

The occurrence of two bill morphs of prions *Pachyptila vittata* on Gough Island

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Abstract Prions *Pachyptila* are abundant seabirds in the Southern Ocean that have been used to infer environmental change, but this relies on an understanding of their morphological diversity. Species limits among prions are largely defined by the size and structure of their bills. The broad-billed prion *P. vittata*, which breeds at temperate islands in the central South Atlantic Ocean and around New Zealand, is the largest species with adult bill widths averaging 21–22 mm. We report local differences in bill sizes on Gough Island, with typical adults breeding in some areas and narrower-billed birds in other areas (average bill width 18–19 mm, although at one site there was a second mode at bill widths of 16–17 mm). The narrow-billed birds have slightly shorter bills, heads and wings (averaging 1–2 % smaller than typical adult broad-billed prions), but the difference in bill width is much more marked (15 %). The small-billed birds differ from typical broad-billed prions in having blue colouration in the upper mandible and are similar in size to MacGillivray's prion *P. [salvini/vittata] macgillivrayi* from Amsterdam and St Paul islands in the temperate Indian Ocean. The occurrence of two prion morphs on Gough Island raises intriguing questions about their ecology and systematics. Small-billed birds breed 3 months later than large-billed birds, suggesting that they are a separate species, not an example of bill polymorphism.

Keywords Allochronous speciation · Broad-billed prion · Gough Island · *Pachyptila* · Resource polymorphism · Tristan da Cunha

Introduction

Prions *Pachyptila* spp. are small (130–200 g) petrels that mainly feed on zooplankton. They are among the most abundant seabirds in the Southern Ocean and have been shown to be sensitive to changes in environmental conditions (Quillfeldt et al. 2008). As such they have been used to infer long-term changes in zooplankton communities (Quillfeldt et al. 2010), but prion diet is related to bill morphology (Cherel et al. 2002), so we need a sound understanding of their morphological diversity if we are to use them as indicators of long-term changes in zooplankton communities in the Southern Ocean.

Prions pose one of the greatest identification challenges among seabirds due to their uniform appearance (Shirihai 2007). Six species typically are recognized (Marchant and Higgins 1990; Brooke 2004), differing mainly in bill size and structure, but species limits within the genus are subject to debate, with authors identifying three to seven species (e.g. Cox 1980; Harper 1980; Warham 1990; Shirihai 2007). The larger-billed species have palatal lamellae along the sides of their upper mandibles, which they use to filter zooplankton in conjunction with their distensible gular pouch and large, muscular tongue (Wilson 1907; Harper 1980; Warham 1990). The number and size of palatal lamellae increases with bill length and especially bill width (Klages and Cooper 1992). These lamellae are best developed in the largest species, the broad-billed prion *P. vittata* (average bill width 21–22 mm), which forages mainly in sub-tropical waters around its breeding islands

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off New Zealand and on Tristan da Cunha and Gough Islands in the central South Atlantic Ocean (Marchant and Higgins 1990). It does not overlap morphologically with the smaller Antarctic prion *P. desolata* (average bill width 13–15 mm) that forages mainly in Antarctic and sub-Antarctic waters while breeding.

The situation is complicated, however, by the occurrence of intermediate-sized populations breeding at islands in the southern Indian Ocean (Bretagnolle et al. 1990). Salvin's prion *P. salvini* (average bill width 16–17 mm) breeds at the sub-Antarctic Prince Edward and Crozet islands, and is slightly smaller than the enigmatic MacGillivray's prion *P. macgillivrayi* (bill width 18–19 mm, assuming 6 % shrinkage of museum skins; Kinsky and Harper 1968). The latter taxon currently is confined to a few hundred birds breeding on a stack off Saint Paul Island (Tollu 1984; Shirihai 2007), but formerly was common at Amsterdam Island as well as St Paul (Worthy and Jouventin 1999). The large overlap in morphology among taxa led Cox (1980) to propose treating *P. vittata-salvini-desolata* as a single, polytypic species, but Bretagnolle et al. (1990) showed that there is limited overlap between adults of each species, and where they bred together, they are segregated by differences in the timing of breeding and nesting habitat. Salvin's prion typically has been linked to the broad-billed prion (Warham 1990), but limited genetic data suggest that it is more closely allied to the Antarctic prion (Nunn and Stanley 1998). There are no genetic data to infer the relationships of MacGillivray's prion (Roux et al. 1986; Bretagnolle et al. 1990), which appears to be the temperate Indian Ocean equivalent of the broad-billed prion (Warham 1990).

Early writers recognized multiple subspecies of prions, mainly reflecting inter-island differences in morphology (e.g. Murphy 1936; Falla 1940). Subsequent authors have largely subsumed these taxa, with only MacGillivray's prion and up to three subspecies of Antarctic prion recognized (Warham 1990). The broad-billed prion is thought to be monotypic (Marchant and Higgins 1990; Brooke 2004). Mathews (1912) suggested that birds from Tristan da Cunha and Gough are paler above than New Zealand birds, recognizing them as *P. v. keyteli*, but this has been refuted (Murphy 1936; Clancey 1981). There has been no suggestion that more than one type of prion breeds at Tristan or Gough Island. The few skulls conforming to the dimensions of Antarctic prions found in subantarctic skua *Stercorarius antarctica* regurgitations on Inaccessible Island in the Tristan archipelago are assumed to have been of non-breeding visitors to the islands' waters (Fraser et al. 1988). Here, we report the occurrence of two morphs of prion on Gough Island that appear to show little spatial overlap, raising intriguing questions about their ecology and systematics.

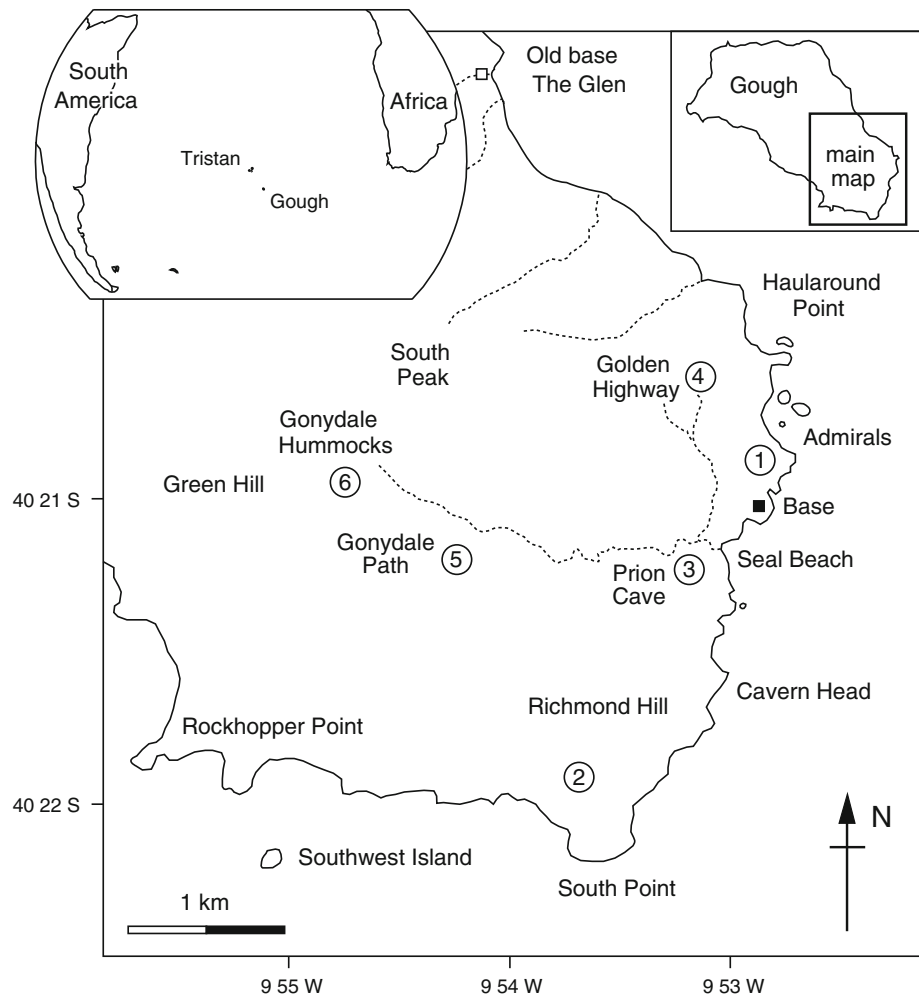
Materials and methods

KB and SD collected skulls of petrels killed by subantarctic skuas on Gough Island in 2011/2012. Examining this material, they noticed that prions from Gonydale (450–480 m elevation) had narrower bills than birds collected around the island's research station (hereafter termed the 'base') near sea level on the island's southeast coast (Fig. 1). However, bill dimensions of prions vary with age, sex and time since death (e.g. Kinsky and Harper 1968; Marchant and Higgins 1990). So in September–October 2013, PGR and BJD examined fresh material at six sites in the southeastern sector of Gough Island (Fig. 1). Three sites were near sea level along the coast in tussock grassland and fern bush vegetation (Ryan 2007): the area around the base between Seal Beach and Admirals, around South Point (from Cavern Head to Rockhopper Point) and in 'Prion Cave' (50 m). Two sites were at mid-elevation in fern bush habitat: along the 'Golden Highway' (230 m) and along the path to Gonydale (mainly adjacent to a series of prion breeding caves at 230 m). The last site was in short, upland wet heath vegetation in the Gonydale 'hummocks' at 460 m, where there are numerous prion breeding caves.

Most birds examined had been killed by skuas, but live birds were caught at night around the base, in the Gonydale hummocks, and during the day in Prion Cave, a cave accessible to people where prions gather to display and breed (Klages and Cooper 1992; Cuthbert et al. 2013). Flash photographs of live prion heads were taken against a standardized pale blue background to compare bill colouration and plumage pattern. Material from 2013 was augmented by a sample of 73 birds killed accidentally at the base during night strikes in October 1984 (previously published by Klages and Cooper 1992). Only a few skua-killed birds could be sexed because the internal organs are usually consumed first, but all birds from 1984 were sexed and aged by inspecting their gonads. Wing length (flattened chord) was recorded to the nearest 1 mm, and tarsus, head (from the bill tip to the cerebellar prominence, with skin still intact), culmen (from the bill tip to the start of the feathers above the nares) and maximum bill width were all measured to the nearest 0.1 mm. All measurements were made by PGR, apart from some bill measures taken by BJD after ensuring that both observers measured the same birds to within ± 0.1 mm. Not all skua prey remains were complete, and so, not all measurements could be made for all individuals. Wings are particularly conspicuous prey remains and often lacked heads and feet, so larger samples of wing measures were taken at each sample area (except Prion Cave; right wings only measured to avoid duplication).

Samples were normally distributed within sites, so simple parametric tests were used to test for differences in prion sizes (ANOVA with post hoc Newman–Keuls range

Fig. 1 The southeast sector of Gough Island, showing the six sampling locations



tests to assess differences among sites, and *t* tests to compare two-sample hypotheses, with $\alpha = 0.05$). Simple univariate tests were preferred over multivariate comparisons because they emphasized how differences were most marked in bill width, and because they will assist field workers to identify birds of unknown provenance from traditional measures of bird size. A χ^2 goodness-of-fit test with Yates’s correction for continuity was used to assess whether bill size differences were sex-linked.

Results

Bill widths of prion skulls collected in Gonydale in 2011/2012 were significantly narrower than those collected around the base on Gough Island ($t_{100} = 6.69, P < 0.001$; Table 1). Birds from around the base were similar in size to broad-billed prions from New Zealand, whereas those from Gonydale were similar to the extinct population of MacGillivray’s prions from Amsterdam Island (Table 1). Although the maximum width recorded in Gonydale was

Table 1 Maximum bill widths of prion skulls collected at two locations on Gough Island, compared with data from broad-billed prions in New Zealand and the extinct population of MacGillivray’s prion from Amsterdam Island (from Worthy and Jouventin 1999)

Location	Average \pm SD	Range	<i>n</i>
Gough Island—base area	19.22 \pm 1.56	16.2–21.6	17
Gough Island—Gonydale	16.59 \pm 1.46	14.6–22.1	85
Amsterdam Island	16.30 \pm 0.74	14.9–17.7	31
New Zealand	18.99 \pm 1.64	15.5–20.5	15

large (22.1 mm), 95 % of individuals had bill widths <20 mm, and 90 % <19 mm.

Bill widths of live or freshly dead birds also differed significantly among the six study sites ($F_{5,281} = 95.2, P < 0.001$; Table 2). The small samples of birds from the Golden Highway and around South Point were not significantly different from that around the base, with all three sites having much broader-billed birds (average 21–22 mm) than the other three sites (average 18–19 mm; Table 2). The combined data set had a strongly bimodal

Table 2 Maximum bill widths of live or freshly dead adult prions collected at six sites on Gough Island and the proportion with bills >20 mm wide

Location	Average \pm SD	Median	Range	<i>n</i>	% >20 mm
Base area	21.5 \pm 1.3	21.7	17.7–24.4	133	87
Golden Highway	21.8 \pm 0.8	21.8	20.8–23.1	10	100
South coast	22.0 \pm 1.3	22.3	18.8–23.2	10	90
Prion Cave	19.2 \pm 1.0	19.1	17.0–23.0	55	13
Gonydale path	18.7 \pm 0.7	18.6	17.4–20.2	28	4
Gonydale hummocks	17.9 \pm 1.3	17.9	15.8–21.9	51	6

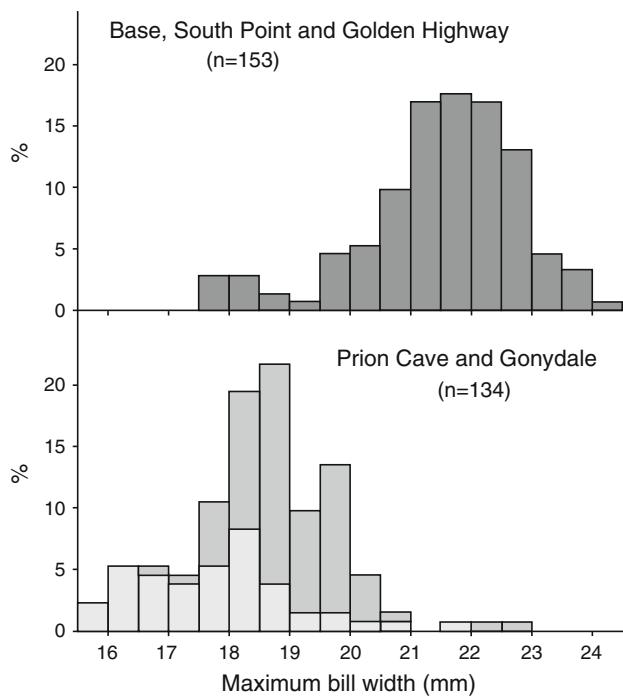


Fig. 2 The frequency of bill widths among prions sampled around the base, South Point and on the Golden Highway compared with birds from Gonydale hummocks (pale grey) and Prion Cave and the Gonydale path (mid-grey)

distribution in bill width, resembling two normal distributions with overlap for bill widths 19–21 mm (Fig. 2). Pooling birds from different sites into two groups on the basis of the predominant bill size resulted in two samples differing in average bill width by 13.8 % ($t_{285} = 19.84$, $P < 0.001$). However, both samples are weakly bimodal (Fig. 2), presumably due to a small number of birds straying outside their ‘typical’ range (also see ‘Discussion’). This inference is supported by the differences between the average and median bill width in each of the six study areas (Table 2). Excluding birds with bills >21 mm from areas where small-billed birds dominated ($n = 3$, 2 %), and birds with bills <19 mm from areas where large-billed birds dominated ($n = 10$, 7 %), we defined two morphs differing by 15.1 % in average bill width (Table 3). Bill and head lengths also differed

statistically between these morphs, but the differences were much less marked (2.0 and 1.4 %, respectively; Table 3). There was no difference in tarsus length, but wings of birds from the Gonydale area averaged 2.3 % shorter than those from around the base (Fig. 3; Table 3).

Among the smaller-billed birds from Prion Cave and the Gonydale area, there was a tendency for bill width to decrease with elevation (Table 2). Post hoc range tests showed that birds from Prion Cave and the Gonydale path averaged larger than those from Gonydale hummocks ($P < 0.001$), with very narrow-billed birds (<17 mm) mainly recorded from Gonydale hummocks (Fig. 2). Indeed, the samples from these sites showed some indication of bimodal distributions, with the Gonydale hummocks birds having most birds with bills 16–16.5 and 18–18.5 mm wide, whereas those from Prion Cave and the Gonydale Path were mainly 18.5–19 or 19.5–20 mm wide (Fig. 2). However, sample sizes were moderate, and more data are needed to assess whether there is indeed a third, very narrow-billed morph at higher elevations in Gonydale. There was no difference in wing length between birds from Gonydale hummocks (211.8 ± 4.3 , $n = 148$) and Prion Cave and the Gonydale path (210.2 ± 4.7 , $n = 34$; $t_{180} = 1.87$, NS).

Only three birds sampled in 2013 could be sexed, but together with the 73 birds collected at the base in 1984, they indicate that variation in bill size is not sex-linked. Given the predominance of samples from close to the base, only a small proportion of these birds had narrow bills, but there was no evidence of sex-linked differences in bill size: 9 of 35 females and 7 of 41 males had bills <20 mm wide ($\chi^2 = 0.41$, NS). Gonadal inspection confirmed that most birds examined were reproductively active, with both small males (minimum bill width 18.0 mm) and females (17.7 mm) having enlarged testes or well-developed ovaries, respectively. Klages and Cooper (1992) reported that males had bills on average 0.8 mm wider than females (based on large part on our 1984 data). However, this result was compromised by the inclusion of small-billed individuals; removing birds with bills <19 mm wide from the sample of known-sex birds reduced the difference in bill width among broad-billed birds attributable to sex to 0.6 mm (males: 21.8 ± 0.87 , $n = 35$; females 21.2 ± 0.84 , $n = 30$).

Table 3 Comparative morphology of the two prion morphs on Gough Island (average \pm SD, n , all units mm)

Measure	Large-billed morph	Small-billed morph	Significance
Wing	216 \pm 4.9 (276)	211 \pm 4.4 (182)	$t_{456} = 10.9$, $P < 0.001$
Tarsus	36.6 \pm 1.38 (121)	36.5 \pm 0.98 (35)	$t_{154} = 0.05$, NS
Head	73.8 \pm 1.67 (100)	72.7 \pm 1.62 (30)	$t_{128} = 3.07$, $P < 0.01$
Culmen	34.9 \pm 1.31 (134)	34.2 \pm 0.94 (40)	$t_{172} = 3.46$, $P < 0.001$
Bill width	21.8 \pm 0.98 (143)	18.5 \pm 1.09 (131)	$t_{272} = 26.4$, $P < 0.001$

Birds were categorized by location, but excluded outliers (bills >21 mm at small-billed sites and <19 mm at large-billed sites)

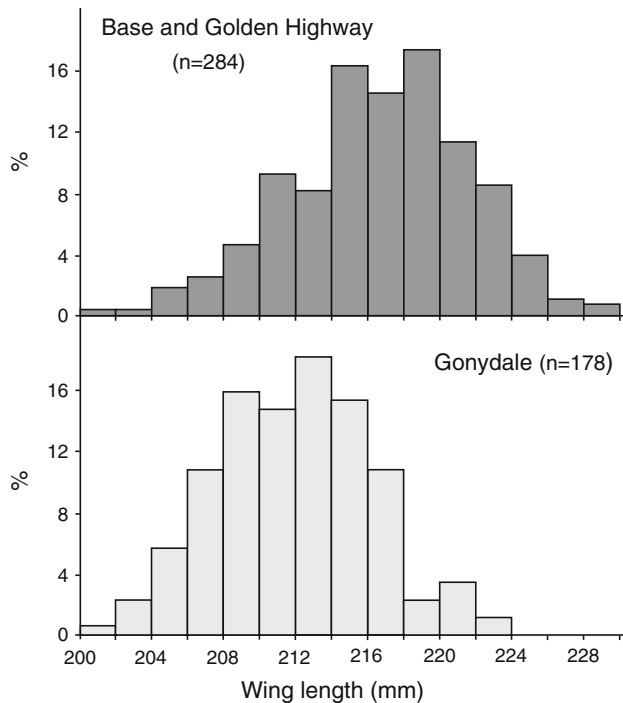


Fig. 3 The frequency of wing lengths among prions sampled around the base and on the Golden Highway compared with birds from the Gonydale path and hummocks

Observations from Prion Cave and limited searches of burrows support the conclusion that bill size differences are not linked to age or sex, and provide some indication of assortative mating among bill morphs. Prions do not breed in the cave during the September–October annual visit to Gough Island, but some birds sit together in apparent pairs, calling together and often allopreening. In 2013, we visited the cave on four occasions. None was measured during a brief visit on 22 September when hundreds of prions were present. On 26 September, only four birds were accessible: a pair of large-billed prions (bill width 22.4 and 23.0 mm) plus two single small-billed birds (18.1 and 19.6 mm). On 30 September, following the passage of a cold front, the cave contained many more prions, all apparently small-billed (bill width range 17.8–20.2 mm, $n = 36$). All three pairs sampled were of small-billed birds (18.2 and

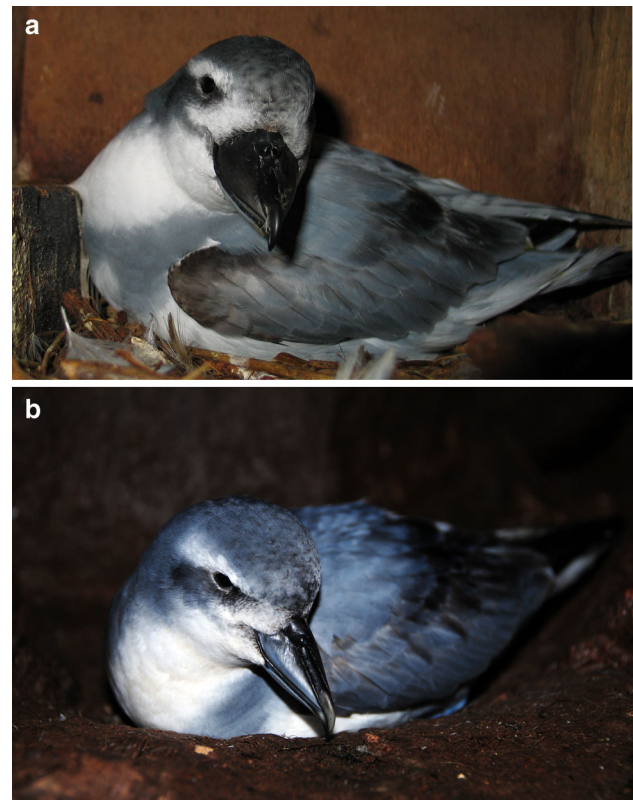


Fig. 4 A typical broad-billed prion with a *blackish upper mandible*, incubating on 15 August 2004 at Gough Base (*top*, photograph by Ross Wanless) has an appreciably broader bill than a prion incubating in Prion Cave, Gough Island, on 20 December 2013 (*bottom*, photograph by Ben Dilley) that has *pale blue sides* and a *grey tip* to the upper mandible. (Color figure online)

19.0 mm, 18.8 and 19.9 mm, and 18.7 and 20.1 mm). The cave contained an intermediate number of birds on 11 October, when again all birds measured were small-billed (range 17.0–20.6 mm, $n = 15$). We were unable to access other Prion Caves in the hummocks or along the Gonydale path, but a burrow near the Prion Cave at 230 m on the Gonydale path also contained a pair of small-billed birds (18.3 and 18.9 mm) on 12 October 2013. Burrows around the base mainly contained small chicks, but a pair of large-billed birds (21.8 and 22.3 mm) was found together in a burrow on Cavern Head on 16 October 2013.

Photographs of measured birds show that most large-billed birds caught around the base have dark grey upper mandibles (Fig. 4a) that contrast with the blue ramicorn (sides of the lower mandible), whereas small-billed birds from Prion Cave typically have some blue in the sides and tip of the upper mandible (Fig. 4b). Using this character, combined with apparent bill width, photographs of prions in Prion Cave on 2 October 2006 and 28 September 2007 show all birds in the cave to be narrow-billed birds, including several consorting pairs. Subsequent observations in November 2013 showed that these birds laid eggs in late November (few birds present on 22 November; 90 birds incubating on 27 November). Birds in Gonydale also bred then, with a bird with an oviduct egg on 30 November 2013.

Discussion

The frequency distribution of prion bills widths on Gough Island is strongly bimodal, indicating the presence of two morphs on the island. Our data from live and freshly dead birds confirm that these differences are not the result of age- or sex-related differences in morphology. Prion fledglings average smaller than adults (Harper 1980), but our sampling took place well before any fledglings leave their nests (see below). Also, the differences in average bill width between adult and fledgling broad-billed prions (1.3 mm, Richdale 1965; Marchant and Higgins 1990) and between adult males and females (0.6 mm) are modest. The difference in average bill width between morphs on Gough Island (3.3 mm) is similar in magnitude to that between prion species breeding sympatrically at Ile de l'Est in the Crozets: 3.1 mm between *P. belcheri* and *P. desolata*, and 3.3 mm between *P. desolata* and *P. salvini* (Bretagnolle et al. 1990).

It might seem surprising that such marked differences in bill size among prions have been overlooked until now. However, there has been limited collecting on Gough island, where prions are the most abundant seabird, breeding virtually throughout the island (Swales 1965; Cuthbert 2004). As a result, samples are readily obtained close to where observers are based. Prior to 1962, this was at The Glen on the east coast (Fig. 1), and since then, it has been around the South African research station on the southeast coast—both areas seemingly dominated by broad-billed birds. Swales (1965) reported that prions from The Glen had an average bill width of 21.6 mm (range 18–25, $n = 129$). Clancey (1981) collected adults from around the current research station and reported bill widths of 20.7 ± 0.87 mm ($n = 12$, range 18.8–22 mm), but he measured them after they had been prepared as museum skins, which reduces bill width by about 6 % (Kinsky and Harper 1968). Compensating for post-mortem shrinkage, his average bill width would have been approximately 21.9 mm (range

~20–23 mm), similar to our samples from around the base (Table 3). Examination of Clancey's specimens in the Durban Natural History Museum confirms that all have blackish upper mandibles typical of broad-billed prions. It thus appears that no significant collections have been made in areas where small-billed birds are abundant.

Our data demonstrate the presence of at least two distinct prion morphs with largely non-overlapping ranges on Gough Island, differing primarily in terms of bill width. Birds conforming to typical broad-billed prions (bill width 21–22 mm) breed at The Glen, along the south and east coasts and adjacent slopes of South Peak, whereas smaller birds (18–19 mm) breed in caves from near sea level to at least 450 m, and a possible third, even smaller morph (16–17 mm) might occur at higher elevations. These findings raise several fascinating questions.

Ecomorphs or cryptic species?

The variation in bill width among Gough Island prions could represent a novel case of resource polymorphism (Skúlason and Smith 1995). Bill width is closely linked to foraging behaviour and diet in prions (Warham 1990) and is correlated with the number of palatal lamellae (Klages and Cooper 1992). Disruptive selection favoured by different prey types could potentially drive the evolution of two or more bill morphs, analogous to that found in *Pyrenestes* finches (Smith 1993) or *Loxia* crossbills (Benkman 1993). However, this explanation fails to address why the morphs are spatially segregated on the island, given that all foraging occurs well offshore. The presence of two cryptic species is perhaps a more plausible explanation for the observed variation, and this hypothesis is supported by apparent differences in bill colour as well as data on the timing of breeding on Gough Island.

One of the features other than breeding season used to separate the broad-billed prion from other prion species is its dark grey upper mandible, lacking any blue on the sides (Falla 1940; Harper 1980; Shirihai 2007; although Marchant and Higgins 1990 note that the maxillary unguis and sides of the latericorn can be tinged blue). At Gough, small-billed prions typically have more blue on the upper mandible than large-billed morphs, although no birds have bills as blue as that shown in the photograph of an adult MacGillivray's prion in Shirihai (2007, p. 194). The bird illustrated in Fig. 4 is at the upper end of the range in terms of the amount of blue on its bill.

Breeding phenology provides a better indication of the specific status of the two morphs. Breeding by prions typically is highly synchronized, varying by no more than a week or two between colonies (Bretagnolle et al. 1990; Warham 1990), but prions have two breeding seasons on Gough Island. The large-billed birds breeding at The Glen and

around the research station lay eggs in late winter (August–September), with chicks hatching from the end of September into October and fledging in early December (Swales 1965, pers. obs.). However, some prions breed several months later. Swales (1965) reported an egg laid in a burrow at The Glen in mid-November, and prions in Prion Cave had newly hatched chicks on 20 January 2009 (Cuthbert et al. 2013), suggesting that eggs were laid there in late November or early December (assuming an incubation period of roughly 45 days; Brooke 2004). Our observations in 2013 confirm that small-billed birds lay in late November, roughly 3 months after the large-billed form. Such temporal segregation of breeding seasons is typical of islands where prion species breed sympatrically (Bretagnolle et al. 1990) and bears a striking similarity to the allochronous speciation of *Oceanodroma castro* (sensu lato) storm petrels (Monteiro and Furness 1998; Bolton et al. 2008).

It will be fascinating to investigate the ecological segregation of the prion morphs on Gough Island. Given the general trend among filter-feeding prions for bill width to increase towards lower latitudes, we might expect the small-billed birds to forage farther south. This also might explain why they have slightly shorter wings when there is no difference in tarsus length, given the stronger wind speeds experienced at higher latitudes (cf. Shaffer et al. 2001).

Links to Indian Ocean prion populations?

The seabirds of Tristan da Cunha and Gough Island share several affinities to seabirds breeding on Amsterdam and St Paul, temperate islands in the central Indian Ocean (Elliott 1957). These biogeographic affinities extend beyond seabirds, with several plants and marine fish confined to these two island groups that are some 8,000 km apart in separate ocean basins (Richardson et al. 2003; Ryan 2007). It is thus intriguing that the small-billed prion morph on Gough is similar in size to MacGillivray's prion from Amsterdam and St Paul Islands. The current consensus is to treat *macgillivrayi* as a subspecies of Salvin's prion based on its blue bill and November laying date (Roux et al. 1986), or perhaps as a separate species (Bretagnolle et al. 1990; Shirihai 2007). Could the small Gough birds be another population of this little-known taxon? And the very small-billed birds sampled in Gonydale fall within the size range of Salvin's prions, which breed at the same time of year farther south in the Indian Ocean at the Prince Edward and Crozet islands (Bretagnolle et al. 1990).

Genetic markers are needed to resolve the relationships among populations on Gough and those breeding in the Indian Ocean. However, it may be that multiple morphs have evolved independently at Atlantic and Indian Ocean islands, as is the case for the allochronous populations of

O. castro (Friesen et al. 2007). Although there is no subfossil evidence of an extinct broad-billed prion at Amsterdam or St Paul (Worthy and Jouventin 1999), early visitors to St Paul reported two breeding seasons, in September and November (Velain 1878), suggesting that two prion species may have bred at these islands before they were extirpated by introduced predators (Falla 1940).

Why are morphs spatially segregated?

It is not clear why there should be such seemingly strong spatial segregation among morphs on Gough Island. In fact, our samples probably underestimate the degree of segregation, given that most samples were killed by skuas, and thus might not have actually been breeding exactly where they were sampled. Such spatial 'fuzziness' might account for the larger proportion of birds excluded from the base sample (7%), close to the coast, than the Gonydale samples (2%), farther inland. However, most (90%) of the birds excluded from the base sample were killed by night strikes in 1984, suggesting that being disoriented by lights is more likely to result in birds being found in the 'wrong' area than being killed by skuas.

When the differences in skull morphology were first detected, we assumed that elevation was the primary factor segregating the two morphs, but small-billed birds were then found close to sea level in Prion Cave, and two sites with similar vegetation and at similar altitude (Gonydale path and Golden Highway) support different bill morphs. The only obvious difference between the sites supporting the different morphs is that all three locations with small-billed birds are adjacent to cave-breeding sites. However, not all small-billed birds are confined to caves, as a pair was removed from a burrow nest along the Gonydale path, and Ross Wanless photographed a large chick in a burrow in the coastal lowlands on 17 March 2004 which showed the features of a narrow-billed bird. Further study is needed to better understand the distribution, breeding habitat preferences and mate selection criteria of the two morphs.

Do small-billed birds breed at Tristan?

Given the presence of a small-billed prion morph on Gough Island, does it also breed at the nearby Tristan archipelago? There is no evidence of this from the limited sampling conducted to date. Prions from Blenden Hall, near sea level on the west coast of Inaccessible Island, have broad bills: Fraser et al. (1988) reported an average bill width of 21.6 mm (range 20–23 mm, $n = 12$), and PGR obtained a similar estimate (22.0 ± 0.8 mm, range 20.2–22.9 mm, $n = 12$). Measurements of freshly dead prions at Nightingale Island in September 2013 also only sampled large-billed birds (21.6 ± 1.0 mm, range 19.8–24.3 mm,

$n = 20$; B.M. Dyer unpubl. data). Hagen (1952) reported a slightly narrower mean bill width from Nightingale (21.0 ± 1.0 mm, range 20.0–22.8 mm, $n = 6$), but his measures probably were taken from skins, thus underestimating fresh bill width.

The timing of breeding at Tristan also conforms to that of the large-billed form. Breeding at Tristan has only been recorded commencing in late winter, with eggs laid in the second half of August and chicks fledging in December (Elliott 1957; Richardson 1984; Fraser et al. 1988). Prions breeding in an accessible cave near Round Hill on the eastern plateau of Inaccessible Island (310 m above sea level) also have this breeding schedule, with birds on eggs on 28 September 2011, on eggs and small chicks on 12 October 2009 and large chicks on 19 November 2009 (PGR unpubl. data). Photographs of these birds suggest that they are of the large-billed form, although at least two birds incubating eggs on 28 September had blue sides to their upper mandibles.

Conclusions

Further research is needed to confirm the taxonomic status of the bill morphs of prions on Gough Island and to investigate their ecological segregation. We also need to understand the distribution and relative abundance of morphs on Gough Island. Swales (1965) estimated at least 10 million pairs of prions bred on Gough in the 1950s, and although their numbers have decreased since then due to predation by introduced house mice *Mus musculus* (Cuthbert et al. 2013), Cuthbert (2004) estimated roughly 1.5–2.0 million pairs of prions at the island in 2000/2001, making Gough still the most important breeding site for this species worldwide (Brooke 2004). We need to assess the contributions of the different morphs to this total and to determine whether small-billed birds also breed in the Tristan archipelago.

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