Plumage variation in Gould's petrel (*Pterodroma leucoptera*): an evaluation of the taxonomic validity of *P. l. caledonica* (Imber & Jenkins 1981)

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Abstract Gould's petrel, *Pterodroma leucoptera*, comprises 2 subspecies: *P. l. leucoptera* that breeds in eastern Australia, and *P. l. caledonica* that breeds in New Caledonia. The latter subspecies was diagnosed primarily on the basis of plumage differences observed between beachcast specimens from New Zealand (presumed to be *P. l. caledonica*) and a small sample of specimens from Cabbage Tree Island in Australia. This study re-examined the diagnosis of *P. l. caledonica* by quantifying plumage variation in both subspecies using live individuals and museum specimens originating from breeding colonies. Variation in supposedly diagnostic plumage characters within the larger sample of the nominate subspecies encompassed almost the entire variation observed in *P. l. caledonica*; though the former tended to be more heavily pigmented. Given the lack of valid diagnostic characters, the retention of *P. l. caledonica* as a distinct taxon is difficult to justify. Gould's petrel should therefore be treated as monotypic.

INTRODUCTION

The genus *Pterodroma* (gadfly petrels; Procellariidae) is the most speciose within the Procellariiformes, comprising at least 32 species (Brooke 2004). The existence of numerous species complexes (*e.g.,* Brooke & Rowe 1996; Browne *et al.* 1997; Jesus *et al.* 2009) within the genus has incited considerable debate and frequent revision of the systematics and taxonomy of *Pterodroma* (*e.g.,* Jouanin & Mougin 1979; Imber 1985; Penhallurick & Wink 2004). One such species complex comprises Gould's (*P. leucoptera*) and collared (*P. brevipes*) petrels, which have been treated either as conspecific (*e.g.,* Marchant & Higgins 1990; Warham 1990; Dickinson 2003) or full species (*e.g.,* Imber 1985;

Spear *et al.* 1992; Brooke 2004). The systematics of this complex has yet to be fully resolved (Gangloff 2010; Tennyson *et al.* 2012). Gould's and collared petrels are superficially similar, but the former is readily distinguishable from the latter primarily by its larger size, proportionately shorter and less tapered tail, and white bases on the underside of the remiges (Murphy 1929; Spear *et al.* 1992; Enticott & Tipling 1997; Brooke 2004; Onley & Scofield 2007; Bretagnolle & Shirihai 2010). Moreover, unlike Gould's petrel, the collared petrel is polymorphic: the breast, belly, flanks and undertail vary along a continuum from entirely white, resembling Gould's petrel, to entirely sooty grey (Watling 1986; Bretagnolle & Shirihai 2010).

Gould's petrel breeds on at least 4 islands off the coast of New South Wales in Australia (primarily on Cabbage Tree Island; Priddel & Carlile 1997;

Carlile *et al.* 2012, 2013; N. Carlile, *pers. comm.*) and on Grand Terre in New Caledonia (Naurois 1978). The species has also been recorded on Raivavae in the Austral Islands (Seitre & Seitre 1991; Raust 2007), but breeding has not been confirmed, and a single specimen was reputedly collected from Makira Island (San Cristobal) in the Solomon Islands between 1878 and 1880 (National Museums Liverpool T.16064). Naurois (1978) considered the birds he found in New Caledonia were a new subspecies, *P. l. caledonica* (hereafter *caledonica*), because they had a paler back, wings and side of the chest, and a more robust bill than specimens of the nominate subspecies collected from Cabbage Tree Island (hereafter *leucoptera*). Bull (1943) had earlier described 10 beachcast Gould's petrels from Muriwai Beach, New Zealand, that exhibited reduced pigmentation on the underside of the manus, a lesser tendency to exhibit 'clouding' across the upper breast (= foreneck), and larger average dimensions than birds from Cabbage Tree Island. Imber & Jenkins (1981) re-examined 4 of these specimens and an additional 4 beachcast specimens from Muriwai and Otaki Beaches. They too concluded the beachcast birds originated from a separate colony, and believed them to be *caledonica*, adding that:

> "...the back and upper tail-coverts [of *caledonica*] are grey, thus contrasting with the rest of the upperparts, which are dark grey to sooty... In [*leucoptera*] the upperparts are darker, the back in particular, and so there is much less contrast" and "the most reliable distinguishing feature seems to be found in the rectrices.... In [*leucoptera*] (two specimens... were examined) the outermost tail feather has its inner web grey to brownish grey, except for the basal half which is off-white. All eight New Zealand specimens.... have the inner web of the outer feather white, or mainly white, but with a variable amount of grey freckling near the tip. At most this freckling extends from about the mid-point near the rachis gradually over the whole width near the tip."

Imber & Jenkins (1981) also examined a specimen from New Caledonia held in the American Museum of Natural History (AMNH), which had "...white inner webs to the outer pair of tail feathers." Shirihai (2008) suggested *caledonica* also differs from *leucoptera* in having paler bases to the underside of the primaries, and potentially a narrower dark tip on the uppertail. Imber & Jenkins (1981) reported that mean culmen, wing, tail, tarsus and mid-toe lengths of Gould's petrels collected in the Pacific Ocean (Loomis 1918; Murphy 1929), New Zealand, near Tonga, near Pitcairn Island, and New

Caledonia (the single AMNH specimen), which they attributed to *caledonica,* were 2–4% larger than *leucoptera* measured by Serventy *et al.* (1971).

Although the subspecific name *caledonica* first appeared in Naurois (1978), Palma & Tennyson (2005) designated Imber & Jenkins (1981) as the author because Naurois (1978) intended to retract his description of a new subspecies, but in an oversight did not remove the name from the manuscript's abstract. Both authors used a small sample of *leucoptera* skins to establish plumage differences between the purported subspecies—indeed this was why Naurois (1978) intended to withdraw his description of a new subspecies (Palma & Tennyson 2005)—and Imber & Jenkins (1981) referred to only a single specimen originating from New Caledonia. These shortcomings cast doubt on the validity of the designation of *caledonica*, especially given the plumage of *leucoptera* may be more variable than these authors realised, as evidenced by variation in pigmentation across the foreneck (Hindwood & Serventy 1941). The aim of this study was to re-evaluate the diagnosis of *caledonica* by quantifying plumage variation in both subspecies, using a larger sample of museum skins and live birds sourced from the 2 main breeding colonies.

METHODS

The extent of pigment on the rectrices, underwing and foreneck of *leucoptera* and *caledonica* was quantified by the author using photographs of museum skins and live individuals. Museum skins had been collected from breeding colonies on Cabbage Tree Island (*leucoptera*; n = 17) and New Caledonia (*caledonica*; n = 16), and at sea off Noumea, New Caledonia (*caledonica*; n = 1) (Appendix 1). The plumage of 188 live adult *leucoptera* was examined in the hand in November (34%), December (61%) or March (5%), during annual population surveys on Cabbage Tree Island (see Priddel & Carlile 2007). These individuals were selected pseudo-randomly without prejudice to plumage characteristics. The rectrices, underwing and foreneck (n = 40), rectrices and underwing only (n = 40), rectrices only (n = 13), or foreneck only (n = 45) were photographed. The forenecks of an additional 50 live *leucoptera* were examined but not photographed. The variable lighting conditions under which photographs were taken is not considered to have affected the results, because the degree of pigmentation rather than characteristics of the pigment (*e.g.*, hue, tone) was examined. Photographs of at least 18 live *caledonica* observed at sea off New Caledonia in March, April and May—taken by Julien Baudat-Franceschi, Thomas A. Blackman, Mike Danzenbaker, John & Jemi Holmes, Jonathan Rossouw, Alan Tate, Nigel Voaden and Kirk Zufelt—and 2 *caledonica*
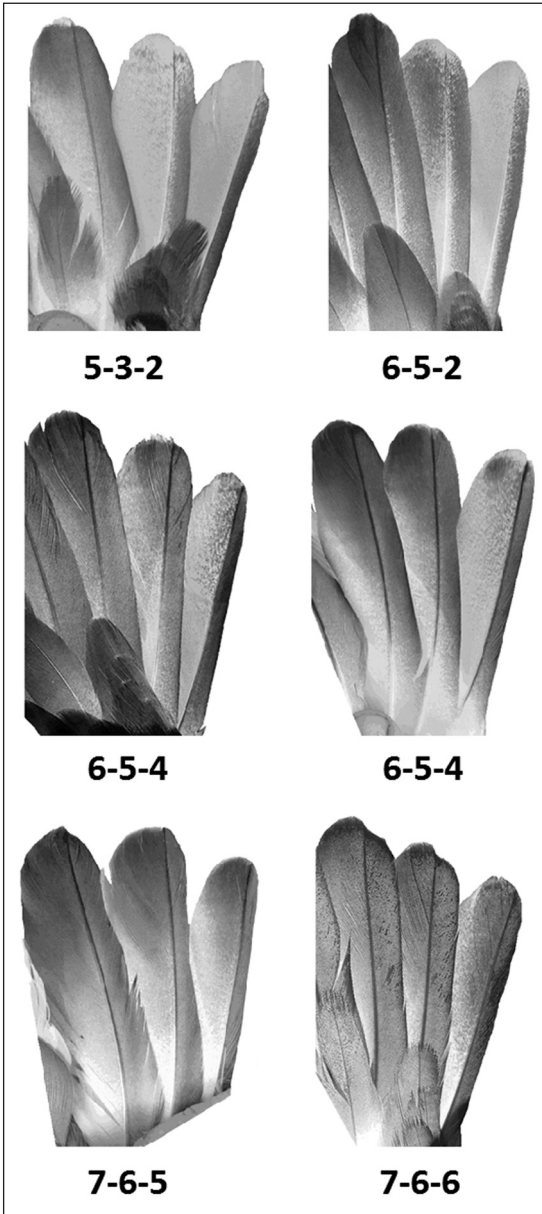
Fig. 1. Variation in the extent of pigment in the outer rectrices of live *leucoptera*. Numbers below each image indicate the scores for each rectrix in the format R4-R5-R6. Left side of tail shown.

photographed in the hand at Mt Dzumac, New Caledonia by Nicholas Carlile were also examined.

Additionally, the plumages of 4 petrels captured on Raivavae (February 1993) was examined using photographs taken by Alain Guillemont. The specific identity of birds from Raivavae has been treated as uncertain, with most authors considering

them to be collared petrels (Onley & Scofield 2007; Tennyson *et al*. 2012; Raust 2015). However, several diagnostic characteristics of Gould's petrel that readily distinguish it from collared petrel—most notably the weakly graduated rectrices and white bases to the underside of the primaries—are apparent in the photographs.

Rectrices

The inner rectrices are grey but progressively lose pigment proximally from the innermost (R1) to outermost (R6) rectrices, becoming increasingly freckled grey against a white background (Hindwood & Serventy 1941). The loss of pigment is greatest on the inner vane, which in the extreme case lacks pigment (Imber & Jenkins 1981). Within a rectrix, the freckling becomes denser and spreads from the inner half of the vane towards the tip and outer edge, where it coalesces to solid grey in more heavily pigmented feathers. Only the outer 3 rectrices (R4, R5 and R6) were examined because variation in the extent of pigment on the inner 3 rectrices was negligible. Although inter-individual variation represented a continuum of increasing pigmentation, the extent of pigment on the inner vane of R4, R5 and R6 on one side of the tail for 110 *leucoptera* (including 17 museum skins) and 17 *caledonica* museum skins was scored as follows (Fig. 1):

1 = no pigment.

2 = limited tiny flecks of pigment in the distal ⅓.

3 = light freckling on distal ¼–⅓ or more rarely distal ½, sometimes coalescing to form tiny blotches.

4 = moderate freckling on distal ⅓–½ with limited coalescing of freckles or, more rarely, a conspicuous small uniform grey blotch within the distal ¼.

5 = uniform grey over most or all of distal ¼ with freckling over remainder of distal ½–¾.

6 = uniform grey distal ⅓ with extensive coalescing of freckles in remainder of distal ½ and freckling over remainder of distal ¾ to entire vane.

7 = uniform grey over most of distal ½ with extensive coalescing of freckles in remainder of distal ⅔ and freckling over much of proximal ⅓.

The rectrices of 40 advanced *leucoptera* nestlings on Cabbage Tree Island were also examined, but the extent of pigment was not quantified because the feathers were not fully grown.

Underwing

The smaller marginal coverts on the manus and along the ulna are partially or wholly dark grey to sooty black, forming a dark ulnar-carpal bar; the remaining coverts are unpigmented. The underwing was examined for 80 live *leucoptera* individuals photographed in November–December, 9 *caledonica* museum skins prepared with one wing partly outstretched, and 17 live *caledonica* photographed at sea (all *leucoptera* and the remaining 8 *caledonica* museum skins were prepared with both wings closed and held against the body). Although inter-individual variation represented a continuum of increasing pigmentation, the extent of pigment within the ulnar-carpal bar was scored as follows (Fig. 2):

1 = conspicuous, usually linear, white (*i.e.*, unpigmented) patch immediately distal to the mid-point of the manus (hereafter mid-manus patch) and a smaller, usually less regular white patch proximal to the mid-manus patch (hereafter basal manus patch). Indistinct to distinct white to light grey fringes on the marginal coverts along the leading edge of the manus.

2 = mid-manus patch reduced, appearing as a small white blotch, thin line or crescent; basal manus patch absent. Fringes of marginal coverts as 1.

3 = mid-manus patch greatly reduced or indistinct, basal manus patch absent, and indistinct to distinct pale fringes largely restricted to the distal coverts along the leading edge of the manus.

4 = manus almost entirely pigmented, except for a limited number of coverts with indistinct thin pale fringes.

The thickness of the ulnar-carpal bar was not scored because the wings of the *caledonica* museum skins were only partly outstretched.

Foreneck

The extent of pigment across the foreneck was scored for 15 *leucoptera* and 17 *caledonica* museum skins, and 135 live *leucoptera* which were examined with the head held horizontally, as follows (Fig. 3):

1 = no pigment.

2 = limited speckles across foreneck.

3 = lightly speckled across foreneck.

4 = indistinct to distinct speckled band across foreneck.

5 = distinct, heavily speckled or mottled band across foreneck.

Fig. 2. Variation in the extent of pigment on the underside of the manus of live *leucoptera*. Scores from top to bottom: 1, 2, 3, 4.

Dorsal plumage

The variable lighting conditions under which museum specimens were photographed proved problematic for quantifying variation in the strength of the contrast between the dark crown and nape and paler mantle and back (hereafter dorsal contrast). Therefore, the dorsal plumages of *leucoptera* and *caledonica* museum skins were only compared qualitatively.

To investigate the effect of wear on the dorsal contrast, the dorsal plumages of live adult *leucoptera* were photographed while sitting in nest boxes in November (n = 26), December (n = 15), March (n = 13) or April (n = 1); 38 of these individuals were also photographed in the hand (see above). Additionally, 13 advanced nestlings were photographed while sitting in next boxes in March–April. All individuals were photographed under similar lighting conditions, both with and without a flash.

Statistical analysis

Spearman rank correlations were performed in SPSS® version 23 to test for positive relationships (*i.e.*, one-tailed test) between the pigmentation score for the outermost rectrix (R6) and the pigmentation

Fig. 3. Variation in the extent of pigment across the foreneck of live *leucoptera*. Scores from left to right: 2, 3, 4, 5 (score 1 not depicted).

Table 1. Variation in the extent of pigment on the underside of the manus, which increases from score 1 through to score 4, for live *leucoptera* (*n* = 80), *caledonica* museum skins (*n* = 9) and live *caledonica* photographed at sea (*n* = 17). Values indicate percent.

Subspecies (sample)	Pigmentation score			
	1	2	3	4
leucoptera (live)	17.5	57.5	21.3	3.4
caledonica (museum)	22.2	66.7	11.1	0.0
caledonica (live)	47.1	52.9	0.0	0.0

score for: (1) the underside of the manus (*n* = 80), and (2) the foreneck (*n* = 40) of *leucoptera*.

RESULTS
Rectrices
The extent of pigment on the outer rectrices, particularly R6, varied considerably in both subspecies, but *leucoptera* tended to have more extensively pigmented rectrices than *caledonica* (Fig. 4): the mean (± sd) of the sum of the scores for R4, R5 and R6 was 15.3 ± 1.81 (*n* = 110) for *leucoptera* and 12.8 ± 3.17 (*n* = 17) for *caledonica*. Only one individual, a *caledonica*, had an entirely white inner vane on R6 (score 1); this individual was unique in that it also had an entirely white inner vane on R5 and an almost completely white inner vane on R4 (score 2). With the exception of this individual, all combinations of scores for R4, R5 and R6 observed in *caledonica* also occurred in *leucoptera*. Eighteen different combinations of scores (in the format R4-R5-R6) were recorded for *leucoptera*, the most common being 6-5-4 (26.4%), 6-5-5 (15.5%), 6-5-3 (13.6%) and 7-6-5 (9.1%) (Fig. 1). Nine combinations of scores were recorded for *caledonica*, with most

individuals having a combined score of 5-3-2 (17.6%), 6-5-4 (17.6%), 7-5-4 (17.6%) or 6-5-3 (11.8%). The extent of pigment decreased from R4 to R6 either gradually (39.1% *leucoptera*, 23.5% *caledonica*; scores of adjacent rectrices usually differed by one) or abruptly. In the latter case, R6 (26.4% *leucoptera*; 23.5% *caledonica*) or R4 (11.0% *leucoptera*; 41.2% *caledonica*) was considerably less or more pigmented than the adjacent 2 rectrices, respectively, and/ or 2 adjacent rectrices had the same score (34.5% *leucoptera*, 11.8% *caledonica*); though the innermost was always slightly more pigmented. Variation among advanced *leucoptera* nestlings was similar to that observed for adults. No difference was discernible in the thickness of the dark tip on the uppertail of *caledonica* photographed at sea and live *leucoptera*.

Underwing
Variation in the extent of pigmentation on the underside of the manus was similar between the 2 subspecies (Table 1). Most (57.5%) live *leucoptera* and most (57.7%) *caledonica* had a prominent, albeit small, white patch almost mid-way along the underside of the manus within the dark ulnar-carpal bar (*i.e.*, score 2; Fig. 2). However, all but one of the remaining *caledonica* had less pigment in the manus, whereas only about half of the remaining *leucoptera* did so. As for the rectrices, the individual with the least amount of pigment was a *caledonica* (photographed at sea); this individual was unique in that the 2 white patches on the manus were enlarged and connected. Unlike *leucoptera*, none of the live *caledonica* had an entirely dark ulnar-carpal bar. There was a weak positive correlation between the extent of pigment on the outermost rectrix and the extent of pigment on the underside of the manus for *leucoptera* (Fig. 5; ρ = 0.193, t_{78} = 1.74, *P* = 0.043).
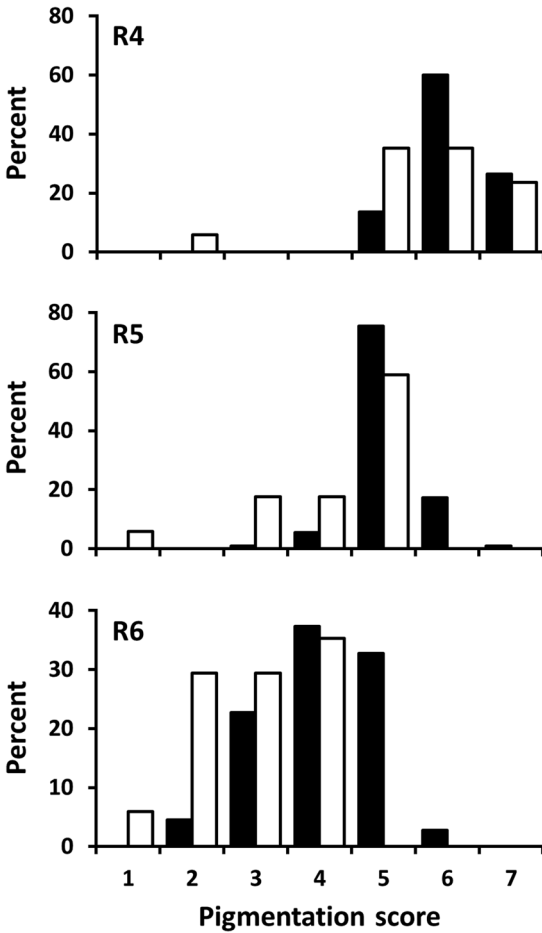
Fig. 4. Distribution of scores for the extent of pigment on rectrices R4 (top), R5 (middle) and R6 (bottom) of 110 *leucoptera* (solid columns) and 17 *caledonica* (open columns). The extent of pigment increases from score 1 through to score 7.
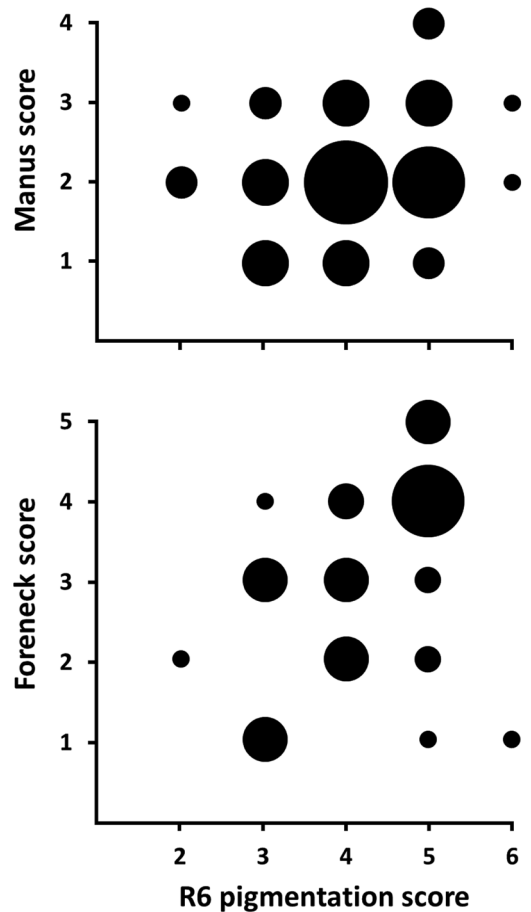
Fig. 5. The relationship between the extent of pigment on the outermost rectrix (R6) and pigmentation on 1) the underside of the manus (top; n = 80), and 2) across the foreneck (bottom; n = 40) in *leucoptera*. Size of circles (smallest to largest) indicate the number of individuals: 1, 2–4, 5–9, 14, 20 (top); 1, 2, 3, 4, 9 (bottom).

The thickness of the ulnar-carpal bar on both the manus and along the forearm, and consequently how close to the body it terminated, varied appreciably among live *leucoptera*. Live *caledonica* photographed at sea showed similar variation, with the exception of the individual described above. Additionally, there was no consistent discernible difference between live *leucoptera* and live *caledonica* in the extent of dark pigment on the underside of the primary remiges.

Foreneck
Most *leucoptera* (85.3%) had a variable degree of pigment across the foreneck, whereas all but 2 *caledonica* museum skins lacked pigment (Table 2). The most heavily pigmented *leucoptera* (a live individual) exhibited a thick, mottled band that

continued as grey speckling and streaking along the flanks. At least 2 of the live *caledonica* photographed at sea had pigment across the foreneck: one bird had an indistinct, thin speckled band, while the other had a thick, solid and well-defined band concolourous with the side of the breast. There was a moderately strong positive correlation between the extent of pigment on the outermost rectrix and the extent of pigment on the foreneck for *leucoptera* (Fig. 5; $\rho = 0.432$, $t_{38} = 2.95$, $P = 0.003$).

Dorsal plumage
The dorsal contrast of juvenile *leucoptera* was striking. It was slightly less pronounced in live adult *leucoptera* in relatively fresh plumage photographed in November–December, partly because the mantle

Fig. 6. Darkening of the mantle and back resulting from plumage wear. Left 3 images show live *leucoptera* photographed using a flash: juvenile in fresh plumage (April; left), adult in relatively fresh plumage (November; middle), adult in heavily worn plumage (April; right). Image at far right shows the lectotype of *caledonica* (AMNH 824271) which was collected in February.

Table 2. Variation in the extent of pigment, which increases from score 1 through to score 5, on the forenecks of *leucoptera* (*n* = 150) and *caledonica* (*n* = 17). Values indicate percent.

Subspecies	Pigmentation score				
	1	2	3	4	5
leucoptera	14.7	24.0	30.7	24.7	6.0
caledonica	82.4	11.8	5.9	0.0	0.0

and back feathers of nestlings had thicker pale fringes. The mantle and back of adults photographed later in the breeding season (March–April) were considerably darker, resulting in a markedly reduced dorsal contrast (Fig. 6). The strength of the dorsal contrast of all museum specimens of both subspecies and live *caledonica* photographed at sea fell within the range observed for live *leucoptera* (Fig. 6). There was no consistent difference in the dorsal contrast between *caledonica* and *leucoptera* museum specimens, including among those collected at an equivalent time in the breeding cycle. Similarly, live *caledonica* photographed at sea in March and April had a similar dorsal contrast to live *leucoptera* photographed in the same months, and the single live juvenile *caledonica* photographed at sea (in May) had a similarly pronounced dorsal contrast as live *leucoptera* nestlings.

Leg colouration
No difference in the colouration of the legs of the 2 live *caledonica* from Mt Dzumac and live *leucoptera* was evident.

Raivavae petrels
Pigmentation on the outer rectrices and underwing of the birds captured on Raivavae fell within the range observed in *leucoptera* and *caledonica*. Two birds had a score of 1–2 for R6 and a probable score of 4 for R5, while a third had more heavily pigmented rectrices (R6 and R5 with scores of ≥3 and ≥5, respectively). Almost the entire underwing was photographed for 2 birds: one had a probable score of 1 and the other a score of 3. The dorsal plumage was photographed for at least 2 birds. The dorsal contrast of these birds was similar to moderately worn dorsal plumages of live *leucoptera*. No other plumage or morphological characteristics that distinguished these birds from *leucoptera*/*caledonica* were evident.

DISCUSSION
The plumage of Gould's petrel is considerably more variable than was previously recognised by Imber & Jenkins (1981). This study examined a much larger sample of individuals originating from breeding colonies on Cabbage Tree Island and Grand Terre, and failed to support Imber & Jenkins (1981) diagnosis of *Pterodroma leucoptera caledonica*. Indeed, there was near-complete overlap in plumage variation between the purported subspecies, which highlights the importance of examining adequate samples of individuals sourced from breeding colonies when diagnosing seabird taxa (see also Tennyson *et al.* 2012). Most notably, a predominantly white inner vane of the outer rectrix—supposedly the most reliable diagnostic characteristic of *caledonica*—was found in multiple individuals from both populations. Although no discrete differences

in plumage between the subspecies were found, *leucoptera* exhibited a tendency towards more extensive pigmentation in the rectrices, underwing coverts and foreneck than did *caledonica*. Moreover, despite the considerably smaller number of *caledonica* examined, the individuals with the least pigment in the rectrices and underwing coverts were of this subspecies. This subtle difference in plumage is minor compared with that observed among populations of the nominate subspecies of both collared (Watling 1986) and Kermadec (*P. externa*; Murphy & Pennoyer 1952) petrels. Plumage wear was unlikely to have confounded the comparisons between subspecies, since most live *leucoptera* (61%) and *caledonica* museum skins (≥47%) were photographed or collected at an equivalent time in the breeding cycle (December and January, respectively; see Priddel *et al.* 2014).

Imber & Jenkins (1981) reported that the mean culmen, wing, tail, tarsus and mid-toe lengths of *caledonica* were 2–4% longer than those of *leucoptera*. These differences are largely unsupported by Bretagnolle & Shirihai (2010), whose measurements of museum skins sourced from breeding colonies indicate that *leucoptera* has a 3% shorter culmen, 5% deeper and 11% wider bill, and 8% longer tail on average than *caledonica*, but wing and tarsus lengths do not differ (V. Bretagnolle, *unpubl. analyses*). Thus *leucoptera* has a slightly more robust bill (*contra* Naurois 1978) and proportionally longer tail than *caledonica*. Mean body mass of *caledonica* incubating eggs (19–22 January) was 224 grams (range 163–237, *n* = 10) for males and 174 grams (range 182–231, *n* = 6) for females, and that of incubating male and female *leucoptera* during an equivalent period of the nesting cycle (28 December to 2 January, see Priddel *et al.* 2014) was 216 grams (range 170–262, *n* = 33) and 199 grams (range 156–220, *n* = 10) respectively (N. Carlile *et al.*, *unpubl. data*). Thus, these limited data do not suggest the 2 subspecies differ in body mass. The relative magnitude of the morphological differences between the subspecies (*i.e.*, the difference between measurements expressed as a proportion of the smaller measurement) is only slightly greater than that between populations of the nominate subspecies of collared petrel for bill depth (4%) and bill width (9%) (Bretagnolle & Shirihai 2010), and is less than that among populations of several monotypic procellariids—Hawaiian (*P. sandwichensis*; Judge *et al.* 2014) and Galapagos (*P. phaeopygia*; Tomkins & Milne 1991) petrels and pink-footed (*Ardenna creatopus*; Guicking *et al.* 2004),wedge-tailed (*A. pacifica*; Peck *et al.* 2007), Cory's (*Calonectris borealis*) and Scopoli's (*C. diomedea*) (Gomez-Diaz *et al.* 2006) shearwaters—for culmen, wing and tarsus lengths, bill depth and bill width (not all measurements were taken for all species), with tail length being the only exception.

Moreover, like Gould's petrel, populations of these species differ structurally rather than in overall size. The morphological differences between *leucoptera* and *caledonica* are therefore of questionable taxonomic significance.

There are several notable differences in the nesting ecology of the 2 subspecies. *P. l. caledonica* breeds on forested mountain slopes at elevations of 400−650 m asl (Naurois 1978; Brooke 2004), whereas *leucoptera* breeds on low (<120 m asl) coastal islands (Fullagar 1976). However, high elevation coastal sites similar to those on Grand Terre are absent in Australia. On Cabbage Tree Island, *leucoptera* breeds in dense colonies of ~250−450 breeding pairs (Priddel & Carlile 2007; *unpubl. data*), while *caledonica* breeds in loose colonies of 50–100 breeding pairs (V. Bretagnolle, *pers. comm.* in Birdlife International 2015). It is unclear whether the smaller, more dispersed colonies of *caledonica* are a result of high predation pressure from feral predators in New Caledonia (see Baudat-Franceschi 2012). Typical of most small to medium sized procellariids (Brooke 2004), *caledonica* nests in burrows that are dug in soil, but also commonly nests under boulders and tree roots (Naurois 1978; N. Carlile, *pers. comm.*). In contrast, *leucoptera* has not been recorded digging a burrow on Cabbage Tree Island—despite extensive areas of soil suitable for digging burrows—and typically nests instead in naturally occurring cavities: amongst boulders and rocks, inside logs, beneath fallen palm fronds, in between buttresses of *Ficus* spp. and under tree roots (Hindwood & Serventy 1941; Fullagar 1976; Priddel & Carlile 2004). The absence of burrowing may result from the high availability of suitable natural cavities on the island and/or nest-site competition with the substantially larger wedge-tailed shearwater (see Ramos *et al.* 1997; Villard *et al.* 2006). Since these differences in nesting ecology may reflect characteristics of the breeding sites, rather than evolutionary divergence in ecology between the subspecies *per se*, they are rather uninformative for evaluating the taxonomic validity of *caledonica*.

Behavioural differences between the subspecies are poorly known. On Mt Dzumac, New Caledonia, *caledonica* rarely vocalise while on the ground (N. Carlile, *pers. comm.*); whereas *leucoptera* on Cabbage Tree Island produce a range of vocalisations while on the ground and inside the nest (*pers. obs.*). The presence of introduced mammalian predators (pigs *Sus scrofa* and cats *Felis catus*) within the Mt Dzumac colony (Baudat-Franceschi 2011) may at least partly explain this difference, since Imber *et al.* (2003) observed that Cook's petrels (*P. cookii*) rarely uttered '*purrr*' calls on the ground before feral cats were eradicated from Hauturu in New Zealand, but often did so following eradication. Since vocalisations play a

key role in species recognition and presumably function as a pre-mating reproductive isolating mechanism (Bretagnolle & Robisson 1991; Cure *et al.* 2012), they can provide considerable insight into the systematics of morphologically cryptic taxa (Rheindt *et al.* 2008), including procellariiform seabirds (*e.g.*, Bretagnolle 1995; Bolton 2007). An investigation of vocal differences among populations of Gould's petrel, including behavioural responses to playback experiments, may shed further light on the evolutionary relationship between populations.

The pelagic distribution, migration and breeding phenologies of *leucoptera* and *caledonica* differ (Priddel *et al.* 2014). Although there is substantial overlap in the pelagic distributions of the 2 subspecies during the breeding season, the core foraging areas utilised in the non-breeding period are associated with different oceanic currents: *leucoptera* in the central tropical Pacific Ocean and *caledonica* in the eastern tropical Pacific Ocean (Priddel *et al.* 2014). Adult *leucoptera* return to the colony prior to breeding in mid- to late October, whereas *caledonica* do so on average 3 weeks later in late October to mid-November (Priddel *et al.* 2014). The 2 subspecies rarely interact socially, since Gould's petrels are solitary at sea away from their breeding colony (at least during the day; Priddel *et al.* 2014) and natal philopatry is strong (at least in *leucoptera*; *unpubl. data*). Spatial and seasonal segregation of breeding populations of Gould's petrel, coupled with limited social contact, suggest the 2 populations may represent independent evolutionary lineages—as has been postulated for populations of other monotypic procellariiform seabirds, including Cook's petrel (Rayner *et al.* 2011), Hawaiian petrel (Welch *et al.* 2012) and Madeiran storm-petrel (*Oceanodroma castro*; Monteiro & Furness 1998; Friesen *et al.* 2007). However, unlike these species, the 2 populations of Gould's petrel are not genetically distinct: no significant genetic differentiation was detected at multiple mitochondrial and nuclear DNA loci (Gangloff 2010; Iglesias-Vasquez *et al.* 2016).

The validity of a taxon relies on diagnosable characters other than geographic distribution as criteria for distinguishing sibling taxa (Cracraft 1983; Tobias *et al.* 2010). Since these are found to be lacking for *caledonica*, the retention of this subspecies as a distinct taxon is difficult to justify. Gould's petrel should therefore be treated as monotypic. Although Iglesias-Vasquez *et al.* (2016) did not discuss the taxonomic validity of *leucoptera* and *caledonica*, their failure to find strong genetic differences between these purported subspecies corroborates the conclusion based on phenotypic variation. Taxonomy aside, the aforementioned behavioural and ecological differences between Australian and New Caledonian populations—coupled with differing conservation challenges facing the 2 main populations—supports their treatment as independent conservation management units (Iglesias-Vasquez *et al*. 2016).

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APPENDIX 1. Source of museum specimens examined in this study. AM = Australian Museum; AMNH = American Museum of Natural History; ANWC = Australian National Wildlife Collection, Canberra; MONZ = Museum of New Zealand Te Papa Tongarewa; PMNH = Paris Museum of Natural History; QM = Queensland Museum; USNM = National Museum of Natural History, United States of America. NSW = New South Wales, Australia. NC = New Caledonia.

Collection	Catalogue No.	Subspecies	Date collected	Location
AM	16503	*leucoptera*	30/10/1910	Cabbage Tree Island, NSW
AM	16504	*leucoptera*	Unknown	Cabbage Tree Island, NSW
AM	16505	*leucoptera*	30/10/1910	Cabbage Tree Island, NSW
AM	16507	*leucoptera*	1910	Cabbage Tree Island, NSW
AM	16975	*leucoptera*	27/02/1912	Cabbage Tree Island, NSW
AM	30237	*leucoptera*	1910	Cabbage Tree Island, NSW
AM	30238	*leucoptera*	1910	Cabbage Tree Island, NSW
AM	30239	*leucoptera*	1910	Cabbage Tree Island, NSW
AM	30240	*leucoptera*	1910	Cabbage Tree Island, NSW
AM	30241	*leucoptera*	1910	Cabbage Tree Island, NSW
AM	35175	*leucoptera*	26/11/1928	Cabbage Tree Island, NSW
AM	35176	*leucoptera*	1926	Cabbage Tree Island, NSW
AM	54193	*leucoptera*	07/11/1980	Cabbage Tree Island, NSW
AM	63491	*leucoptera*	20/03/1991	Cabbage Tree Island, NSW
AM	65628	*leucoptera*	29/02/1992	Cabbage Tree Island, NSW
AM	73281	*leucoptera*	12/12/2006	Cabbage Tree Island, NSW
QM	11154	*leucoptera*	16/10/1910	Cabbage Tree Island, NSW
QM	22177	*leucoptera*	01/01/1984	Cabbage Tree Island, NSW
AM	61920	*caledonica*	15/03/1990	Parc Forestier, Noumea, NC
AMNH	824271*	*caledonica*	19/02/1978	Mt Dzumac, NC
ANWC	17832†	*caledonica*	1974	At sea off Noumea, NC
MONZ	23109†	*caledonica*	18/07/1978	Mt Dzumac, NC
PMNH	1978-1019	*caledonica*	30/01/1978	Mt Dzumac, NC
PMNH	1978-1021	*caledonica*	10/01/1978	Mt Dzumac, NC
PMNH	1978-1022	*caledonica*	25/03/1978	Mt Dzumac, NC
PMNH	1978-1023	*caledonica*	1978	NC
PMNH	1978-1024†	*caledonica*	02/1978	Mt Dzumac, NC
PMNH	1978-1025†	*caledonica*	30/01/1978	Mt Dzumac, NC
PMNH	1978-1026†	*caledonica*	18/01/1978	Mt Dzumac, NC
PMNH	1978-1027†	*caledonica*	18/01/1978	Mt Dzumac, NC
PMNH	1978-1028†	*caledonica*	30/01/1978	Mt Dzumac, NC
PMNH	1999-3100	*caledonica*	1978	NC
PMNH	1999-3101†	*caledonica*	1978	NC
PMNH	1999-3102†	*caledonica*	1978	NC
USNM	474215	*caledonica*	11/01/1961	Bae de la Conception, NC

* lectotype of *P. l. caledonica* (Palma and Tennyson 2005)
†skin prepared with one wing outstretched