

The dark-morph Herald Petrel *Pterodroma heraldica*

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SUMMARY.—Whether dark-morph Herald Petrel *Pterodroma heraldica* exists or not has been debated for many years. We summarise previous contributions on the subject, provide indisputable evidence of the dark morph, describe its plumage based on museum specimens and live birds, highlight differences between dark, light and intermediate morphs, and enumerate characters that relatively easily separate the dark morph from ‘all-dark’ Henderson Petrel *P. atrata*. Dark-morph Herald Petrel is scarce and local. Since the 1970s, records have been restricted to the central South Pacific at Mangareva Island (Gambier Islands) and Ua Pou (Marquesas Islands).

Background

The following three taxa have been central to the debate as to the existence or not of dark-morph Herald Petrel.

Trindade Petrel *Pterodroma arminjoniana* Polymorphic. Breeds in the South Atlantic on Trindade Island (Murphy & Pennoyer 1952, Luigi *et al.* 2009, Flood & Fisher 2013), with a small population on Round Island, in the south-west Indian Ocean (Murphy & Pennoyer 1952, Brown *et al.* 2010, 2011).

Herald Petrel *P. heraldica* Polymorphic (see below). Wide-ranging, breeds across the tropical South Pacific, from Raine Island, Australia, in the west, to Easter Island in the east (Brooke 2004, Thibault & Cibois 2017, Howell & Zufelt 2019, Harrison *et al.* 2021), with small numbers on Round Island, south-west Indian Ocean (Brown *et al.* 2010, 2011).

Henderson Petrel *P. atrata* Monomorphic. Breeds in the South Pacific on Henderson Island (Brooke & Rowe 1996, Thibault & Cibois 2017), with c.10 pairs nesting on Moto Nui, off Easter Island (Jaramillo *et al.* 2008, Marin & Caceres 2010). Harrison *et al.* (2021) stated without supporting evidence that ‘Henderson Petrel may once have bred on Ducie Atoll and Pitcairn Island, possibly in the Gambier Islands and Marquesas Islands.’ We report evidence of dark-morph Herald Petrel at the Gambier and Marquesas Islands.

Nowadays, the three taxa are considered species, as listed above, but this has not always been the case. Herald Petrel was once considered the Pacific race of Trindade Petrel, but a split into two species is now generally accepted based on biometrics (Murphy & Pennoyer 1952, Brooke & Rowe 1996), genetics (Booth-Jones *et al.* 2017) and intestinal structure (Imber 1985).

Murphy & Pennoyer (1952) considered Herald Petrel polymorphic by incorporating the dark petrels that breed on Henderson Island (Henderson Petrel). This taxonomy remained unchanged until Brooke & Rowe (1996) reported compelling evidence to the contrary, i.e. genetic differences, the darker brownish-black coloration of Henderson Petrel, and strict assortative breeding with a different breeding period on Henderson Island. The split into two species is now widely accepted.

This leaves an unresolved question, does Herald Petrel occur only as a light morph? Doubts as to whether a dark morph exists were expressed by Howell & Zufelt (2019), partly



Figure 1. Light-morph (bottom) and dark-morph (top) Herald Petrels *Pterodroma heraldica*, c.1.5 miles off east coast of Ua Pou, Marquesas Islands, French Polynesia, South Pacific, 5 October 2021; the dark morph shows the same basic underwing pattern as the light morph, whilst Fig. 2D shows the same dark morph (Mike Danzenbaker)

due to a lack of confirmatory photographs, although they stated that ‘At-sea observations indicate that, unlike Henderson Petrel, some presumed dark-morph Heralds have white underwing primary flashes, like light-morph Herald, and a greyish ground colour to the plumage (H. Shirihai, pers. comm.).’ Bailey *et al.* (1989), Marchant & Higgins (1990) and Harrison *et al.* (2021) illustrated this plumage, but Bailey *et al.* did not distinguish Henderson Petrel from Herald Petrel and presented both underwing plumages as variation within Herald Petrel.

In East Polynesia, away from Henderson Island, light-morph Herald Petrel and a much scarcer dark petrel form pairs (Murphy & Pennoyer 1952, Thibault & Cibois 2017). Unlike Henderson Petrel, these dark petrels possess the same basic underwing pattern as light-morph Herald Petrel (Fig. 1) and biometrics are mainly consistent across morphs (Table 1) supporting the hypothesis that they are dark-morph Herald Petrel and invalidating any suggestion of a hybrid origin and introgression involving Henderson Petrel.

TABLE 1
Biometrics in mm (mean on upper line, standard deviation on lower line) of Herald Petrel *Pterodroma heraldica* (light morph $n = 132$, intermediate morph $n = 2$, and dark morph $n = 7$). All birds are museum specimens measured by VB.

Species	Wing	Tail	Tarsus	Culmen	Bill depth	Bill gape
Herald light	276.40 6.29	113.40 4.91	34.52 1.33	27.09 0.82	10.12 0.41	13.07 0.69
Herald intermediate	278.50 16.26	112.50 6.36	34.60 3.53	28.00 1.56	10.90 1.27	12.65 0.21
Herald dark	276.40 6.06	112.90 5.27	34.80 0.95	26.90 1.13	10.00 0.67	12.65 0.66

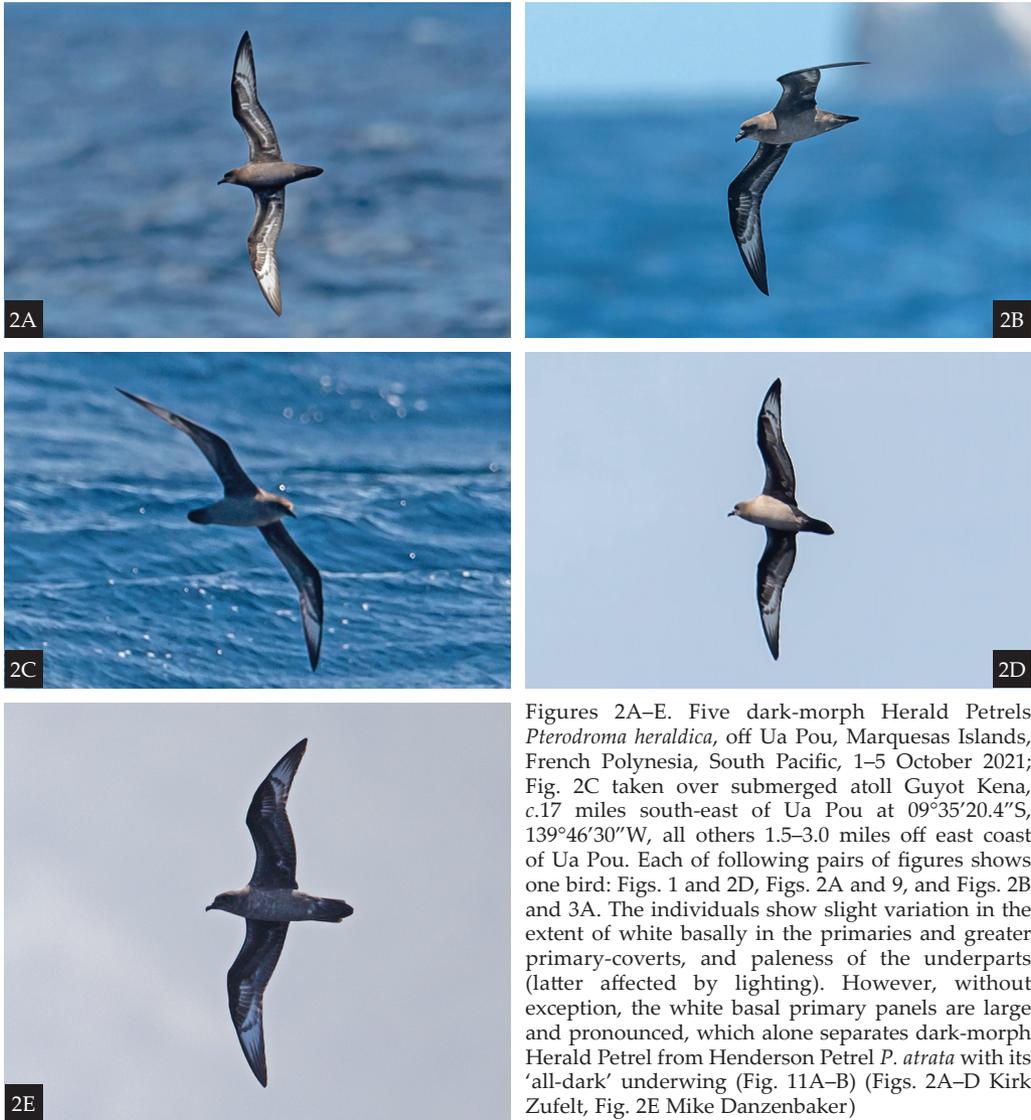
Further, to our knowledge, hybrid *heraldica* × *atrata* have not been documented. On Henderson Island, of 86 pairs engaged in aerial courting, two were mixed *heraldica* × *atrata*; however, of 19 pairs that actually bred (Brooke & Rowe 1996) and 25 pairs that bred (Oppel *et al.* 2017), none was mixed *heraldica* × *atrata*. Occasional isolated cases cannot be ruled out given growing evidence of hybridisation in *Pterodroma* petrels (e.g., Brown *et al.* 2010, 2011, Tennyson *et al.* 2013, Booth-Jones *et al.* 2017). Even so, an occasional isolated case of hybridisation would not invalidate our confirmatory evidence for dark-morph Herald Petrel.

Description of dark-morph Herald Petrel

The term ‘polymorphism’ in ornithology refers to a panmictic population of a species with two or more phenotypes clearly differentiated by plumage coloration and pattern. All individuals of a panmictic population are potential partners with no mating restrictions, behavioural or genetic, and occupy the same breeding location at the same time (Ford 1965, Galeotti *et al.* 2003, Roulin 2004). On Ua Pou, in the Marquesas Islands, and possibly elsewhere, Herald Petrels meet this criterion. Specimens and live birds (see below) represent an island population that interbreeds, producing light (common), dark (scarce) and intermediate (rare) offspring. They differ in the coloration and pattern of plumage, but not in structure or biometrics (Table 1). The number of dark birds rules out aberration and we assign them to morphs. There are few intermediates, but given acceptance of light and dark morphs, it is reasonable to accept intermediate morph.

Dark morph.—The following description is based on photographs of five birds taken at sea during a recent expedition circumnavigating the Marquesas Islands (Figs. 1–3), led by RLF & KZ, and in-hand examination of eight specimens by VB & HS (five shown in Figs. 4–6).

Ground colour Dark grey-brown, typically a tone or so darker than the light morph (if seen side by side in the same light conditions; see below), but can appear warmer brown in strong tropical sunlight, and old feathers bleach browner. **Head and neck** Dark grey-brown in slight contrast to subtly paler aspect of underparts. **Throat patch** Varies from whitish to dusky, some intermixed with dark feathers. Note, the patch is whitish on most specimens and mostly dusky on birds photographed at sea. **Upper breast** Broad diffuse dark breast-band. **Lower breast to undertail-coverts** Subtle ghosting of light morph’s whitish underparts, being rather uniform darkish grey-brown, flanks and undertail-coverts slightly darker. Subtle hooded appearance, most obvious when underparts lit, but border with lower breast not clear-cut. **Underwing** White ‘tongues’ basally in inner web of primaries extend 30–60% the length of the visible feather. At longer range, ‘tongues’ may appear to coalesce and form a single white triangular panel. White basally in greater primary-coverts may exclude innermost ones, forms short and narrow to long, broad and pronounced white crescent. Coverts can be mainly white and join with the white in the primaries, forming a striking, very large white triangular panel. Inner median primary-coverts typically show several splayed white ‘tongues’ (white basally running most of length of inner web). Median secondary-coverts may be white basally, typically barely perceptible, but can form a white line across outer part of inner wing. Lesser secondary-coverts may be white basally, again barely perceptible, but can form white line on innermost wing. All show chequered whitish / dark marginal forewing linings to some degree. **Comments** The underside of two birds have irregular small areas of pale / whitish feathers (Figs. 2A, 2E and 9; Figs. 2A and 9 same bird), whilst the upperside of two had irregular small / large patches of pale grey-brown, mainly on the nape to back and inner forewing, partly explained by feather wear and bleaching. **Lighting** Strong sunlight on the underparts can exaggerate dark morph’s



Figures 2A–E. Five dark-morph Herald Petrels *Pterodroma heraldica*, off Ua Pou, Marquesas Islands, French Polynesia, South Pacific, 1–5 October 2021; Fig. 2C taken over submerged atoll Guyot Kena, c.17 miles south-east of Ua Pou at 09°35′20.4″S, 139°46′30″W, all others 1.5–3.0 miles off east coast of Ua Pou. Each of following pairs of figures shows one bird: Figs. 1 and 2D, Figs. 2A and 9, and Figs. 2B and 3A. The individuals show slight variation in the extent of white basally in the primaries and greater primary-coverts, and paleness of the underparts (latter affected by lighting). However, without exception, the white basal primary panels are large and pronounced, which alone separates dark-morph Herald Petrel from Henderson Petrel *P. atrata* with its ‘all-dark’ underwing (Fig. 11A–B) (Figs. 2A–D Kirk Zufelt, Fig. 2E Mike Danzenbaker)

subtle ghosting of light morph plumage, suggesting intermediate morph (e.g., Figs. 2A and 9 show same bird under different lighting conditions, Fig. 9 suggesting intermediate morph).

Light morph.—The following is based on photographs of several hundred live birds (e.g., Fig. 1) and 149 specimens (e.g., Figs. 5–6) from numerous locations. *Ground colour* Mid grey-brown. *Head and neck* Mid grey-brown in strong contrast to whitish underparts. *Face* Whitish nose-band and throat patch. *Upper breast* Diffuse dark breast-band of variable depth. *Lower breast to undertail-coverts* Whitish with variably darker flanks and undertail-coverts. *Underwing* Light and dark morphs share the same basic underwing pattern (see dark morph), but light morph more variable (Thibault & Cibois 2017). Marginal forewing linings typically more pronounced than dark morph.

Intermediate morph.—The following is based on photographs of two specimens at the American Museum of Natural History (AMNH 191642, Fig. 5; AMNH 191366, Fig. 6) and



Figures 3A–B. Dark-morph Herald Petrels *Pterodroma heraldica*, 1.5–3.0 miles off east coast of Ua Pou, Marquesas Islands, French Polynesia, South Pacific, 3 and 5 October 2021 respectively; note slight variation in dorsal coloration, though true colour may be affected by lighting and feather wear (Fig. 3A Mike Danzenbaker, Fig. 3B Kirk Zufelt)



Figures 4A–D. Dark-morph Herald Petrel *Pterodroma heraldica* specimens at American Museum of Natural History (AMNH). Figure 4A. AMNH 194339 (top), AMNH 194338 (bottom), Ua Pou, Marquesas Islands, South Pacific, 14–15 September 1922. Figure 4B. AMNH 191756, Ducie Atoll, Pitcairn Islands, South Pacific, 30 March 1922. Figure 4C. AMNH 191770, Ducie Atoll, Pitcairn Islands, South Pacific, 30 March 1922. Fig. 4D. AMNH 191592, Ducie Atoll, Pitcairn Islands, South Pacific, 20 March 1922 (also shown in Figs. 5, 6 and 10) (Tubenoses Project/Vincent Bretagnolle)

one bird at sea (Fig. 8). *General plumage* In all respects, the palest intermediates approach light morph, and the darkest approach dark morph. *Lower breast to undertail-coverts* There is a gradation in plumage from dusky (AMNH 191366, Fig. 6) to darkish (AMNH 191642, Fig. 5), and in between (Fig. 8). The key difference from light morph is that the breast to undertail-coverts are at least wholly dusky (Fig. 6); and from dark morph this area manifests reasonably clear ghosting of light-morph plumage, with a relatively clear border between the dark upper breast and paler lower breast; Fig. 8).



Figure 5. Comparison of light, intermediate and dark-morph Herald Petrels *Pterodroma heraldica* (left-hand three specimens) with Henderson Petrels *P. atrata* (right-hand two specimens), at American Museum of Natural History (AMNH), from left to right: (1) light-morph Herald Petrel (AMNH 191569), Ducie Atoll, Pitcairn Islands, South Pacific, (2) intermediate-morph Herald Petrel (AMNH 191642), Henderson Island, Pitcairn Islands, South Pacific, (3) dark-morph Herald Petrel (AMNH 191592, also shown in Figs. 4D, 6, 10), Ducie Atoll, Pitcairn Islands, South Pacific, 20 March 1922, (4) Henderson Petrel (AMNH 191753), Henderson Island, Pitcairn Islands, South Pacific, (5) Henderson Petrel (AMNH 191553), Henderson Island, Pitcairn Islands, South Pacific; note that (1) is a typical light-morph Herald Petrel, (2) an intermediate-morph Herald Petrel with a complete dark-flecked dusky lower breast to undertail-coverts, (3) a typical dark-morph Herald Petrel, and (4) and (5) are typical Henderson Petrels (Tubenoses Project/Hadoram Shirihai)

Separation from Henderson Petrel

Onley & Scofield (2007) incorrectly stated that 'Plumage of dark-phase Herald Petrel appears to be exactly the same as Henderson Petrel and there is no known way of telling them apart at sea.' Rather, photographic documentation of more than 300 Henderson Petrels at Henderson Island during 2003–17 confirms that the species invariably has a uniformly dark underside to the primaries (RLF, HS & KZ pers. obs.; Fig. 11). Care must be taken, however, to recognise a Henderson Petrel showing pale grey reflection off the shiny underside, which can suggest dark-morph Herald Petrel (Fig. 11B), but never truly mimics the extensive white basal primary 'triangle' characteristic of the latter (Figs. 1–2). Similarly,



Figure 6. Herald Petrel *Pterodroma heraldica* specimens, Ducie Atoll, Pitcairn Islands, South Pacific. Light morphs, except intermediate morph AMNH 191366 (left row, third from bottom, collected 20 March 1922), and dark morph AMNH 191592 (far right, collected 20 March 1922, also shown in Figs. 4D, 5 and 10). Note, some light morphs have dusky markings encroaching onto the belly (e.g., left row, second from bottom), but in our definition the intermediate morph uniquely has a complete dusky lower breast to undertail-coverts, plus an enlarged diffuse dark breast-band (Tubenoses Project/Vincent Bretagnolle)



7A



7B

Figure 7A–B. Dark-morph Herald Petrels *Pterodroma heraldica*, collected in Tuamotu Islands, on Vanavana Island (AMNH 191656; left) and Tenarunga Island (AMNH 191658; right) (Augie Kramer, © American Museum of Natural History, New York)



Figure 8 (left). Intermediate-morph Herald Petrel *Pterodroma heraldica*, 1.5–3.0 miles off east coast of Ua Pou, Marquesas Islands, French Polynesia, South Pacific, 5 October 2021; breast to undertail-coverts darkish with a quite clear ghosting of light-morph plumage (e.g., clearly delineated border between darker upper breast and paler lower breast). Multiple photographs were checked to eliminate the possibility that this is an effect of lighting (cf. Fig. 9). (Shoko Tanoi)

Figure 9 (right). Dark-morph Herald Petrel *Pterodroma heraldica*, 1.5–3 miles off east coast of Ua Pou, Marquesas Islands, French Polynesia, South Pacific, 3 October 2021; light catching the underparts can exaggerate subtle ghosting of light-morph underparts plumage, suggesting intermediate morph. Fig. 2A shows same bird under different light conditions, confirming it is a 'classic' dark morph. (Kirk Zufelt)

any white in the greater primary-coverts is less extensive than even the narrowest but still bold white crescent of dark-morph Herald Petrel. The whitish marginal forewing lining on average is better developed in Henderson Petrel. Furthermore, Henderson Petrel is often incorrectly described and / or illustrated with uniformly dark underparts (e.g., Brooke 2004, Onley & Scofield 2007). Howell & Zufelt (2019) were uncertain whether 'ghosting of Herald Petrel's dark hood' (i.e., paler underparts) represents paler extremes in Henderson Petrel, dark variations in Herald Petrel, or possibly even hybrids. The fact is that most Henderson Petrels show paler underparts, with darker breast, flanks and undertail-coverts, not unlike dark-morph Herald Petrel (Fig. 11B), whilst Henderson Petrel with uniformly dark underparts is rather scarce. This underscores the importance of differences in their underwing patterns to separate the two species.

As for structure, prolonged views of Henderson Petrel in flight confirm its characteristically slenderer form than Herald Petrel, with a smaller head, narrower wings, slimmer body and longer tail (Fig. 11A). A bird's behaviour and the angle of view can momentarily create a more compact appearance, meaning care should be taken with single photographs (e.g., compact impression, Fig. 11B; truer slenderer form, Fig. 11A). Conversely, a single photograph of a Herald Petrel can capture a moment when the bird looks slenderer in appearance versus the impression gained from prolonged views (e.g., compare apparent structures in Figs 1–3).



Figure 10A–B. Dark-morph Herald Petrel *Pterodroma heraldica* (Fig. 10A), Ducie Atoll, Pitcairn Islands, South Pacific (AMNH 191592, also Figs. 4D, 5–6); Henderson Petrel *P. atrata* (Fig. 10B, also Fig. 5), Henderson Island, Pitcairn Islands, South Pacific (AMNH 191753). Note, dark-morph Herald Petrel shows a white tongue basally on inner web of underside to primaries (only p10 visible here) and white basally in greater primary-coverts (outermost few visible here), both of which are dark in Henderson Petrel (though white basally on greater primary-coverts can be just visible; as here, be aware of light reflecting off the underside of the primaries) (Tubenoses Project/Hadoram Shirihai)

Records of intermediate-morph and dark-morph Herald Petrel

Below, we consolidate all records known to us of intermediate-morph and dark-morph Herald Petrel (specimens and live birds). Since the 1970s, records have been restricted to Ua Pou and Mangareva, with the majority from Ua Pou, but this may reflect observer coverage.

Specimens. — We know of seven dark-morph and two intermediate-morph Herald Petrel skins in museums (below). The percentages of dark and intermediate birds from named locations are listed here with the caveat that collectors may have taken a disproportionate number of the rarer intermediate and dark birds (Murphy & Pennoyer 1952).

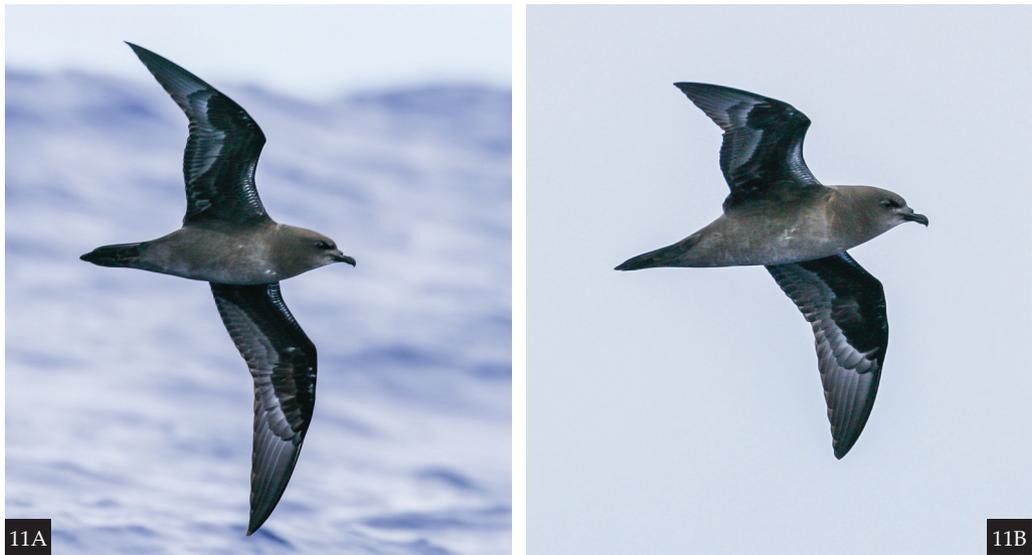
Ua Pou (Marquesas Islands): two dark of 28 (c.7%) specimens at the American Museum of Natural History, New York (AMNH), collected 14–15 September 1922 (AMNH 194338 and 194339, Fig. 4A; Murphy & Pennoyer 1952).

Ducie Atoll (Pitcairn Islands): of 46 specimens held at AMNH, one intermediate (c.2%) (AMNH 191366, 20 March 1922, Fig. 6) and three dark (c.6.5%), 20 March 1922 (AMNH 191592, Figs. 4D, 5–6) and 30 March 1922 (AMNH 191756, Fig. 4B; AMNH 191770, Fig. 4C).

Henderson Island (Pitcairn Islands): of four specimens at AMNH, one (25%) intermediate (AMNH 191642, 8 April 1922; Fig. 5).

Tuamotu Islands: two dark of five specimens (40%), one collected 23 June 1922 on Vanavana Island (AMNH 191656, Fig. 7A) and one taken 18 June 1922 (AMNH 191658, Fig. 7B) on Tenarunga Island (Murphy & Pennoyer 1952). No recent record of breeding at these localities (J.-C. Thibault pers. comm. to VB), but a recent record of breeding by light morph from Morane, Tuamotu (HS pers. obs.).

'All-dark' birds collected in the Pacific Ocean by L. B. Spear & R. L. Pitman, held at the Natural History Museum of Los Angeles County (LACM), show the characters



Figures 11A–B. Henderson Petrels *Pterodroma atrata*, off Henderson Island, Pitcairn Islands, South Pacific, July 2006, showing slight individual variation in underwing markings and body plumage. However, both lack dark-morph Herald Petrel's diagnostic underwing markings; extensive white basal primary 'triangle' and bold white greater primary-coverts 'crescent'. Do not be misled by a pale grey reflection off shiny underside to primaries, or limited white basally in the greater primary-coverts of some Henderson Petrels (Fig. 11B). Note Henderson Petrel's typically paler belly, with darker breast, flanks and undertail-coverts (rarely uniform). Differences in underwing pattern are key to separating Henderson and Herald Petrels. In flight, the former is characteristically more slender than Herald Petrel (Fig. 11A), but as shown in Fig. 11B the bird's behaviour and angle of view can momentarily yield a more compact appearance (Tubenoses Project/Hadoram Shirihai)

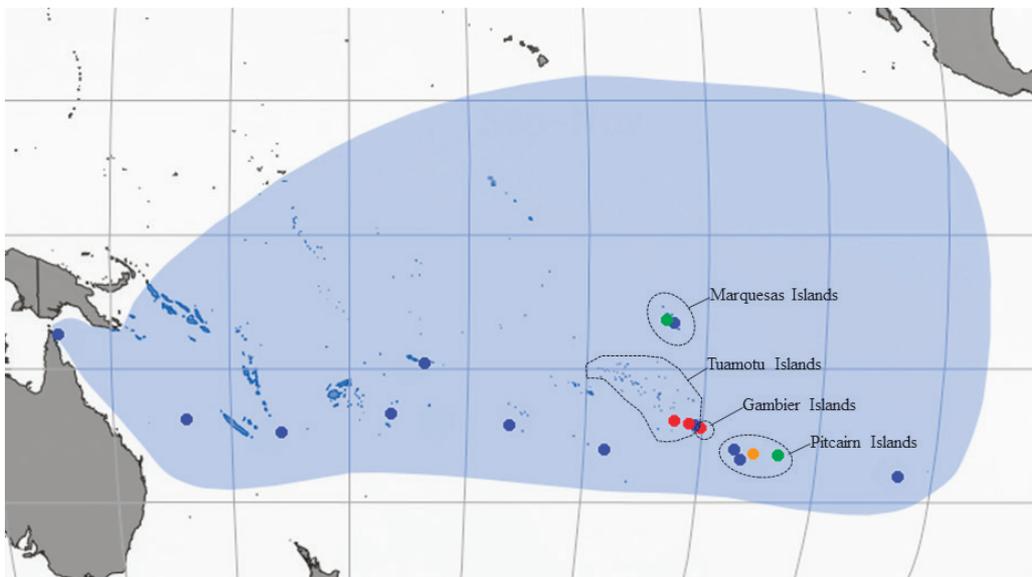


Figure 12. Distribution of Herald Petrel *Pterodroma heraldica* in the Pacific Ocean, showing island groups where light, intermediate and dark morphs are, or previously were, recorded (see text for records of intermediate and dark morphs; blue = light morph, orange = light and intermediate morphs, red = light and dark morphs, green = all three morphs). Made with Natural Earth.

of Henderson Petrel, but LACM 103086 warrants further inspection (determined from photographs supplied by the museum).

Sight records. — Ua Pou (Marquesas Islands), October 1971: 25 dark of *c.*50 birds (*c.*50%), at breeding colony (Holyoak & Thibault 1984), though retrospectively these figures are uncertain (J.-C. Thibault pers. comm. to VB). July 1975: *c.*1.5% dark of 200–300 individuals at breeding colony (Holyoak & Thibault 1984). 15 February 1990: two dark of 100–120 birds (*c.*2%) at main colony (VB). August 1998: nine dark among 300 birds (*c.*3%) at breeding colony (J.-C. Thibault). 1–4 October 2021: five dark of *c.*180–200 birds (*c.*3%) (Figs. 1–3); four birds 1.5–3.0 miles offshore, one *c.*17 miles south-east; one intermediate (*c.*0.5%), 1.5–3.0 miles offshore (Fig. 8) (Flood *et al.* 2022).

Mangareva Island (Gambier Islands), August 1996: six dark among 44 birds (*c.*14%) at cliff-nesting colony (Thibault & Bretagnolle 1999). October 2019: no dark individuals among five birds at cliff-nesting colony (J.-C. Thibault & A. Cibois pers. comm. to VB).

Fig. 12 shows the range of Herald Petrel in the Pacific Ocean (based on Spear *et al.* 1992, Howell & Zufelt 2019), indicating the locations of at-sea sightings and specimens of intermediate and dark morphs listed above. Note, to our knowledge, only light-morph birds have been confirmed north of the Marquesas (northernmost islands *c.*07°30'S). For example, only light-morph *Pterodroma* have been confirmed in Hawaiian waters, with five dark *Pterodroma* on 21–29 November 2002 that could have been Henderson Petrels (Pyle & Pyle 2017) or, based on known range, more likely Murphy's Petrels *P. ultima*.

Further research

As mentioned above, hybrid *heraldica* × *atrata* cannot be eliminated and it is unknown if offspring from such hybridisation events could result in birds that resemble intermediate-morph or dark-morph Herald Petrel. In addition, the extent of mixed morph pairings among Herald Petrels is unknown. Lastly, further insights into morphs of Herald Petrel may be found in the genetics and inheritance of colour morphs.

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References

- Bailey, S. F., Pyle, P. & Spear, L. B. 1989. Dark *Pterodroma* petrels in the North Pacific: identification, status, and North American occurrence. *Amer. Birds* 43: 400–415.
- Booth Jones, K., Nicoll, M. A. C., Raisin, C., Dawson, D. A., Hipperson, H., Horsburgh G. J., Groombridge, J. J., Ismar, S. M. H., Sweet, P., Jones, C. G., Tatayah, V., Ruhomaun, K. & Norris, K. 2017. Widespread gene flow between oceans in a pelagic seabird species complex. *Mol. Ecol.* 26: 5716–5728.
- Brooke, M. 2004. *Albatrosses & petrels across the world*. Oxford Univ. Press.
- Brooke, M. de L. & Rowe, G. 1996. Behavioural and molecular evidence for specific status of light and dark morphs of the Herald Petrel *Pterodroma heraldica*. *Ibis* 138: 420–432.
- Brown, R. M., Nichols, R. A., Faulkes, C. G., Jones, C. G., Bugoni, L., Tatayah, V., Gottelli, D. & Jordan, W. C. 2010. Range expansion and hybridization in Round Island petrels (*Pterodroma* spp.): evidence from microsatellite genotypes. *Mol. Ecol.* 19: 3157–3170.

- Brown, R. M., Jordan, W. C., Faulkes, C. G., Jones, C. G., Bugoni, L., Tatayah, V., Palma, R. L. & Nicols, R. A. 2011. Phylogenetic relationships in *Pterodroma* petrels are obscured by recent secondary contact and hybridization. *PLoS ONE* 6: e20350.
- Flood, R. L. & Fisher, A. 2013. *North Atlantic seabirds: Pterodroma petrels*. Pelagic Birds & Birding Multimedia ID Guides, Scilly.
- Flood, R. L. & Fisher, A. 2016. *North Atlantic seabirds: albatrosses & fulmarine petrels*. Pelagic Birds & Birding Multimedia ID Guides, Scilly.
- Flood, R. L., Tanoi, S. & Zufelt, K. 2022. Pelagic observations during a circumnavigation of the Marquesas Islands, French Polynesia, September–October 2021. Pacific Seabird Group Tech. Rep. 4. <https://pacificseabirdgroup.org/psg-publications/technical-publications/>.
- Ford, E. B. 1965. *Genetic polymorphism*. Faber & Faber, London.
- Galeotti, P., Dunn, P., Rubolini, D. & Fasola, M. 2003. Colour polymorphism in birds: causes and functions. *J. Evol. Biol.* 4: 635–646.
- Harrison, P., Perrow, M. & Larsson, H. 2021. *Seabirds: the new identification guide*. Lynx Edicions, Barcelona.
- Holyoak, D. T. & Thibault, J.-C. 1984. Contribution à l'étude des oiseaux de Polynésie orientale. *Mém. Mus. Natl. Hist. Nat., Paris (sér. A), Zool.* 127: 1–209.
- Howell, S. N. G. & Zufelt, K. 2019. *Oceanic birds of the world: a photo guide*. Princeton Univ. Press.
- Imber, M. J. 1985. Origins, phylogeny and taxonomy of the gadfly petrels *Pterodroma* spp. *Ibis* 127: 197–229.
- Jaramillo, A., Johnson, M. T. J., Rothfels, C. J. & Johnson, R. A. 2008. The native and exotic avifauna of Easter Island: then and now. *Bol. Chil. Orn.* 14: 8–21.
- Luigi, G., Bugoni, L., Fonseca-Neto, F. P. & Teixeira, D. M. 2009. Biologia e conservação do petrel-de-Trindade, *Pterodroma arminjoniana*, na Ilha da Trindade, Atlântico Sul. Pp. 225–263 in Mohr, L. V., Castro, J. W. A., Costa, P. M. S. & Alves, R. J. V. (eds.) *Ilhas oceânicas brasileiras: da pesquisa ao manejo*, vol. 2. Ministério do Meio Ambiente, Brasília.
- Marchant, S. & Higgins, P. J. 1990. (eds.) *Handbook of Australian, New Zealand & Antarctic birds*, vol. 1A. Oxford Univ. Press, Melbourne.
- Marin, M. & Cáceres, P. 2010. Sobre las aves de Isla de Pascua. *Bol. Mus. Nac. Hist. Nat.* 59: 75–95.
- Murphy, R. C. & Pennoyer, J. M. 1952. Larger petrels of the genus *Pterodroma*. *Amer. Mus. Novit.* 1580: 1–43.
- Onley, D. & Scofield, P. 2007. *Albatrosses, petrels and shearwaters of the world*. Christopher Helm, London.
- Oppel, S., Lavers, J. L., Donaldson, A. H., Forrest, A. K., McClelland, G. T. W., Bond, A. L. & Brooke, M. de L. 2017. Population status, breeding success and ecology of the Henderson Petrel after a failed rat eradication on Henderson Island. *Emu* 117: 151–159.
- Pyle, R. L. & Pyle, P. 2017. The birds of the Hawaiian Islands: occurrence, history, distribution, and status. B.P. Bishop Museum, Honolulu. Version 2 (1 January 2017) <http://hbs.bishopmuseum.org/birds/rlp-monograph>.
- Roulin, A. 2004. The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biol. Rev. Cambridge Philos. Soc.* 79: 815–848.
- Shirihai, H. & Bretagnolle, V. in prep. *Albatrosses, petrels and shearwaters of the world: a handbook to their taxonomy, identification, ecology and conservation*, vol. 1. Bloomsbury, London.
- Spear, L. B., Howell, S. N. G. & Ainley, D. 1992. Notes on the at-sea identification of some Pacific gadfly petrels (genus: *Pterodroma*). *Colonial Waterbirds* 15: 202–218.
- Tennyson, A. J. D., Lawrence, H. A., Taylor, G. & Imber, M. J. 2013. A hybrid gadfly petrel suggests that soft-plumaged petrels (*Pterodroma mollis*) had colonised the Antipodes Islands by the 1920s. *Notornis* 60: 290–295.
- Thibault, J.-C. & Bretagnolle, V. 1999. Breeding seabirds of Gambier Islands, Eastern Polynesia: numbers and changes during the 20th century. *Emu* 99: 100–107.
- Thibault, J.-C. & Cibois, A. 2017. *Birds of Eastern Polynesia: a biogeographic atlas*. Lynx Edicions, Barcelona.
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