverts, which can appear like a distinct upperwing panel, even if ragged; a feature we did not see in Mascarene. However, this is much reduced with wear and only visible in certain light, angles or close views. Many appear as uniformly dark as Mascarene. Head and body plumage is identical except for one feature that might be consistent: Mascarene has faint straw-yellow spots and streaks on the neck, although these vary individually. We studied enlarged photographs of 50+ Great-winged Petrels and none showed this feature, but it requires further checking with birds of different ages and feather wear.

Separation from Wedge-tailed Shearwater.—The dark morph of this shearwater is common off Réunion, and elsewhere in the Indian Ocean, and should prove straightforward to identify if the slender bill is seen. There are two issues to consider. Firstly, the low, lethargic flight of Mascarene Petrel is reminiscent of shearwaters, especially this species. Secondly, they are similar, in that both glide low over the water, moving from low arcing and banking into the wind to slow bursts of wingbeats of short duration. For these reasons, we thought we were being approached by a Wedge-tailed Shearwater only to find it was a Mascarene Petrel and vice versa, but at closer range bill alone identified the species.

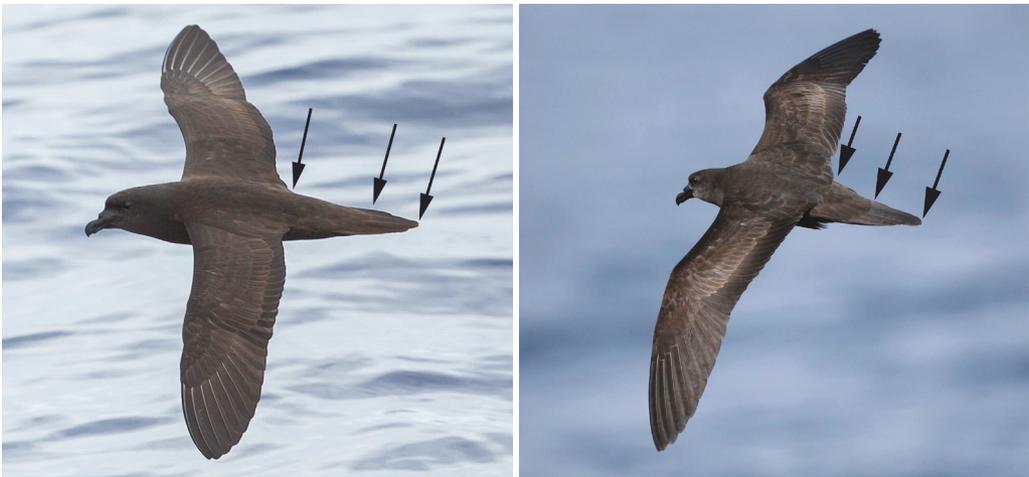


Figures 24–25. Comparison between Mascarene Petrel *Pseudobulweria aterrima* (left) and Wedge-tailed Shearwater *Ardenna pacifica* (right) off Réunion, December 2012, photographed at the same distance; note how they resemble each other in shape and colour, but it is possible to ascertain diagnostic differences in bill, head / neck and tail structures (Hadoram Shirihai, © Tubenoses Project)

We noted that Wedge-tailed Shearwaters off Réunion appeared smaller than in the Pacific. We are unsure if this is geographical variation, or perhaps age-related, but because local Wedge-tailed Shearwaters can appear the same size as Mascarene Petrel, the latter could be overlooked especially among flocks of shearwaters. Confirmation that the approaching bird is a shearwater may require views at 300–500 m and sometimes much closer, 100–200 m, to confirm the bill. Their plumage is rather similar including underwing pattern. The tail of Wedge-tailed is usually longer and the wedge-shaped tip often visible.

Separation from Jouanin's and Bulwer's Petrels.—The two *Bulweria* are dark-plumaged petrels closely related to Mascarene. The larger, Jouanin's, is close in size to Mascarene and can have a quite similar upperwing pattern. Bulwer's Petrel with its smaller size, lighter build, faster and typically fluid flight, and pale upperwing-coverts bar, is usually safely identifiable at sea, but observers need to evaluate size correctly and be aware that, in some lights and certain angles, the upperwing can appear uniform. Bulwer's Petrel breeds on Round Island, off Mauritius, the only known breeding site in the Indian Ocean, and was rather frequently recorded by us, whereas Jouanin's Petrel was uncommon (Table 4). Seasonality of either in Réunion waters is largely unknown. Veit *et al.* (2007) recorded 21 Jouanin's north of Réunion during four days at sea between Mauritius and Mayotte in January 2004. Therefore, any claim of Mascarene Petrel will need to eliminate especially Jouanin's Petrel.

Compared to Mascarene, Jouanin's is smaller and sligher. The leaner silhouette comes from a relatively small head, thin neck, and slim posterior body with proportionately long tail. The square-shaped head with steep forehead and dark lores appear similar, although both species when on the sea can show a rounded crown. When fresh Jouanin's can have uniform upperwings, like Mascarene, though some worn birds have a pale panel on the greater coverts. This feature is highly variable depending on feather wear, and its prominence alters with angle and light. Underwing pattern in both species is similar but Mascarene can show stronger contrast between the brown shading and dark 'frame', whereas the underwing of Jouanin's is more uniform. There may be overlap and the effect of light may render these differences of limited use. We found only two plumage features



Figures 26–27. Comparison between Mascarene Petrel *Pseudobulweria aterrima* (left: off Réunion, December 2012; Hadoram Shirihai, © Tubenoses Project) and Jouanin's Petrel *Bulweria fallax* (off Muscat, Oman, September 2006; © Hanne & Jens Eriksen): some Jouanin's have a characteristic pale upperwing-coverts bar, but note Mascarene's relatively shorter exposed tail-feather projection beyond the longest uppertail-coverts.



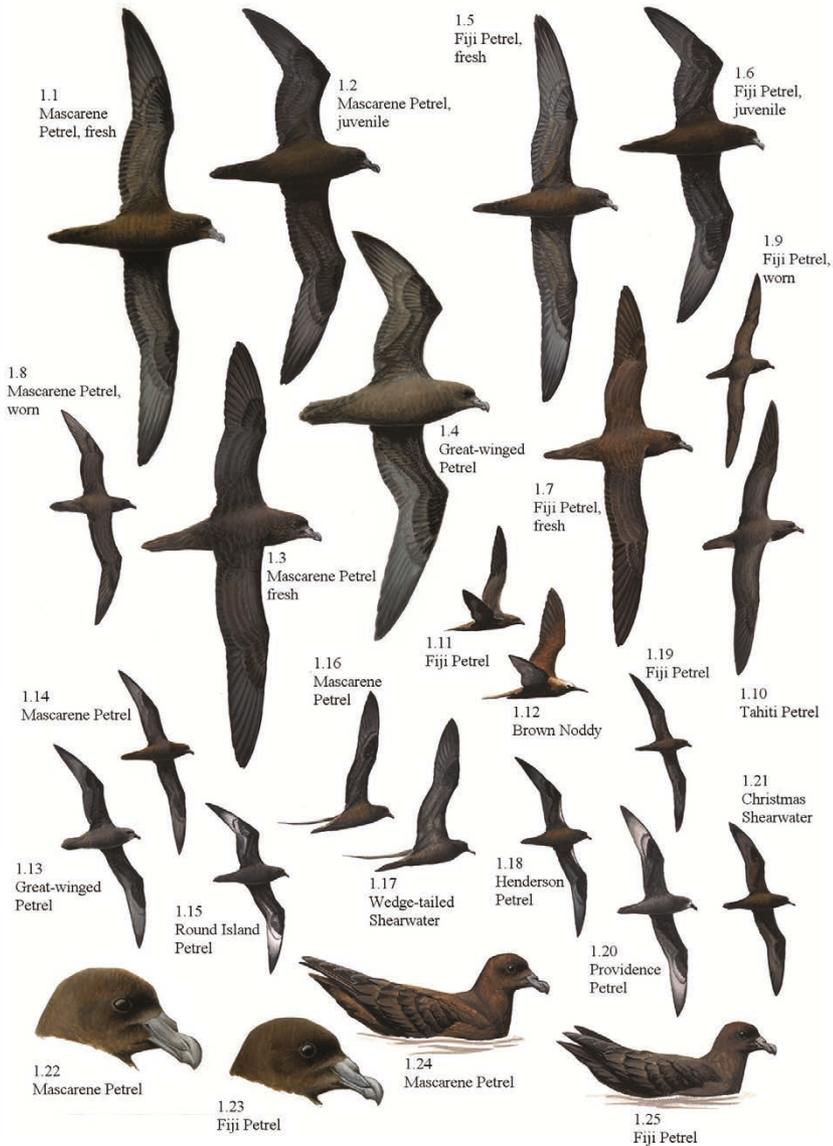
Figures 28–29. Comparison between Mascarene Petrel *Pseudobulweria aterrima* (left: off Réunion, December 2012; Hadoram Shirihai, © Tubenoses Project) and Jouanin's Petrel *Bulweria fallax* (off Hasik, Oman, November 2005; © Hanne & Jens Eriksen): note similar plumage from below, but Jouanin's is smaller, more slender, has a narrow neck, long bill (usually held forwards and downwards) and typically a different flight; several older records of Mascarene Petrel did not eliminate this species.

that could help: 1. Mascarene has unique delicate straw-yellow markings on the neck; and 2. Jouanin's often has some dull greyish to slate-blue hue on the head and / or neck and often the upperparts, especially scapulars. However, these features vary individually, requiring cautious use and close views. Identification of Mascarene and Jouanin's rests therefore on correct evaluation of size and shape, flight mode and behaviour.

Their wing lengths are identical, although they have different wingspans, *c.*880 mm in Mascarene vs. *c.*790 mm in Jouanin's; overall length is longer also, *c.*350 mm vs. *c.*310 mm, whilst body mass is 28% larger for Mascarene at mean 222 g vs. 173 g for Jouanin's (Table 3). The proportionately longer wings of Mascarene are frequently held stiff and the flight is less erratic than Jouanin's, which flies low to the water zigzagging, changing height and altering direction more rapidly with shorter glides and arcs. In calm conditions Jouanin's has graceful flight, consistent and purposeful with deep elastic wingbeats, reminiscent of a small skua, followed by glides. Jouanin's wings may appear more angular, the 'arms' often pointing forwards so the carpal is the most forward point of the wing, the 'hands' swept backwards producing an impression of effortless flight.

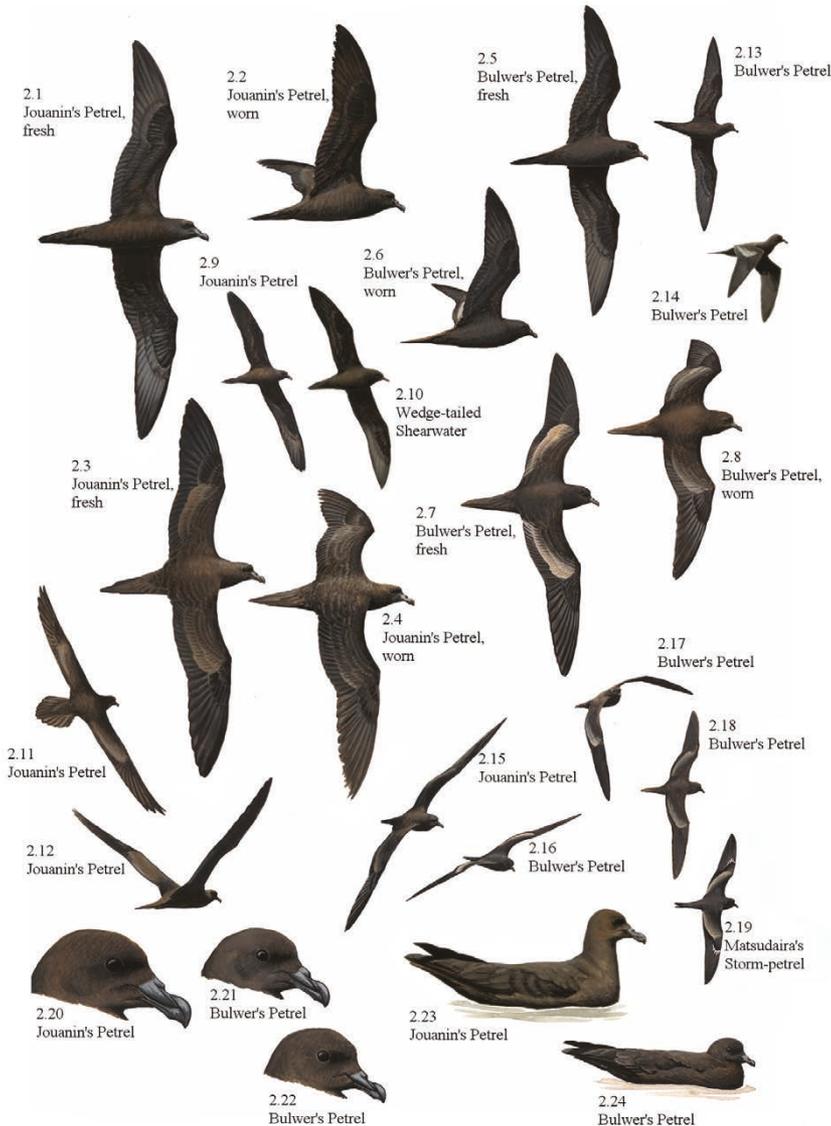
The posterior body of Jouanin's is more streamlined than Mascarene. When Jouanin's is seen with the tail fully folded, the projection of the posterior body is *c.*60% longer than that of the head and neck before the wing, and *c.*30% longer than the anterior section to the bill tip, vs. *c.*50% and *c.*20% respectively in Mascarene (Figs. 26–29). Thus, both have similar proportions, and any differences should be used cautiously in comparing the two species, especially as the tails of *Bulweria* can be shorter due to wear, and the outline of a bird may alter with flight mode and angle.

Jouanin's has a proportionately longer tail than Mascarene. It is graduated with a noticeable 'step' midway along the outer tail. Tail to wing ratio is 98.7% compared to 97.7% in Mascarene. The length of the exposed central rectrices, beyond the uppertail-coverts, is half the total posterior body (from the trailing edge) yet in Mascarene the exposed tail feathers comprise only one-third of the total posterior body (Figs. 26–27). Jouanin's has a



Plates 1–2: Plate 1: Mascarene Petrel *Pseudobulweria aterrima* and other dark, medium–large petrels and shearwaters of the Indian Ocean, plus various Pacific Ocean species that could be confused with Mascarene (and Fiji *Pseudobulweria macgillivrayi*) Petrel. Plate 2: the closely related, all-dark, medium–small Jouanin’s *Bulweria fallax* and Bulwer’s Petrels *B. bulwerii*. Identifying Mascarene from the very similar Great-winged Petrel *Pterodroma macroptera* is the greatest challenge, followed by Jouanin’s Petrel. Dark-morph Wedge-tailed Shearwater *Ardenna pacifica* and ‘Round Island’ Petrel *Pterodroma arminjoniana* (and hybrids) also require eliminating. Mascarene and Fiji Petrels are extremely similar, differing principally in size; both are illustrated, being possible vagrants, for example, to parts of the Pacific; in this region other all-dark tubenoses may occur, so Henderson *Pterodroma atrata* and Providence Petrels *P. solandri*, together with Christmas Shearwater *Puffinus nativitatis*, are included.

Variation between fresh adult **Mascarene Petrel** (1.1, 1.3), worn (1.8) and juvenile (1.2) with its slimmer bill and more uniformly dark plumage; the latter exaggerated in poor light. Corresponding variation shown within **Fiji Petrel** i.e. fresh adult (1.5, 1.7), worn (1.9) and similar/darker juvenile (1.6). Fresh adult **Great-winged Petrel** (1.4) is portrayed, the similarity between the two shown in 1.13 and 1.14. Dark-morph ‘**Round Island**’ Petrel (1.15), here a relatively well-marked bird with clear white primary bases (a rare variation has darker underwings). For size comparison, relevant around Fiji, **Tahiti Petrel** *Pseudobulweria rostrata* is included; its white belly is diagnostic, but is sometimes invisible from above (1.10). At first glance, or distant view, narrow bill of dark-morph **Wedge-tailed Shearwater** (1.17) cannot be seen, and it can be



confused with Mascarene and Fiji Petrels. **Christmas Shearwater** (1.21) is confusable with Fiji Petrel (1.19), e.g. when arcing or gliding. **Brown Noddy** *Anous stolidus* (1.12) could appear superficially similar, if seen briefly in low flight between waves, or at distance (cf. Fiji Petrel 1.11). **Providence Petrel** (1.20) and the poorly known all-dark, slender **Henderson Petrel** (1.18) are shown for comparison; note underwing patterns. The head / bill profiles, and postures on water, of both adult Mascarene (1.22, 1.24) and Fiji Petrels (1.23, 1.25) are illustrated.

Jouanin's Petrel, here showing fresh (2.1, 2.3) and worn (2.2, 2.4) adults, their jizz changing with posture, and corresponding plumages of **Bulwer's Petrel** (2.5–2.8). Dark-morph **Wedge-tailed Shearwater** (2.10) shown here for jizz and size comparisons with Jouanin's Petrel. Different flight modes of Jouanin's and Bulwer's Petrels showing variation and impressions, e.g. particularly large, bulky and dark Bulwer's Petrel (2.8), and when head-on (2.16), compared to an atypical slim Jouanin's Petrel (2.12, 2.15), with a spread tail (2.11) imparting a more rounded shape. Bulwer's Petrel in flight (2.13, 2.14, 2.17) showing typical elastic flight of both *Bulweria*, which compare (2.18) with all-dark **Matsudaira's Storm Petrel** *Oceanodroma matsudairae* (2.19). Head / bill profiles and postures on water of adult Jouanin's (2.20, 2.23) and Bulwer's Petrels (2.21, 2.22, 2.24) also depicted.

Plates by Tim Worfolk, © Tubenoses Project, from *Albatrosses, petrels and shearwaters of the world: a handbook to their taxonomy, identification, ecology and conservation* (Shirihai & Bretagnolle, illustrated by T. Worfolk, in prep., Christopher Helm, London).

proportionately smaller head and more slender neck, with a deep and long bill, often held forwards and downwards. Correct evaluation of bill size and structure, including formation and relative sizes of the plates could prove crucial with any photographic identification.

Potential confusion with other dark-coloured petrels and shearwaters.—The location of Réunion and its relationship to the Subtropical Convergence to the south, where tropical, temperate and much colder waters merge, brings various tubenose species together in varying numbers. These include several dark-coloured petrels and shearwaters that could be confused with Mascarene Petrel: dark-morph Trindade Petrel *Pterodroma arminjoniana* plus hybrids from Round Island, Mauritius (collectively 'Round Island Petrel'), Kermadec *P. neglecta*, Soft-plumaged *P. mollis*, Kerguelen *Lugensa brevirostris*, White-chinned *Procellaria aequinoctialis* and Spectacled Petrels *P. conspicillata*, and Sooty *Ardenna grisea* and Flesh-footed Shearwaters *A. carneipes*. Fortunately, all these possess diagnostic features and are readily identifiable, despite having all-dark or mostly dark plumage.

Genetic analysis has confirmed that Trindade Petrel on Round Island is interbreeding with Kermadec and Herald Petrels *Pterodroma heraldica* (Brown *et al.* 2010) resulting in mixed plumages. Nevertheless, recent studies by HS has shown that all dark-morph individuals retain sufficiently obvious white / pale patches on the underside of the primaries and always lack the all-dark underwings of Mascarene Petrel.

Dark-morph Soft-plumaged Petrel is fully described in Shirihai (2007) and is more common in the Indian Ocean than elsewhere. It is unclear if dark individuals represent a gradual cline in variation, possibly being phases and not morphs, as there is broad variation with extremes looking almost all dark. When fresh these are greyish in ground colour but when worn are more brownish-tinged; even these are easily eliminated vs. Mascarene. They have pale inner underwing-coverts, at least a trace of the species' usual breast-band and upperwing 'M' pattern, a shorter tail, and typical *Pterodroma* shape and flight.

Kerguelen Petrel occurs in subantarctic and Antarctic waters, and is generally all dark. Many guides do not describe its uniqueness well; it is a squat-bodied, large-headed petrel with distinctive long arched wings and a short tail. Flight includes towering above the water surface. When close, it has diagnostic silver-grey flashes to the primaries, greater primary-coverts and lesser and marginal forewing-coverts, especially in strong light (Shirihai 2007). It is very different to Mascarene Petrel.

The two *Procellaria*, White-chinned and Spectacled Petrels, are wholly, or largely, blackish brown but readily separated from Mascarene by their much larger size, different structure and proportions, including shorter tail. Both have a mainly yellowish bill, and Spectacled has distinctive though variable white 'spectacles' (*cf.* Shirihai 2007).

The two *Ardenna* are readily separated by shape and flight, but Flesh-footed Shearwater can adopt a casual direct flight with less flapping, superficially resembling a petrel when distant. It has a distinct pinkish base to the bill. Sooty Shearwater has diagnostic silvery linings / flashes in the underwings. Both have a slim bill, very different to that of Mascarene Petrel. Sooty Shearwater might be considered an unlikely confusion species, yet in Fiji (Shirihai *et al.* 2009) we witnessed experienced observers misidentify it for Fiji Petrel.

Mascarene versus Fiji Petrel.—The extremely similar and very rare Fiji Petrel is known only from the island of Gau. The prospect of it reaching the western Indian Ocean appears highly unlikely, but possible vagrancy of Fiji and Mascarene Petrels to the north-east Indian or south-west Pacific Oceans, e.g. off south-east Australia, cannot be ignored. They are virtually identical in structure and plumage (Pl. 1) but differ markedly in size: Mascarene wingspan 880 mm, total length 350 mm; Fiji Petrel 730 mm and 290 mm, respectively (Shirihai *et al.* 2009). Even the bill, including the plates, is the same, although that of Fiji Petrel is clearly smaller. The variable straw-yellow markings on the neck of Mascarene

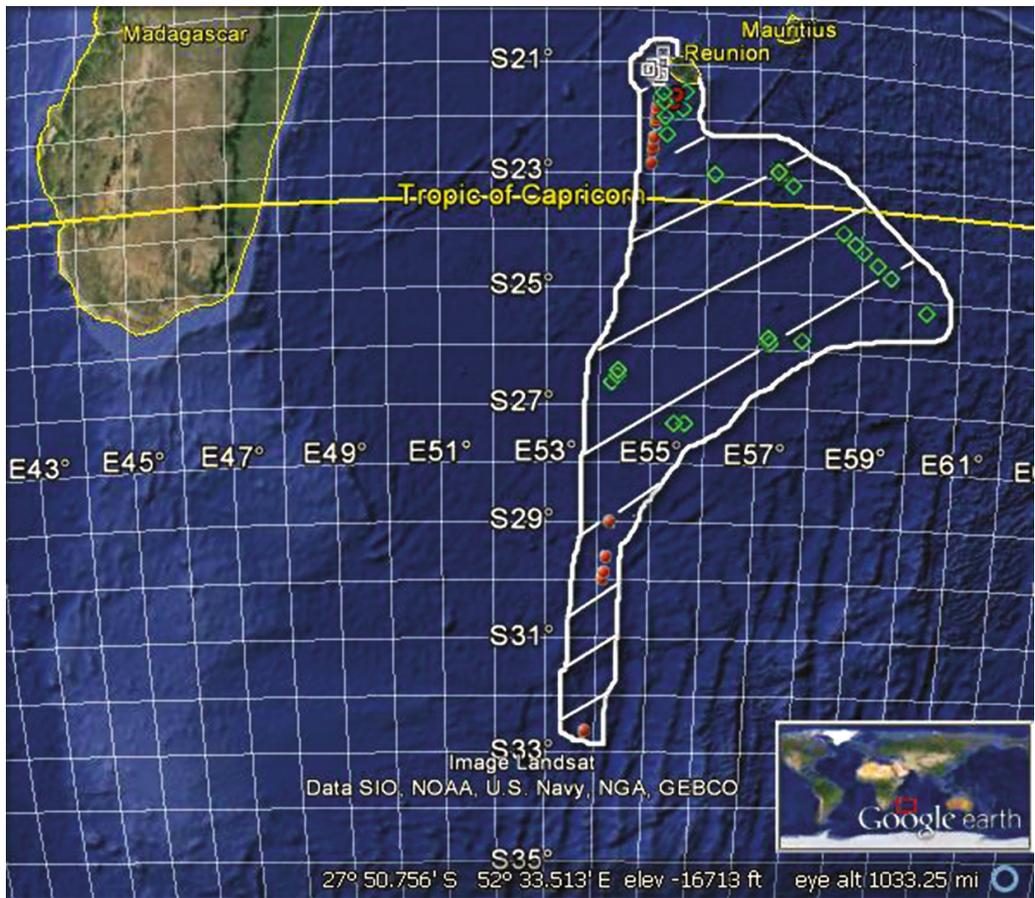


Figure 30. Distribution of Mascarene Petrel *Pseudobulweria aterrima* showing all ‘probable’ and ‘certain’ records at sea, to December 2012 (hatched area), $n = 80$, with records mainly close to Réunion as expected. See Fig. 5 for precise coordinates of our expedition. Note that all records were between south-east and north-west of Réunion and in November–March. Pelagic distribution in non-breeding season unknown. Legend: green open diamonds = records from Attie *et al.* 1997; red-filled circles = records from Hyrenbach (2003); white open squares = records from S. Jaquemet (*in litt.* 2013); and red open circles = this expedition. Satellite images courtesy of Google Inc. All rights reserved © 2013 DigitalGlobe.

appear to be lacking in Fiji Petrel. Vagrants of either species would be extremely difficult to confirm without biometric measurements and / or genetic analysis.

Past records of Mascarene Petrel at sea

Errors in the literature.—The literature has repeatedly described the species wrongly, with inaccurate illustrations of profile, proportions, tail shape, etc. Emphasis has been placed on the wrong features, and erroneous and misleading statements have been perpetuated. Most recently, Safford & Hawkins (2013) stated that ‘head and tail protrude equally either side of wings’ and ‘tail always appears rounded rather than pointed’. Skerrett & Disley (2011) mistakenly described the tail as ‘short’ and ‘squarish’. Onley & Scofield (2007) placed undue emphasis on underwing pattern, describing it incorrectly, i.e. ‘presence of silvery underwing should separate Mascarene from most dark petrels and shearwaters’,

an error that possibly arose from photographs of grounded birds in which camera flash had reflected ('burnt') the paler bases to the underwing-coverts (an illusion reported in Shirihai *et al.* 2009). The plates in all these works illustrate these misconceptions, adding to the perplexity.

Also, with no certain at-sea field descriptions, many authors have assumed the flight of Mascarene to be the same as most *Pterodroma*. For example, Harrison (1987) stated 'probably swift, bounding in high arcs with rather heavy powerful jizz' and Enticott & Tipling (1997) 'probably swift with typical high *Pterodroma* arcs'. The regional field guide (Sinclair & Langrand 1998) stated 'flight action similar to Great-winged Petrel but more agile' so correctly compares it with the principal confusion species, but is difficult to interpret even with knowledge of Great-winged. These descriptions do not convey the build or outline of Mascarene Petrel, or describe the flight, at least in the usual conditions off Réunion. All of these errors, taken together, have led unsurprisingly to uncertainty and misidentifications.

At sea records off Réunion and elsewhere.—Several claimed Mascarene Petrel records have since proven spurious due to lack of knowledge of confusion species, e.g. a specimen from Mumbai recently confirmed as a Jouanin's Petrel (Praveen & Kelvin 2013) and a record from Oman now also known to be of Jouanin's Petrel (*cf.* Jouanin 1970, 1996, Bourne 1996).

Attié *et al.* (1997) listed 28 sightings, involving 31 birds, between 7 November and 29 March, 1978–95, of which ten were ranked 'certain'; all were at latitudes south of Réunion with the furthest 580 km from the island. The other records were classed as 'possible' (four) and 'probable' (17). Jaquemet *et al.* (2004) recorded seven Mascarene Petrels during 36 research cruises from Réunion in February 2001–October 2002; most trips were west of the island, their records of Mascarene were in the sector north-west to south-west. In January 2003 multiple observers undertaking the Southern Indian Ocean Marine Bird and Mammal Survey, aboard a research vessel that departed Réunion for Western Australia, recorded 14 Mascarene Petrels; all were south-southwest of Réunion, the furthest 1320 km from the island (Hyrenbach 2003). It is notable that another scientific cruise, the 38-day Southern Indian Ocean Seamounts that departed Réunion on 12 November 2009, heading south-east then west to South Africa, recorded 36 seabird taxa but no Mascarene Petrels (Rogers *et al.* 2010).

There have been other claims, for example in trip reports by visiting birders and casual sightings reported on the internet. One involved a posting to Birding-Aus (<http://birding-aus.org>) entitled 'Mascarene Petrel, first record for Australia' (<http://bioacoustics.cse.unsw.edu.au/archives/html/birding-aus/2002-12/msg00335.html>), which claimed >45 Mascarene Petrels during a cruise from Mauritius to the islands of the South Indian Ocean, and finishing in Australia, with one bird in Australian territorial waters. It was stated this record would be submitted to the Birds Australia Records Committee, but it was never received. Hansbro (2004) later wrote that 20 seen between Amsterdam Island and Australia were reconsidered to be Great-winged Petrels. He stated that Mascarene Petrels had followed the ship the second day after leaving Mauritius (behaviour not recorded but possible, whereas Great-winged Petrels certainly do approach and will briefly accompany ships). Photographs were apparently taken of Mascarene Petrels but despite many requests, from HS & TP, the only ones we have seen, as separate communication to others and in a printed flyer advertising a birding cruise, show Great-winged Petrels.

We cannot verify the validity of all records above, nor trace any photographs (by all accounts none were taken), though we assume many were Mascarene Petrels, e.g. given that Attié *et al.* (1997) described the flight and jizz correctly, they could critically check accounts and descriptions. From now, we recommend that any record or photograph be reviewed and judged against the criteria presented here.

Mascarene Petrel behaviour at sea off Réunion

Feeding technique.—Mascarene Petrels took no interest in our small boat, birds flying close, within 10 m, to feed on food floating on the water surface. They appeared to locate the chum slick using smell and sight. Approach was focused, with no hesitation, on shallow strong wingbeats, some gliding and slight banking before any change of direction to chum scraps. They appeared more determined than other *Pseudobulweria* but this might have reflected the lack of any larger competitors as Mascarene was usually alone. When landing, wings were held aloft and partially open, remaining so whilst taking food. Take-off involved flapping and the feet running across the water surface before becoming airborne. No calls were heard.

Clearly Mascarene Petrel surface feeds and will scavenge at floating offal, and this behaviour, together with a lack of fear of boats, probably means the species is attracted to bycatch, and is therefore at risk from long-lining and other fishing practices.

Return from pre-laying exodus.—On 22 December 2012 a Mascarene Petrel was photographed at sea with a large egg in the uterus, the protrusion being obvious in the contour of the underbody. The swollen area is just above the cloaca, indicating that it is indeed an egg and not an abnormality or growth (Fig. 36). Petrels are known to have disproportionately huge eggs. We believe this to be the first record of a petrel or any other sea- or landbird to be photographed in flight with an obvious egg inside the body.

This bird was returning from the pre-laying exodus and it is highly likely the egg would have been laid the same night. The unexpectedly large number of Mascarene Petrels recorded on 18 December (14 birds) and 22 December (17) may include, and indicate, an influx of other such individuals.

We were positioned in just one sector of ocean, meaning these numbers may represent a concentration of birds heading towards land from the deep ocean, with numbers increasing closer to land, added to which there was an influx as dusk approached. The two interpretations are either that many more Mascarene Petrels were elsewhere, also heading shorewards or, more probably, that we discovered the principal approach route to the breeding sites.

Range at sea.—All at-sea records, probable or certain, of Mascarene Petrels, have been from south-east clockwise to north-west of Réunion, during November to March inclusive (the breeding season), with the furthest some 1,320 km from the island (Fig. 30). Pelagic range in the non-breeding season is wholly unknown.

Breeding distribution on Réunion

Of the four species of petrels breeding on Réunion it is Mascarene that is elusive. VB began searching for breeding sites in 1987, and continued virtually annually until 2002, in conjunction with a complete breeding survey of Tropical Shearwaters on the island (Bretagnolle *et al.* 2000). Almost all mountains were visited at night and at least once in November–March (austral summer). The first confirmation of a Mascarene Petrel breeding site came when an unidentified call was tape-recorded by C. Attié at l'Entre-Deux in September 1988. Bretagnolle & Attié (1996) wrongly suggested that the call was of an unidentified scops owl, given some similarity to a bird from the Comoros. When VB heard Mascarene Petrel for the first time, on 26 December 1997 at Grand Bassin, he realised their mistake. High-quality tape-recordings were obtained and these confirmed that the bird heard by C. Attié in 1988 was also a Mascarene Petrel. Repeated searches undertaken around Grand Bassin between 1997 and 2002 led eventually to the discovery of nine presumed burrows (i.e. birds calling from the ground) at six separate sites, with one on



Figures 31–35. Adult Mascarene Petrels *Pseudobulweria aterrima*, off Réunion, December 2012, showing feeding behaviour at chum: top image (31) gliding in leisurely flight over the slick, low to the water, to investigate frozen chum block (bottom left). When slowing to land, tail spread briefly and appears rounded; centre-left image (32), patrolling the slick, head-on, wings held slightly lower, forming shallow arc; centre-right image (33), lands on water, swims towards floating food, wings held partially open; bottom-left image (34), hesitancy to examine the food. Only surface food taken, wings always kept open against wind; bottom-right image (35), after feeding, takes off by running on water with wings spread (Hadoram Shirihai, © Tubenoses Project)



Figure 36. Adult female Mascarene Petrel *Pseudobulweria aterrima*, off Réunion, December 2012, with a large egg in the uterus (Hadoram Shirihai, © Tubenoses Project)

27–28 December 1997 having at least four birds calling simultaneously. No burrows were seen, nor searched for, as a decision was taken to avoid climbing on cliffs and ledges that could open pathways for cats or rats. At all times observers stayed strictly to marked paths or riverbeds.

In subsequent years, nocturnal searches were organised by Société d'Études Ornithologiques de la Réunion (SEOR), some years involving as many as 30 people. The most recently published data (Riethmuller *et al.* 2012) show that, in the 2008/09 season, Mascarene Petrels were heard on 17 nights of 34 at one known site, yet during the 2009/10 season the species was heard on just three nights of 55 in the field. The most birds calling simultaneously, at any site over the ten-year period, 2001–10, was three. An online media journal in Réunion (<http://www.clicanoo.re>) reported that SEOR positioned an automatic listening station within the breeding area in 2012 and though operated for >800 hours no calling Mascarene Petrels were recorded. Based on maps in Riethmuller *et al.* (2012), it is presumed that the breeding site described by these authors is one of the six original sites located by VB, although a calling bird in January 2001 was at lower altitude (c.1,150 m, vs. above 1,300 m in Riethmuller *et al.* 2012). Apart from the single at l'Entre-Deux, all known sites where ground-calling birds have been found are in Grand Bassin, within 25 km² and at altitudes of c.500 m to c.1,150 m (most below 900 m). There were additional records of birds calling in flight at several places, all within the same 25 km² area.

Birds calling repeatedly from the ground at night were considered to be males, at the entrance to a burrow, attempting to attract females, which behaviour is observed in other petrels, especially Tahiti Petrel (VB pers. obs.). There is some evidence that these are non-breeders, presumably young birds, searching for a mate with calling continuing for several hours. They could be heard on successive nights at exactly the same sites, but not necessarily in consecutive years, e.g. the site with four calling in 1997 had just two in 1998, and one in 1999 and 2002. Hopefully, these lone birds had found mates and thus call less, as known for other rare species with small numbers like Magenta Petrel *Pterodroma magentae*

(G. Taylor pers. comm.). At the site monitored by Riethmuller *et al.* (2012), steadily less calling was witnessed, which they interpreted as reflecting a declining population, even extinction, but we suggest that any single male had found a partner.

Breeding ecology

Attié *et al.* (1997) summarised breeding phenology and Riethmuller *et al.* (2012) provided additional precision, based on grounded fledglings. Mascarene Petrels return to their colonies in July or August. Riethmuller *et al.* (2012) suggested that copulation occurs during this period, but this is very unlikely as the female would need to store sperm in the oviduct for *c.*3 months. According to Riethmuller *et al.* (2012), egg laying is in October, incubation in October–December, and fledging in March–April. Using the dates of collection of 12 fledglings (assuming this being the day they left the burrow), between 1 March and 4 April, plus one on 27 April, with incubation lasting 48–50 days and chick rearing 73–82 days (based on Warham 1990), egg laying is actually mainly 20 October–20 November, with a single extreme late date on 15 December. Our observation of a female with an egg on 22 December is even later than these dates and the suggested influx of females returning to lay in late December does not match known fledging dates. Tropical petrels in general, and Tahiti Petrel in particular (Villard *et al.* 2006), usually display unsynchronised laying and extended laying periods. We cannot exclude this for Mascarene Petrel since fledglings have been recovered over a two-month period.

Peak calling activity recorded by VB was between 25 December and 30 January. Most vocalising birds would have been non-breeders, which visit the colony most frequently and in largest numbers during the chick-hatching period, as is true in most other petrels (VB pers. obs.). Calling activity started around 20.00 h, on average *c.*1 hour later than that of Tropical Shearwaters.

Population size and conservation

Attié *et al.* (1997) suggested that the world population was *c.*1,000 individuals, and proposed a breeding population of 45–400 pairs, although they suggested that the true total was probably at the lower end of this spectrum. This estimate was published before the first colony was discovered. When VB discovered 9–10 burrows, within the 25 km² area, it was thought that perhaps just 25 breeding pairs survived. That 33 different individuals were seen at two locations at sea in just three days possibly demands a reassessment of estimated numbers. It is implausible that only ten pairs are breeding, more likely the total is in the order of *c.*100 breeding pairs (though an even higher figure is possible), which may further fit with the numbers of Barau's Petrels (>500) and Wedge-tailed Shearwaters (*c.*200) seen at sea (Table 4), given their supposed breeding populations on Réunion (3,000–5,000 pairs and a few hundred pairs, respectively). Obviously Mascarene Petrel must also breed outside the currently identified area of 25 km², or the breeding density is much greater than just ten burrows. Optimistically, our at-sea records suggest there are more Mascarene Petrels than concerted efforts to find breeding sites on Réunion currently reflect. It raises hopes that there are more individuals than thought, and that unknown colonies somewhere on the island have ensured the future of this enigmatic bird, at least for now.

Acknowledgements

We dedicate this paper to Batia Shirihai who became critically ill during our expedition. Throughout her life, as a schoolteacher, she taught children to admire and respect wildlife. She followed our research with enthusiasm, regularly enquiring about our progress. Following months in a coma, she is now almost fully recovered. Her fight for survival parallels that of Mascarene Petrel whose continued existence hangs in the

balance—it too, so easily, could be gone forever. We acknowledge the many efforts made by the Société d'Études Ornithologiques de la Réunion (SEOR) to safeguard this petrel, in particular the established and highly respected community programme to rescue any grounded birds. SEOR is now leading the French National Action Plan for the species, and has started a programme of predator control at known colony sites. We thank those that answered our requests for at-sea photographs of putative Mascarene Petrels. Thanks to David Allan, Niall Perrins and Martin Taylor for organising pelagic trips for HS off Durban, South Africa, in November 2013, especially to study variation in Great-winged Petrels. Grateful thanks to the curators and staff of the following museums for access to, or supplying, specimens: American Museum of Natural History, New York (AMNH), University Museum of Zoology, Cambridge, UK (UMZC), Naturalis, Leiden (RMNH), Musée d'Histoire Naturelle, Saint-Denis (MHNR), Muséum National d'Histoire Naturelle, Paris (MNHN), Australian Museum, Sydney (AMS), Museum of New Zealand Te Papa, Wellington (NMNZ), Natural History Museum, Tring (BMNH) and Fiji Museum, Suva (FM). Special appreciation to Tim Worfolk, artist of the forthcoming *Albatrosses, petrels and shearwaters of the world: a handbook to their taxonomy, identification, ecology and conservation*, who spent nearly two months working with us to accurately illustrate some of these species for the first time. Nigel Redman at Bloomsbury Publishing Plc (Christopher Helm) kindly permitted their use. Trevor Hardaker and Peter Ryan supplied images used to study plumage variation in Great-winged Petrels, and Hanne & Jens Eriksen permitted use of Jouanin's Petrel images. TP thanks Sébastien Jaquemet for supplying further details and records from the research pelagics in 2001 and 2002. Edward Soldaat was always helpful in answering questions on petrel morphology and osteology. Richard Klim kindly accessed a specific reference. VB thanks Carole Attié for her dedicated help over nearly 15 years in searching for breeding sites of Mascarene Petrels on Réunion. François Mougeot and Alexandre Millon aided the field work in 1996 and 2002, respectively. Carole Pym gave much-appreciated assistance with logistics on Réunion during the 2012 expedition, and in the production of this paper, which forms part of ongoing research for the Tubenoses Project. Finally, Michael Brooke and an anonymous referee contributed helpful comments.

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- Addresses:* Hadoram Shirihai, Emek Ayalon 39, Shoham 60850, Israel, e-mail: albatross_shirihai@hotmail.com. Tony Pym, Southcott, Pewsey, Wiltshire SN9 5JF, UK, e-mail: tony_pym@hotmail.com. Maria San Román, Ausserdorfstraße 6, 8052 Zurich, Switzerland, e-mail: marsaro100@hotmail.com. Vincent Bretagnolle, CEBC-CNRS, Beauvoir sur Niort, France, e-mail: breta@cebc.cnrs.fr

Taxonomic status of Scaled Ground Cuckoo *Neomorphus squamiger* Todd, 1925

by Daniel Honorato Firme, Claydson Pinto de Assis, Gary R. Graves
& Marcos André Raposo

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SUMMARY.—Scaled Ground Cuckoo *Neomorphus squamiger* Todd, 1925, is a rare and poorly known taxon from Pará and Amazonas, Brazil. Most taxonomic authorities have treated it as a subspecies of Rufous-vented Ground Cuckoo *N. geoffroyi* owing to plumage similarities and distribution. The aim of this study was to review the taxonomic status of *N. squamiger* in the light of a new specimen from the east bank of the rio Xingu, representing a significant eastward range extension. Examination of the 17 known specimens of *N. squamiger* revealed that the diagnostic characters are relatively invariable across its restricted geographic range in the Madeira–Tapajós–Xingu–Tocantins interfluvia. The rio Xingu specimen exhibits no signs of intergradation with the nearest population of *N. geoffroyi*, east of the rio Tocantins. The absence of intergradation and the previously reported difference in mitochondrial DNA between *N. squamiger* and *N. geoffroyi* suggest that *N. squamiger* should be treated as a species.

Neotropical ground cuckoos of the genus *Neomorphus* Gloger, 1827, are rare terrestrial birds that inhabit humid forests (to 1,000 m above sea level) from Nicaragua to south-east Brazil (Haffer 1977, Meyer de Schauensee 1982). The genus comprises four or five species depending on taxonomy (Haffer 1977, Payne 1997, 2005, Dickinson 2003), differing in plumage pattern and colour, and coloration of the bill and orbital skin. Red-billed Ground Cuckoo *N. pucheranii* (Deville, 1851) and Rufous-vented Ground Cuckoo *N. geoffroyi* (Temminck, 1820), are polyphyletic (Haffer 1977, Payne 1997, 2005), and some of the named subspecies may warrant elevation to species status (Raposo *et al.* 2009). Two other species, Banded Ground Cuckoo *N. radiolosus* Sclater & Salvin, 1878, and Rufous-winged Ground Cuckoo *N. rufipennis* (G. R. Gray, 1849), are considered monotypic. The fifth species, Scaled Ground Cuckoo *Neomorphus squamiger* Todd, 1925, was described from a male (Fig. 1)



Figure 1. Lateral view of the type specimen of *Neomorphus squamiger* Todd, 1925 (CMNH 74615) (Marcos A. Raposo)



Figure 2. Dorsal and ventral view of *Neomorphus squamiger iungens* (type, MCZ 173564; top in each panel) and *N. s. squamiger* (MCZ 173562) (Marcos A. Raposo)

collected at Colônia do Mojuy, near Santarém, on the east (right) bank of the rio Tapajós, in central Amazonia (Todd 1925). Although Todd (1925) did not provide a comparative diagnosis for *N. squamiger*, his description highlighted several plumage characters that differentiated it from *N. geoffroyi*. Todd (1925) was followed by Pinto (1938, 1964) and Meyer de Schauensee (1966, 1982). Peters (1940) opined that the two taxa would prove to be conspecific, but he continued to treat *N. squamiger* specifically because the ranges of *N. squamiger* and *N. geoffroyi* were so imperfectly known. One year later, Griscom & Greenway (1941) described *N. squamiger iungens* on the basis of a female from Boim, on the west (left) bank of the rio Tapajós (Fig. 2). This taxon was soon considered invalid by Gyldenstolpe (1945) and Pinto (1964).

In recent decades, *N. squamiger* has frequently been treated as a subspecies of *N. geoffroyi* (Haffer 1977, Payne 1997, 2005). Haffer (1977) considered *N. squamiger* part of a clinal group of subspecies in Amazonia, including *N. g. geoffroyi*, *N. g. amazonicus* and *N. g. australis*. However, he acknowledged that this hypothesis would only be confirmed if additional specimens from the upper rio Tapajós drainage, the lower rio Madeira, and the rio Xingu exhibited smooth clinal intergradation with geographically adjacent populations of *N. geoffroyi*. Sibley & Monroe (1990) noted the absence of intergradation between *N. squamiger* and geographically proximate populations of *N. geoffroyi*, but considered *N. squamiger* to be an allospecies of the *N. geoffroyi* superspecies complex. Payne (1997) likewise retained *N. squamiger* as a subspecies of *N. geoffroyi*, but remarked that it might better be treated specifically. Subsequently, Payne (2005) classified *N. squamiger* as a subspecies of *N. geoffroyi*, while observing that specimens across the geographic range of *N. g. geoffroyi*, *N. g. australis* and *N. squamiger* displayed intergradation in plumage characters. However, neither Payne (1997, 2005) nor Sibley & Monroe (1990) were aware of a recently collected specimen of *N. squamiger* from the right bank of the rio Xingu, which represents a significant eastward range extension (Graves & Zusi 1990). The aim of the present study is to address

the implications of this specimen for the taxonomic status of *N. squamiger* and to evaluate the validity of *N. s. iungens*.

Methods

We examined 83 specimens, including 17 of *N. squamiger*, 66 of *N. geoffroyi*, and the type specimens of both (Raposo *et al.* 2009; Appendix 1). Analyses focused on plumage pattern and colour, particularly of the ear-coverts and malar regions, and the size and shape of the breast-band. Specimen localities transcribed from museum labels were mapped according to geographical coordinates obtained from ornithological gazetteers (Stephens & Traylor 1983, Paynter & Traylor 1991, Paynter 1992, 1993, 1997). Geographical coordinates for localities in Central America were obtained from Global Gazetteer (2009). The program ArcView 3.2 (ESRI 1999) was used to elaborate the maps.

Results and Discussion

Comparative analysis of specimens revealed that the diagnostic plumage characters of *N. squamiger* are relatively uniform across its geographic range in the Madeira–Tapajós–Xingu–Tocantins interfluvia (Fig. 3). Consistent with Pinto (1964), all specimens of *N. squamiger* examined by us possess a rudimentary breast-band and unmarked cinnamon-buff ear-coverts and malar regions, rather than a well-developed breast-band and barred ear-coverts and malar, which typify the nearest populations of *N. g. amazonicus* (Fig. 4). Of special importance, the recently collected specimen of *N. squamiger* from the right (east) bank of the rio Xingu (USNM 572531; see Appendix 1 for museum acronyms) exhibited no evidence of intergradation with *N. geoffroyi* (Fig. 4). As there are no major rivers between the Xingu and Tocantins, it is probable that *N. squamiger* ranges east as far as the last-named

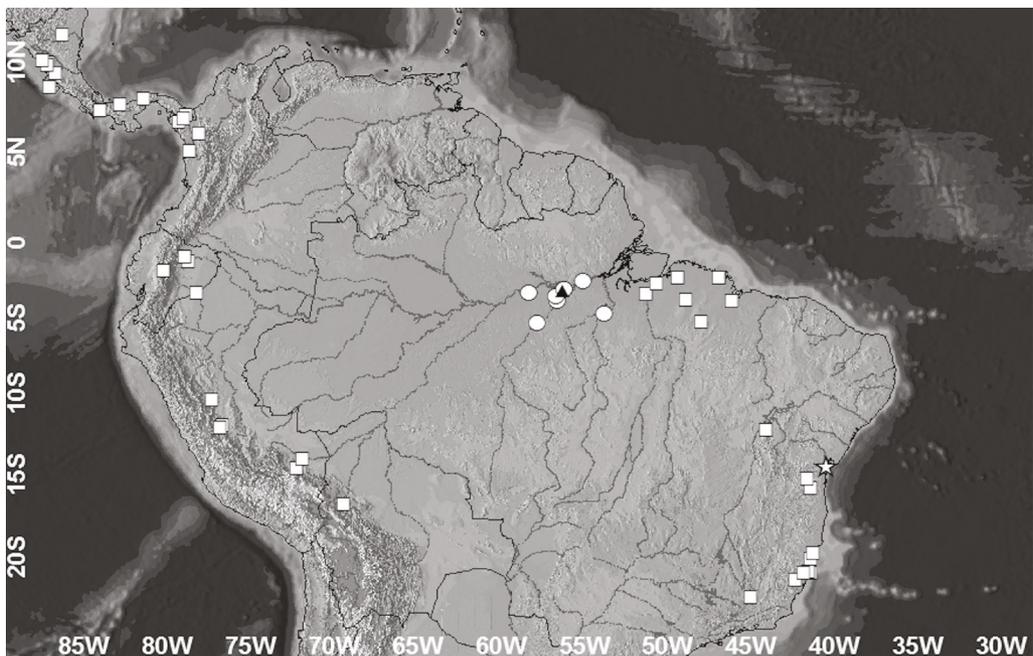


Figure 3. Distribution of specimens of *Neomorphus geoffroyi* (white squares) and *N. squamiger* (white circles) examined in this study. The black triangle and white star represent, respectively, the type localities of *N. squamiger* (Santarém, Pará, Brazil) and *N. geoffroyi* (rio Jaguaribe, Bahia, Brazil).

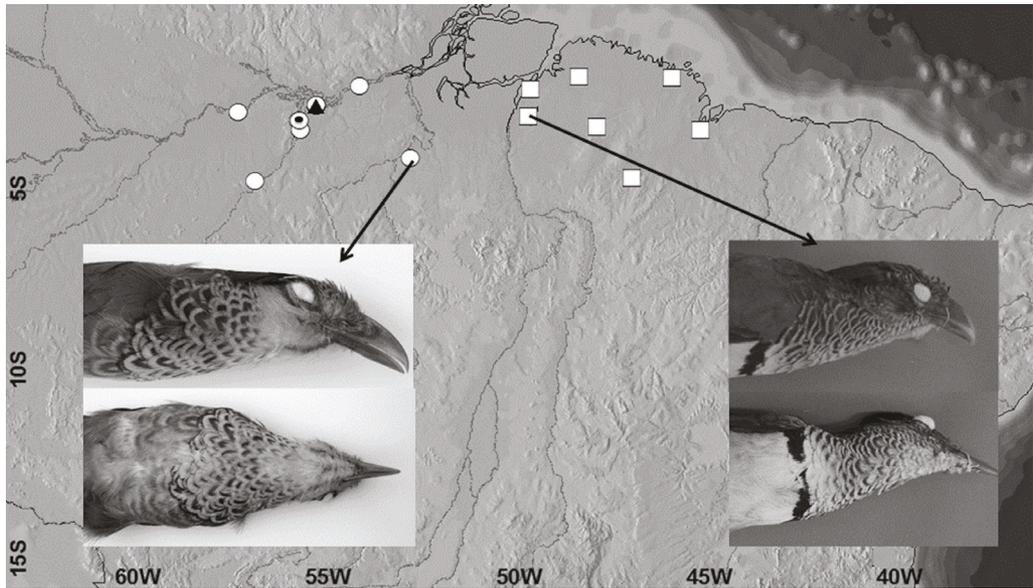


Figure 4. Detailed range of *Neomorphus geoffroyi* specimens from Pará and Maranhão (white squares) and *N. squamiger* (white circles) examined in this study. The photographs depict specimens of *N. geoffroyi* (right, AMNH 430468—Baião, rio Tocantins, Pará: Marcos A. Raposo) and *N. squamiger* (left, USNM 572531—east bank of rio Xingu above the mouth of the rio Iriri, Pará: Gary R. Graves). The black triangle and white circle with black spot represent, respectively, the type localities of *N. s. iungens* (Boim, left bank of rio Tapajós, Pará).

river. The westernmost specimens of *N. g. amazonicus* (AMNH 430467, 430468, 430469) were taken at Baião, on the east (right) bank of the rio Tocantins c.350 km north-east of the Xingu specimen of *N. squamiger*. These specimens show no evidence of intergradation with *N. squamiger* (Fig. 4).

Griscom & Greenway (1941) proposed that *N. s. iungens* could be distinguished from nominate *N. s. squamiger* in (1) having feathers of the forehead and crown buffy brown tipped dull bluish and with bluish centres, (2) a slightly more bronzy-green mantle, (3) greener and less coppery-red secondaries, (4) ear-coverts much deeper cinnamon-buff, (5) chin and throat uniform rich buff instead of 'soiled' whitish or greyish, (6) dark subterminal area on breast feathers less extensive, and (7) in having a more distinct breast-band. Based on a comparison of specimens of *N. s. iungens* and *N. s. squamiger* housed in the Swedish Museum of Natural History, Gyldenstolpe (1945) concluded that the supposed distinguishing characters were due to age differences and individual variation. Our analysis confirms that of Gyldenstolpe. Forecrown coloration in *N. squamiger* exhibits significant individual variation unassociated with geography (Fig. 5). Mantle colour is even more variable and some specimens from opposite sides of the rio Tapajós are virtually identical (Gyldenstolpe 1945, Pinto 1964). Our analysis of the colour of the ear-coverts, chin and throat also agree with the conclusions of Gyldenstolpe (1945); there are no consistent differences between specimens collected on opposite banks of the Tapajós (Fig. 5). Nor are there any consistent differences in the extent of the dark subterminal portions of the breast feathers in specimens from the left and right banks of the Tapajós (Figs. 5–6). For example, in the type series of *N. s. squamiger*, from Colônia do Mojuy, the dark subterminal parts of the breast feathers in CMNH 74616 (Fig. 6) are less extensive than in the other specimens from this locality (CMNH 74542, 74615, 75075), and far less extensive than in the type of



Figure 5. Lateral and ventral views (top to bottom) of *N. s. squamiger* (NRM 570204, Prainha, right bank of rio Tapajós), *N. s. squamiger* (NRM 570205, Caxiricatuba, right bank of rio Tapajós) and *N. s. iungens* (NRM 570206, Patinga, left bank of rio Tapajós) (© Göran Frisk, Swedish Museum of Natural History, Stockholm)

N. s. iungens (Fig. 2). The breast-band is similarly variable in specimens from the left and right banks of the Tapajós (Figs. 2, 5, 6). In conclusion, we concur with Gyldenstolpe (1945) and Pinto (1964) that the supposed diagnostic characters of *N. s. iungens* reflect individual variation. Consequently, *N. s. iungens* Griscom & Greenway 1941, must be treated as a junior synonym of *N. squamiger* Todd, 1925.

On the other hand, *N. squamiger* should be treated as a species restricted to the Madeira–Tapajós–Xingu–Tocantins interfluvia, based on the geographic uniformity of the unmarked cinnamon-buff ear-coverts and malar regions. The extent to which the geographic range of *N. squamiger* approaches some Amazonian populations of *N. geoffroyi* in eastern Pará is unknown. Doubts over the correct identification of some sight records at Alta Floresta, northern Mato Grosso, discussed by Lees *et al.* (2013) are adequately resolved by a photographic record of *N. squamiger* from that locality ([www.wikiaves.com.br; WA1203910](http://www.wikiaves.com.br;WA1203910)).

The lumping of *N. squamiger* with *N. geoffroyi* by several authorities (Haffer 1977, Sibley & Monroe 1990, Payne 1997, 2005) reflects a conservative philosophy, in vogue among avian taxonomists in the mid-20th century, which has resulted in substantial underestimation of species diversity among Amazonian birds. Recent molecular, morphological and behavioural investigations have suggested that dozens of populations currently treated as subspecies should be afforded specific status (e.g., Ribas *et al.* 2006, 2012, Isler *et al.* 2007, Oppenheimer & Silveira 2009). Payne (2005) classified *N. squamiger* as a subspecies of *N. geoffroyi* because the genetic distance in two mitochondrial genes (12S and ND2) observed between one specimen of *N. squamiger* (AMNH 278613) and a specimen of *N. geoffroyi salvini* from Panama was less than that between those specimens and other ground cuckoos. However, we note that the genetic distance between *N. squamiger* and *N. geoffroyi* was greater than that between some other pairs of cuckoos deemed by Payne to be species. Moreover, genetic distance is only one of several indicators of speciation in the Cuculidae



Figure 6. Individual variation in feather pattern and development of breast-band in three specimens of *N. s. squamiger* from Colônia do Mojuy, Pará (left to right: CMNH 75075, 74616 and 74542) (Marcos A. Raposo)

(Payne 1997, 2005). Differences in song and the colour of the facial skin, bill, and the head, neck and breast plumage, may also provide clues to species limits in *Neomorphus*. In this case, the distinctive differences in the facial plumages of *N. squamiger* and *N. geoffroyi*, combined with those in neck and breast plumage provide additional evidence of species-level differences. We anticipate that a more extensive molecular investigation of the *N. geoffroyi*–*N. squamiger* clade will reveal complex patterns of population differentiation and speciation. Confirmation of the validity of *N. squamiger* emphasises the need to evaluate the conservation status of this poorly known species, as it is threatened by the degradation, fragmentation and loss of habitat as well as hunting in the Amazon basin (BirdLife International 2014).

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Addresses: Daniel Honorato Firme, Universidade de São Paulo, Instituto de Biociências, Depto. Zoologia, Rua do Matão, Travessa 14, 101 Butantã, CEP 05508-090, São Paulo, SP, Brazil, and Setor de Ornitologia, Depto. Vertebrados, Museu Nacional / UFRJ, Quinta da Boa Vista s/n, CEP 20940-040, Rio de Janeiro, RJ, Brazil, e-mail: danielfirme@hotmail.com. Claydson Pinto de Assis, Setor de Ornitologia, Depto. Vertebrados, Museu Nacional / UFRJ, Quinta da Boa Vista s/n, CEP 20940-040, Rio de Janeiro, RJ, Brazil, e-mail: claydsonassis@yahoo.com.br. Gary R. Graves, MRC-116, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington DC 20013-7012, USA, and Center for Macroecology, Evolution and Climate, Univ. of Copenhagen, 2100 Copenhagen Ø, Denmark, e-mail: gravesg@si.edu. Marcos André Raposo, Setor de Ornitologia, Depto. Vertebrados, Museu Nacional / UFRJ, Quinta da Boa Vista s/n, CEP 20940-040, Rio de Janeiro, RJ, Brazil, e-mail: raposo@mn.ufrj.br

Appendix 1: Specimens examined

American Museum of Natural History, New York (AMNH); Carnegie Museum of Natural History, Pittsburgh (CMNH); Field Museum of Natural History, Chicago (FMNH); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP); Museu Nacional, Rio de Janeiro (MN); Museu Paraense Emílio Goeldi, Belém (MPEG); Museum of Comparative Zoology, Cambridge, MA (MCZ); National Museum of Natural History, Smithsonian Institution, Washington DC (USNM); Academy of Natural Sciences, Philadelphia (ANSP) and Swedish Museum of Natural History, Stockholm (NRM).

Neomorphus squamiger: BRAZIL: Amazonas: Parintins, rio Amazonas (02°36'S, 56°44'W), ♂, AMNH 278613. Pará: Colônia do Mojuy, near Santarém (02°26'S, 54°42'W), ♀, CMNH 74542, 74616; ♂, CMNH 74615 (holotype *N. s. squamiger*), 75075. East bank of the rio Xingu above the mouth of the rio Iriri (03°50'S, 52°40'W), ♂, USNM 572531. Tauari, right bank of rio Tapajós (03°05'S, 55°06'W), MCZ 173562; ♂, MCZ 173563. Boim, left bank of rio Tapajós (02°49'S, 55°10'W), ♀, MCZ 173564 (holotype, *N. s. iungens*). Cuçari (01°54'S, 53°33'W), ♀, MPEG 3791. Villa Braga, rio Tapajós (04°25'S, 56°17'W), ♀, MPEG 13715. Prainha, right bank of rio Tapajós, ♀, NRM 570204. Caxiricatuba, right bank of rio Tapajós, ♂, NRM 570205. Patinga, left bank of rio Tapajós, ♂, NRM 570206; ♀, NRM 570207. Piquiatuba, right bank of rio Tapajós (02°24'S, 54°41'W), ♀, MZUSP 17464; ♂, MZUSP 21102. Morro do Pau da letra, left bank of rio Tapajós (02°24'S, 54°41'W), MZUSP 40646.

Neomorphus geoffroyi: NICARAGUA: Peña Blanca, ♂, AMNH 103705, 103706. Matagalpa: rio Tuma, ♀, AMNH 103577. Savala, ♂, AMNH 102493. Rivas: San Emilio, Lago Nicaragua, ♀, FMNH 21874. COSTA RICA: Carrillo (09°52'N, 85°30'W), ♀, AMNH 415938. Cerro Santa María (10°81'N, 85°31'W), MCZ 20732. Alajuela: La Bijagua, MCZ 20731. PANAMA: Chiriquí, Obaldía, ♂, MCZ 155254; ♀, MCZ 156093. Darién, Caña, ♂, MCZ 140546. Citaro, rio Capé, ♀, AMNH 136495; ♂, AMNH 136494. Tacarcuna, ♀, AMNH 135485. Tapalisa, ♀, AMNH 136496. Panamá: Perme, ♀, MCZ 155253. Barro Colorado (91°10'N, 79°56'W), ♀, AMNH 228920. Veraguas: rio Calovébora, ♂, AMNH 246610; ♀, AMNH 246611. COLOMBIA: Antioquia: Alto Bonito (07°05'S, 76°30'W), ♀, AMNH 133204. Chocó: Serranía de Baudó (06°00'S, 77°00'W), ♀, AMNH 123274. ECUADOR: Tungurahua: rio Pastaza, ♂, FMNH 101047. Napo: rio Suno (00°42'S, 77°08'W), ♂, AMNH 179092. San José Nuevo (00°26'S, 77°20'W), AMNH 199094; ♂, AMNH 179093, 199095. Pastaza: rio Bobonaza, Sarayacu, ♂, FMNH 77375. PERU: Cuzco: Quincemil (13°31'S, 71°59'W), ♀, FMNH 208174, 208175. Huánuco: La Divisoria (09°05'S, 75°46'W), ♀, FMNH 187766. Junín: Yurinaqui Alto (10°47'S, 75°13'W), ♂, FMNH 282558. Madre de Dios: rio Colorado (12°39'S, 70°20'W), ♀, FMNH 222888. Pasco: Cacazú (10°19'S, 75°05'W), FMNH 296598. BOLIVIA: La Paz: rio Mapiri, Guanay (15°25'S, 67°49'W), ♀, ANSP 120763 (holotype of *N. g. australis*). BRAZIL: Bahia: Fazenda Santa Maria, rio Gongogi, ♂, MCZ 169388. Jequié (13°51'S, 40°05'W), ♂, MZUSP 14146. rio Jaguaribe (13°06'S, 38°56'W), AMNH 6086 (lectotype of *N. g. geoffroyi sensu Raposo et al.* 2009). Espírito Santo: ♀, MZUSP 6380; ♂, MZUSP 6379. Fazenda Boa Lembrança, rio Itaúnas, Conceição da Barra (18°35'S, 39°45'W), ♂, MN 44335. Lagoa Juparanã, Fazenda Santa Anna (19°35'S, 40°18'W), ♀, MN 4057. Norte, ♂, MN 26147. Patrimônio da Palha, rio São José, ♀, MN 39535; rio Doce, ♂, MZUSP 6723. São Mateus (18°44'S, 39°51'W), ♂, MN 12096. Mato Grosso: rio Manuel Corrêa, upper rio São Miguel, MN 4273. Goiás: Espírito Santo do Peixe, rio Tocantins, MN 4098. Maranhão: Buriticupú (04°20'S, 46°24'W), ♀, MPEG 37332. Rio Mearim, Pedreiras (03°04'S, 44°35'W), ♂, MN 44336. Turiaçu (01°41'S, 45°21'W), ♀, FMNH 64074, 64075, MN 32348; ♂, FMNH 64073, MN 4272. Minas Gerais: rio Doce, ♂, MZUSP 24784, 24785. Rio Matipó (10°53'S, 42°33'W), MZUSP 10364, 18365. Rio São José, upper rio Doce, ♂, MN 26361. Pará: Baião, rio Tocantins (02°41'S, 49°41'W), ♀, AMNH 430469; ♂, AMNH 430467, 430468. Capim (01°40'S, 47°47'W), ♀, MZUSP 43959, 43960. Paragominas (03°00'S, 43°18'W), ♂, MPEG 28441. Rio Capim, Ressaca (01°40'S, 47°47'W), ♀, MPEG 1391.

Courtship display of Rufous-breasted (Chiriquí) Quail-Dove *Zentrygon chiriquensis*

by Daniel M. Brooks

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Rufous-breasted (Chiriquí) Quail-Dove *Zentrygon chiriquensis* is endemic to the highlands (300–3,100 m) of Costa Rica and western Panama (Kirwan 2010). It is a relatively little-known species, with natural history accounts containing large gaps in knowledge (e.g., Baptista *et al.* 1997, Gibbs *et al.* 2001, Kirwan 2010, BirdLife International 2013). Similarly, little (Gibbs *et al.* 2001) to no information (Baptista *et al.* 1997) exists in general Columbidae synopses regarding components of the courtship display in *Geotrygon* and *Zentrygon*.

Banks *et al.* (2013) split the genus *Geotrygon* into three groups based on genetic data. These are: (1) the nine species of *Geotrygon* (Indigo-crowned *purpurata*, Sapphire *saphirina*, Crested *versicolor*, Ruddy *montana*, Violaceous *violacea*, Grey-fronted *caniceps*, White-fronted *leucometopia*, Key West *chryisia* and Bridled Quail-Doves *mystacea*), (2) Olive-backed Quail-Dove *Leptotrygon veraguensis*, and (3) eight species in the newly proposed *Zentrygon* (Tuxtla *carrikeri*, Buff-fronted *costaricensis*, Purplish-backed *lawrencii*, White-faced *albifacies*, White-throated *frenata*, Lined *linearis*, Russet-backed *chiriquensis* and Russet-crowned Quail-Doves *goldmani*). However, no information was provided on how these species are related morphologically or behaviourally.

Behavioural characters comprising innate fixed-action patterns can be used to help elucidate avian phylogenies. Studies utilising behavioural characters to elucidate relationships among birds have been undertaken at specific (Gaucher *et al.* 1996), generic (García & Brooks 2007), familial (Archibald 1976, Hughes 1996) and ordinal (Kennedy 1996) levels. The purpose of this note is to describe the heretofore unknown courtship display of *Z. chiriquensis*, and to determine its phylogenetic context in light of recent data (Banks *et al.* 2013).

Data were collected anecdotally from observations of a male housed outdoors in the subtropical climate of Houston, Texas (housing and feeding described in Brooks 2010). The bird (banded DWA 515 right leg) was on loan for two years (29 September 2010–24 September 2012) from the Dallas World Aquarium (DWA), Texas. The male cohabited with a female conspecific from its arrival until 18 November 2010, and again from 26 February 2011 until both were returned to DWA. Birds were recently descended from stock imported from Chiriquí province (Panama), and were naturally reared by, and with, conspecifics to ensure natural behaviour.

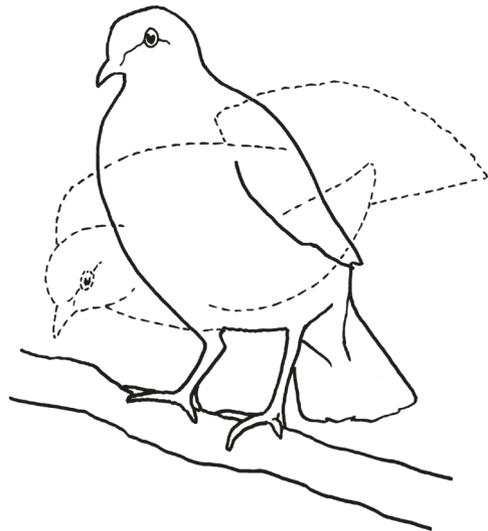


Figure 1. Courtship display of Rufous-breasted (Chiriquí) Quail-Dove *Zentrygon chiriquensis*. Solid line = normal position, dashed line = courting position with head bobbing downwards as tail is raised (drawing by Beverly Garland)

TABLE 1
Courtship components in six species of quail-doves, three each of *Geotrygon* and *Zentrygon*.

Species	stationary head down and tail up	pumping head down with tail up	wings in normal position	wings open or quivering	on perch	low perch or ground
<i>Geotrygon</i>						
<i>G. versicolor</i>	x	-	-	x	-	x
<i>G. montana</i>	-	x	x	-	-	x
<i>G. caniceps</i>	x	-	-	x	-	x
<i>Zentrygon</i>						
<i>Z. frenata</i>	-	x	-	x	-	x
<i>Z. linearis</i>	-	x	-	x	-	x
<i>Z. chiriquensis</i>	-	x	x	-	x	-

Courtship component present (x) or absent (-).

Gibbs *et al.* (2001) provided brief courtship descriptions for four species: *G. montana*, *G. caniceps*, *Z. frenata* and *Z. linearis*. Additional data for *G. versicolor* (DMB unpubl.) and *Z. chiriquensis* (provided herein) permits rudimentary analysis of innate courtship display components among these six species.

The study individual hatched in March 2010 and, on 12 November 2011, was first observed displaying when 20 months old. Displays were subsequently witnessed on multiple occasions over the following ten months until the bird was returned to DWA. Displays occurred irrespective of whether the male was housed with a female. The display (Fig. 1; supporting video clip: hmns.org/quaildove) involved bobbing the head down simultaneously with the tail being raised (*c.*1 second), then tail down as the head returned to normal position (*c.*1 second). The wings remained tucked in their usual position but the tail was fanned during the display. The display was always performed on a branch 0.7–1.7 m above ground, but never while on the ground.

Z. chiriquensis is the only quail-dove known to fan its tail during courtship, as well as to display from a perch and never on the ground (Table 1). Although two other species of *Zentrygon* (*Z. frenata* and *Z. linearis*) share similar components of the courtship display noted for *Z. chiriquensis* (bobbing the head downwards as the tail is raised and vice versa), other components of *Z. frenata* and *Z. linearis* courtship are more similar to *Geotrygon* (*G. versicolor* and *G. caniceps*). Perhaps the species most parsimonious to *Z. chiriquensis* in terms of courtship display components is *G. montana*, which holds its wings in the normal position as it performs the bobbing head down as tail goes up pattern.

Broader sampling of *G. montana* throughout its range may reveal significant intraspecific variation. Given the species' widespread distribution, it is possible that various cryptic forms (Bickford *et al.* 2007) have not been discovered, which may explain the parsimony between the phylogenetically divergent *Z. chiriquensis* and *G. montana* (R. C. Banks pers. comm.).

The results of this rudimentary analysis of courtship displays may be biased by inadequately detailed or the complete lack of descriptions. For example, Gibbs *et al.* (2001) indicated that all species of *Geotrygon* and *Zentrygon* call from the ground or a low perch. However, such behaviour was never observed during ten months of observation in the male *Z. chiriquensis*; moreover this bird was rarely, if ever, seen utilising the ground, preferring to remain arboreal. More rigorous analyses must await additional and more

detailed descriptions of *Geotrygon* and *Zentrygon* courtship behaviour to provide more robust results.

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- Address: Houston Museum of Natural Science; Dept. of Vertebrate Zoology, 1 Hermann Circle Drive, Houston, TX 77030-1799, USA.

Recent observations of White-eyed Starling *Aplonis brunneicapillus* on Guadalcanal, Solomon Islands

by Petter Z. Marki, Markus Lagerqvist & Ashley Banwell

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White-eyed Starling *Aplonis brunneicapillus* is a poorly known Solomon Islands endemic. Since its description, based on a single male specimen from Buin, Bougainville (Danis 1938), additional records have come from Choiseul, Rendova and Guadalcanal (Amadon 1943, Beecher 1945, Cain & Galbraith 1956, Gibbs 1996, Dutson 2011). However, there have been very few recent records, with all of those in the last decade at Mt. Austen on the outskirts of Honiara, Guadalcanal, where 1–5 birds were seen on c.25% of visits in 1990–2010 (G. Dutson *in litt.* 2014). The species is potentially threatened by the ongoing felling of nest trees to eat the young, combined with high rates of habitat degradation and deforestation



Figure 1. White-eyed Starling *Aplonis brunneicapillus*, Guadalcanal, Solomon Islands, July 2013, showing characteristic features including white iris and distinctively shaped tail streamers that help separate this species from Metallic Starling *Aplonis metallica* (Ashley Banwell)

Figure 2. White-eyed Starling *Aplonis brunneicapillus*, Guadalcanal, Solomon Islands, July 2013 (Ashley Banwell)

Figure 3. White-eyed Starling *Aplonis brunneicapillus* carrying nesting material, Guadalcanal, Solomon Islands, July 2013 (Markus Lagerqvist)

Figure 4. White-eyed Starling *Aplonis brunneicapillus*, Guadalcanal, Solomon Islands, July 2013 (Markus Lagerqvist)

(BirdLife International 2012). Thus, given the general paucity of records and a probably small, fragmented and possibly declining population estimated at 1,000–2,499 individuals, *A. brunneicapillus* is currently treated as Endangered (BirdLife International 2012).

On 12 July 2013 a nesting colony of *A. brunneicapillus* was discovered by the authors, and our local guides, along the upper reaches of the Tenaru River, North Guadalcanal (09°35.588'S, 159°58.781'E; 500 m). We observed and photographed (Figs. 1–4) the starlings for c.10 minutes. The colony was in the crown of a tall emergent tree atop a steep, forested

ridge above a stream. The tree appeared to be dead or dying, and was festooned with epiphytic ferns and mosses. We estimated that 10–15 birds were present, but probably more; bad light and the distance made counting difficult. Individuals and pairs appeared to use regular perches, with frequent visits to presumed nests sited in the dense epiphytic ferns. Several birds were carrying nesting material, chiefly ‘strings’ of moss (Fig. 3). Many individuals appeared to have broken or reduced tail streamers. We also observed what appeared to be courtship, with the displaying individual pointing the tail vertically upwards, before thrusting it downwards toward the other bird. Further downstream (09°35.815’S, 159°58.280’E; 481 m) on the same date, we encountered another flock of c.20–30 starlings flying along a forested ridge, before perching in the dense canopy of a tall tree. Four or five *A. brunneicapillus* were visible, but we cannot exclude the possibility that other species were present in the flock. The birds appeared to be feeding on small fruit and there was no indication that this was a nesting tree. Despite spending four days within the species’ known altitudinal range, these were our only records. We were unable to confirm whether local people still fell nesting trees to eat the young.

Discussion

Our record appears to constitute only the third breeding colony of *A. brunneicapillus* and to be the first since the discovery of one near Kieta, Bougainville, in 1985 (Kaestner 1987). Our observations on choice of nest tree, colony size and behaviour, including possible courtship, closely mirror the detailed notes of Cain & Galbraith (1956) and Kaestner (1987). However, the Bougainville colony was apparently in lowland forest, whereas the Guadalcanal records, including ours, were in hill forest. Due to the reports of predation by local people (Cain & Galbraith 1956) and a subsequent lack of records by more recent visitors (Gibbs 1996; G. Dutson pers. obs. 1997), it was suggested that the species may have been extirpated around Betilonga (BirdLife International 2012), even though Cain & Galbraith (1956) stressed that they spent almost one month there before detecting it. Our records confirm its continued presence in this area.

Several additional factors may contribute to the apparent rarity and possible decline of *A. brunneicapillus*. Deforestation and absence of old trees might place a constraint on continued survival in the lowlands, although the species is also tolerant of somewhat disturbed habitats, including native gardens (Beecher 1945, Gibbs 1996). In addition to deforestation, possible threats include competition with congeners and predation by introduced mammals. Competition with other starlings, including the closely related Metallic Starling *A. metallica* may have caused declines, possibly induced by deforestation and habitat alteration. According to taxon-cycle theory, island species undergo successive stages of expansion and contraction, with recent colonisers occupying disturbed lowland habitats, gradually replacing older relictual taxa, whose ranges will retreat to interior hill and montane forest (Wilson 1959, Wilson 1961, Ricklefs & Cox 1972). Thus, in cases where closely related taxa co-occur on an island, they are expected to segregate by habitat and / or altitudinal distribution, and the morphological space occupied. A recent study has found support for patterns of range expansions and contractions, with significant segregation in habitat, elevation and morphological space among sympatric insular taxa of *Pachycephala* whistlers (Jönsson *et al.* 2014). Given similar patterns of range size variation in *Aplonis* starlings, with some species being widespread across large archipelagos, others highly disjunct or restricted to single, montane islands, it is conceivable that similar processes could be at work in the range dynamics of these starlings.

A potentially analogous situation to that of *A. brunneicapillus*, could be that of Yellow-eyed Starling *A. mystacea* in New Guinea. This species is also widespread, but is

decidedly rarer and less frequently encountered than the sympatric *A. metallica* and Singing Starlings *A. cantoroides*. Susceptibility to avian pathogens may also contribute to increasing replacement of *A. brunneicapillus* by species such as *A. metallica*. It has been suggested that sympatry of ecologically similar species may be inhibited when parasites are less virulent in widespread, recent colonisers (e.g. *A. metallica*) but are pathogenic in localised endemics (e.g. *A. brunneicapillus*) that possibly lack recent exposure to the parasites concerned, thus potentially tipping the balance in favour of one species (Ricklefs & Bermingham 2007, Ricklefs 2010, 2011). Introduced mammals, including rats and cats, may pose an additional threat, not only to this species, but other indigenous taxa. Finally, *A. brunneicapillus* may primarily be restricted to hill forest, a habitat rarely visited by ornithologists due to access problems. Recent records of small numbers in mixed starling flocks such as those recorded on Mt. Austen, may relate to stragglers from nearby hill forest rather than residents. However, records of a nesting colony on Bougainville suggest that lowland forest is appropriate habitat and that it is deforestation that has wrought a significant population decline in such areas.

These recent records indicate that significant numbers of *A. brunneicapillus* may survive in hill forest on Guadalcanal, and possibly on other islands within its range, including those from which it is currently unrecorded. *A. brunneicapillus* has a unique geographical range, with no other bird taxon being confined to the same set of islands. Hence, establishing if the species is truly absent on islands from which it is so far unrecorded would be of great interest. Further surveys are required to assess population size of this and other poorly known species in the mountains of Guadalcanal and the Solomons in general.

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Addresses: Petter Zahl Marki, Hanneviktoppen 8, NO-4629 Kristiansand, Norway, e-mail: zoothera87@hotmail.com. Markus Lagerqvist, Askims r sev g 37, 43640 Askim, Sweden, e-mail: markus.lagerqvist@usa.net. Ashley Banwell, 2 Waterworks Cottages, The Street, Marham, King’s Lynn, Norfolk PE33 9JN, UK, e-mail: otusbrooki@aol.com

First record of White-crowned Manakin *Dixiphia pipra* in western Ecuador

by Juan F. Freile

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White-crowned Manakin *Dixiphia pipra* occurs from montane Costa Rica south to Amazonian Bolivia and the Atlantic Forest of eastern Brazil (Snow 2004, Kirwan & Green 2011). Thirteen subspecies are currently recognised but plumage variation is complex and not yet fully understood (Kirwan & Green 2011). Most authors have suggested that several species might be involved given morphological, vocal and behavioural differences across subspecies (Ridgely & Greenfield 2001, Snow 2004, Ridgely & Tudor 2009, Kirwan & Green 2011).

Subspecies distribution over the species' wide range is unresolved. Most subspecies have small ranges, with some occupying narrow altitudinal distributions in the east Andean foothills (Kirwan & Green 2011). Until recently, a single subspecies was believed to occur in Ecuador, namely *D. p. coracina* (Ridgely & Greenfield 2001). However, Freile *et al.* (2014) reported the first records of *D. p. occulta*, from extreme south-east prov. Zamora Chinchipe, in the río Nangaritza valley. They also discussed subspecific affinities of populations in the eastern lowlands and Andean foothills, suggesting that *D. p. discolor* occurs in the former, with *D. p. coracina* and *D. p. occulta* in the foothills.

While examining specimens at the Museo Ecuatoriano de Ciencias Naturales (MECN), Quito, I located a *D. pipra* in female plumage misidentified as Green Manakin *Xenopipo holochlora litae*. The specimen (MECN 2734) was collected by M. Olalla at San Javier, prov. Esmeraldas (01°03'N, 78°46'W; 100 m; *cf.* Paynter 1993) on 5 November 1966. This is the first record of *D. pipra* from the western lowlands of Ecuador (Fig. 1), although Chapman (1926) apparently envisaged its occurrence there.

San Javier is c.250 km south-west of the type locality of *D. p. minima* (Chapman 1914) but just c.90 km south-west of Río Ñambí reserve, the species' nearest-known locality in the lowlands and foothills of western dpto. Nariño, Colombia (Hilty & Brown 1986, Calderón-Leytón *et al.* 2011). I was unable to compare MECN 2734 with other specimens, but photographs of birds in south-west Colombia indicate that it resembles those from the Pacific slope of the West Andes of Colombia. Therefore, I tentatively identified the specimen as *D. p. minima*.

The description of *D. p. minima* is based on size and minor plumage differences in males, but no comparative description of female-plumaged birds was provided (Chapman 1914, 1917). The single Ecuadorian specimen resembles some female-plumaged *D. p. coracina* at MECN (Fig. 2). Although no detailed description of female *D. p. minima* exists, Snow (2004) and Kirwan & Green (2011) suggested that western subspecies resemble each other in the amount of grey on the head and yellow in the underparts.

The MECN specimen differs from *D. p. coracina* in the amount of bluish grey in the crown, which is more uniform olivaceous grey, especially on the forecrown (Fig. 1). Two specimens of *D. p. coracina* at MECN also lack bluish grey in the crown, which has a more olive tone with a few scattered bluish-grey feathers. Likewise, one collected in the Nangaritza Valley, prov. Zamora Chinchipe, deposited at the Museo de Zoología, Universidad Católica del Ecuador (QCAZ 3342), also has little grey in crown. Remaining upperparts of the San Javier specimen resemble *D. p. coracina* in being bright yellowish olive, brighter than the



Figure 1 (left). Female-plumaged specimen of White-crowned Manakin *Dixiphia pipra* collected by M. Olalla at San Javier, prov. Esmeraldas, Ecuador, deposited at Museo Ecuatoriano de Ciencias Naturales (MECN) (MECN 2734), Quito (J. F. Freile)

Figure 2 (below). Female-plumaged specimens of White-crowned Manakin *Dixiphia pipra* from Ecuador deposited at Museo Ecuatoriano de Ciencias Naturales, Quito; MECN 2734, collected at San Javier, prov. Esmeraldas, is on the extreme right (J. F. Freile)



upperparts of the eastern lowlands specimens examined (Fig. 2). Most underparts are yellowish but the throat is whiter and duller, approaching the underparts of *D. p. coracina*.

Specimens from the eastern Ecuadorian lowlands are more reminiscent of eastern subspecies *sensu* Snow (2004) and Kirwan & Green (2011) in being duller olive-green above, lacking bluish grey in the crown, and having duller and greyer underparts. A consistent size difference is also apparent between western subspecies—including the San Javier specimen—and those from the eastern lowlands, all of which look smaller. A more thorough revision of racial variation in *D. pipra* is required, especially in female plumage, as most subspecies are delineated solely on the basis of male characters.

I cannot eliminate the possibility that the San Javier specimen represents an undescribed taxon, but additional specimens are needed, and further field work is required to elucidate the taxonomy and distribution of *D. pipra* in north-west Ecuador.

Few previous records of *D. p. minima* exist from south-west Colombia (Calderón-Leytón *et al.* 2011), but none from north-west Ecuador, even in areas subject to fairly intensive surveys (Jahn 2011). Nevertheless, other recent discoveries in this region, such as Slaty-backed Forest Falcon *Micrastur mirandollei* (Brinkhuizen & de Bruin 2013) and Thicket Antpitta *Hyllopezus dives* (Moore *et al.* 2013) suggest that ornithological knowledge of the Ecuadorian Chocó is still far from complete. That the specimen of *D. pipra* had been overlooked for >40 years also suggests that museum material might still provide insights, and that further collecting work is needed.

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Address: Casilla Postal 17-12-122, Quito, Ecuador, e-mail: jfreileo@yahoo.com

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