



Variation among species and populations in bill shape and size in three planktivorous petrels

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Abstract

Morphological variation in biological structures may be driven by genetic and environmental factors, such as inter- and intraspecific competition for resources. In seabirds, although the bill is also involved in vocalization, olfaction, sexual selection and defence, the main drivers of high morphological plasticity in bill size and shape appear to relate primarily to diet and thus to niche differentiation. Here, we combined geometric morphometrics and comparisons of linear measurements as a precise tool for measuring shape variation in anatomical features, to investigate the differences among species and populations (island groups) in bill shape of three planktivorous petrels (Antarctic prion *Pachyptila desolata*, blue petrel *Halobaena caerulea* and thin-billed prion *Pachyptila belcheri*). Fieldwork was carried out in South Georgia (54° 0' S, 38° 3' W), Falkland (51° 42' S, 57° 51' W), Diego Ramírez (56° 31' S, 68° 44' W) and Kerguelen (49° 20' S, 69° 20' E) Islands, from 2010 to 2021. Results show that the bills of Antarctic prions were more robust and shorter, appropriate for filtering large amounts of small prey. Blue petrels and thin-billed prions had narrower and longer bills, effective for catching and tearing large single prey. Also, Antarctic prions and blue petrels from Kerguelen had longer and narrower bills than conspecifics from other colonies, which could potentially be explained by geographic variation in diet. In conclusion, prey availability and diversity appear to be important factors influencing variation in bill morphology. This study highlights the utility of geometric morphometrics for investigating bill shape variation in seabirds. Nevertheless, further studies are needed to better understand selective pressures leading to morphological variation of biological structures.

Keywords Bill morphology · Character displacement · Ecological segregation · Geometric morphometrics · Niche differentiation · Seabirds

Introduction

Morphological variation is known to be shaped by abiotic and biotic conditions, and their interaction. For instance, genes provide the potential for a particular phenotype,

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but environmental factors determine how this potential is expressed through selective pressures (Grant and Grant 1989; Aldrich and James 1991). In seabirds, selective pressures can be related to environmental conditions, predation, disease, and interspecific and intraspecific competition for resources, such as food or nest sites (Buckley and Buckley 1980; Warham 1996). Suitable breeding sites are limited in number and hence multiple species of seabirds often breed in sympatry (Warham 1996; Brooke 2004). As seabirds are often very abundant, and foraging ranges are subject to the central-place constraint during breeding (i.e., the need to return to incubate eggs or feed chicks), interspecific and intraspecific competition around colonies is particularly intense (Lewis et al. 2001; Phillips et al. 2005; Wakefield et al. 2014). Seabirds have therefore evolved diverse ecological strategies which allow coexistence, including segregation of foraging areas, behaviour or diet (Quillfeldt et al. 2013; Navarro et al. 2013; Corman et al. 2016), as well as allochrony to reduce overlap in the periods of higher demand for prey, including chick-rearing and moulting (Cherel et al. 2016; Jones et al. 2020). Selective pressures differ between regions and thus morphological variation might reflect adaptation to local conditions in different populations (i.e., breeding at different island groups) of the same species (Mayr and Diamond 2001; Bull et al. 2004; Bull 2006).

Common examples of variation among birds in specific morphological traits include the shape and size of feeding structures such as the bill. This is widely established, for example, in different species of Darwin's finches (Coerebinae), in which bill morphology is associated with interspecific variability in foraging strategies (Boag and Grant 1981; Kleindorfer et al. 2006; Foster et al. 2008). Similar patterns occur in boobies (*Sula* spp.) in the Pacific, and little penguins (*Eudyptula minor*) in south Australia, in which wing and bill size differ between colonies in relation to prey selection and competition with sympatric species, and with variation in environmental conditions, respectively (Colombelli-Négrel 2016; Van Oordt et al. 2018). In seabirds, the bill is of great ecological and biological importance since it provides essential functions related to food intake, vocalization, olfaction, sexual selection or defensive and territorial behaviour (Warham 1996; Nebel 2005; Gémard et al. 2019). Given its versatile role, the bill is subject to strong selective forces and it shows wide morphological plasticity and divergence (Schluter 2000; Van Oordt et al. 2018; Masello et al. 2021). Many studies have pointed out the association between bill shape and size, and diet and niche differentiation (Nebel et al. 2005; Bull 2006; Trallero et al. 2019), presumably driven by interspecific competition and natural selection (Navarro et al. 2013; Corman et al. 2016; Masello et al. 2021).

In spite of sometimes wide geographic separation between colonies, breeding populations of seabirds often

show limited genetic variability (Moum and Árnason 2001; Wojczulanis-Jakubas et al. 2014). This applies to Antarctic prions (*Pachyptila desolata*) blue petrels (*Halobaena caerulea*), and thin-billed prions (*Pachyptila belcheri*) breeding at South Georgia, Kerguelen and Falkland Islands, even though the island groups are far apart and the populations exploit different trophic niches (Quillfeldt et al. 2017). Therefore, morphological variation among individuals and populations in the bill might be related to environmental factors such as relative availability of different prey (Croxall and Prince 1980). Based on previous studies, the diet of Antarctic prions at South Georgia is composed mainly of small copepods and Antarctic krill *Euphausia superba*, followed by the amphipod *Themisto gaudichaudii*, small fish and cephalopods (Prince 1980; Croxall et al. 1997; Reid et al. 1997). At Kerguelen, although crustaceans are also important, Antarctic prion preys mainly on *T. gaudichaudii*, and only rarely on Antarctic krill and copepods (Cherel et al. 2002b). Blue petrels at South Georgia feed mostly on crustaceans and small myctophids, whereas conspecifics from Kerguelen also catch larger fish such as *Paradiplosinus gracilis* and consume substantial numbers of cephalopods (Prince 1980; Cherel et al. 2002a). The diet of thin-billed prions at Kerguelen is also mainly composed by crustaceans and myctophids, while individuals from Falkland feed mostly on crustaceans and cephalopods (*Gonatus antarcticus*) (Cherel et al. 2002b; Quillfeldt et al. 2010). The targeting of distinct prey could therefore drive morphological differences between these colonies. Cherel et al. (2002b) suggested that while other crustaceans can be caught individually, large numbers of small copepods might be ingested at once by Antarctic prions through filter feeding. Moreover, it has been suggested that long and narrow bills in blue petrels and thin-billed prions, could be indicative of surface dipping, and tearing of large single prey (Prince 1980; Harper 1987; Quillfeldt et al. 2010). Although there are other environmental factors that can induce morphological variation, the bill, as the anatomical structure most directly related to diet, might be determinant for detecting phenotypical variation within these genetically similar populations.

Geometric morphometric analysis represents a precise tool for measuring shape variation in anatomical features (Adams et al. 2013), providing insights into relationships between morphological structures and ecological strategies (Adams 1999; Zelditch et al. 2004; Farré et al. 2016b), including in seabirds (Foster et al. 2008; Navarro et al. 2009; Berns and Adams 2010; Trallero et al. 2019). With this approach, it is possible to accurately compare biological form in statistical terms, since the effect of the non-shape variation (size, orientation, deformation etc.) was mitigated (Adams et al. 2004; Zelditch et al. 2004). In a previous study (Trallero et al. 2019), we quantified differences among species and sexes in bill morphology of Antarctic prions, blue

petrels, and two species of diving petrels (*Pelecanoides* spp.) all breeding at South Georgia, South Atlantic. Here, we extend this by investigating the differences in bill shape among populations of three abundant planktivorous petrels (Antarctic prion, blue petrel and thin-billed prion) which have circumpolar distributions in the Southern Ocean. Although diet proportions might be similar in terms of prey classes, the three species differ in terms of the main crustacean, fish and cephalopod species consumed (Prince 1980; Cherel et al. 2002a, b) which might explain the striking spatial and ecological segregation among species and populations (Quillfeldt et al. 2013, 2015; Navarro et al. 2013, 2015). Hence, our initial hypothesis was that these differences in foraging ecology would be reflected in bill-character displacement. While species differences have been described with traditional methods, geometric morphometric analyses can reveal subtler contrasts and offer a precise tool to analyse less obvious differences, as may be found between populations.

Materials and methods

Study species

The work focused on three monogamous, small-bodied and ecologically important procellariiform species that inhabit in abundant colonies in different islands along all the Southern Ocean: Antarctic prion, blue petrel and thin-billed prion. All can feed 100 s or 1000 s of km from the colony and spend most of their time at sea (Quillfeldt et al. 2013, 2014). They breed in burrows or rock crevices in dense colonies and show the typical procellariiform pattern of single-egg clutch and slow chick development (Warham 1996; Brooke 2004). Both the Antarctic prion and blue petrel feed mainly on crustaceans, and small fish (myctophids) (Table 1), but the particular prey species vary, presumably related to relative availability in the environment (Ainley et al. 1992). Similarly, thin-billed prions prey mostly on crustaceans (amphipods and krill), myctophid fish and squid (Table 1).

Table 1 Review of the diet of Antarctic prions and blue petrels breeding in South Georgia and the Kerguelen Islands, and thin-billed prions breeding in the Kerguelen and Falkland Islands

| Species | Colony | Type of prey | Average frequency of occurrence (%) | Prey preferences | References |
|-------------------|-------------------|--------------|-------------------------------------|---|---|
| Antarctic prion | South Georgia | Cephalopod | 11.1 | | Prince (1980), Croxall et al. (1997) and Reid et al. (1997) |
| | | Fish | 28.2 | Myctophidae | |
| | | Crustacean | 96.8 | <i>Euphausia superba</i> , Amphipoda (<i>Themisto gaudichaudii</i>), Copepoda | |
| | Kerguelen Islands | Cephalopod | 15.4 | <i>Oegopsida</i> sp. | Cherel et al. (2002b) |
| | | Fish | 31.7 | Myctophidae | |
| | | Crustacean | 100 | Amphipoda (<i>T. gaudichaudii</i>) | |
| Blue petrel | South Georgia | Cephalopod | 6.4 | | Prince (1980) |
| | | Fish | 83.3 | Myctophidae | |
| | | Crustacean | 97.4 | <i>E. superba</i> | |
| | Kerguelen Islands | Cephalopod | 14.3 | <i>Oegopsida</i> sp. | Cherel et al. (2002a) |
| | | Fish | 81.0 | Myctophidae, <i>Paradiplospinus gracilis</i> | |
| | | Crustacean | 100 | Amphipoda (<i>T. gaudichaudii</i>), <i>Thysanoessa</i> sp. | |
| Thin-billed prion | Kerguelen Islands | Cephalopod | 23.5 | Squid (<i>Gonatus antarcticus</i>) | Cherel et al. (2002b) |
| | | Fish | 41.2 | Myctophidae | |
| | | Crustacean | 100 | Euphausiids, Amphipoda (<i>T. gaudichaudii</i>) | |
| | Falkland Islands | Cephalopod | 55.9 | Squid (<i>G. antarcticus</i>) | Quillfeldt et al. (2010) |
| | | Fish | 12.5 | | |
| | | Crustacean | 68.6 | Euphausiids, Amphipoda (<i>T. gaudichaudii</i>) | |

There are no published studies of the diet of blue petrels at the Diego Ramírez Islands

Study areas

Fieldwork was conducted in breeding colonies at four sub-Antarctic island groups > 1000 km apart (Fig. 1): Bird Island, South Georgia (54° 0' S, 38° 3' W), New Island, Falkland Islands (Malvinas) (51° 42' S, 57° 51' W), Gonzalo Island, Diego Ramírez Islands (56° 31' S, 68° 44' W) and, Île Mayes and Île Verte, Kerguelen Islands (49° 20' S, 69° 20' E). Antarctic krills are particularly abundant around and to the south of South Georgia (Atkinson et al. 2001). Prey availability for seabirds is high in the waters surrounding the Falkland Islands, which are characterised by low temperatures, strong winds and turbulent waters (Armstrong and Forbes 1997). At Diego Ramírez, temperatures are low and there are strong westerly winds and high annual rainfall (Schlatter and Riveros 1997). The Kerguelen Islands are also in a region characterized by low temperatures and high winds, with strong upwellings (Zhou et al. 2014).

Sampling and morphological data acquisition

During the breeding period, a total of 60 Antarctic prions and 29 blue petrels were sampled at Bird Island (November 2010–February 2011); 54 Antarctic prions and 37 blue petrels at Île Verte (December 2018–January 2019), 29 blue petrels at Gonzalo Island (November 2020–January 2021), 7 thin-billed prions at Île Mayes (February 2021) and 27 thin-billed prions at New Island (February 2019). For each individual, digital pictures were taken of the right profile and dorsal view of the bill using a compact digital camera in a consistent orientation: the bill was supported using a wooden board with a ruler underneath for scale, and the camera lens was always perpendicular to the bill surface. Any pictures that were not standardized in this

way were excluded from morphological analyses. In addition, three biometric measurements were taken in the field: maximum bill depth, bill depth at nares and culmen length as shown in Trallero et al. (2019). All measurements were made using digital callipers (± 0.1 mm) (Fig. 2).

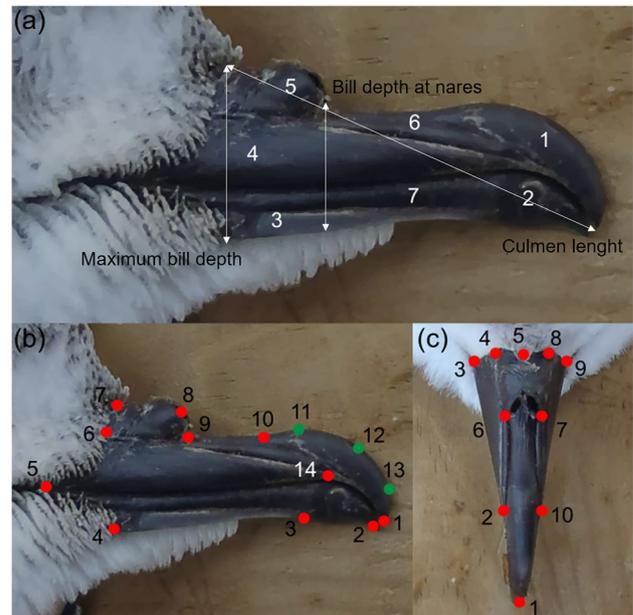
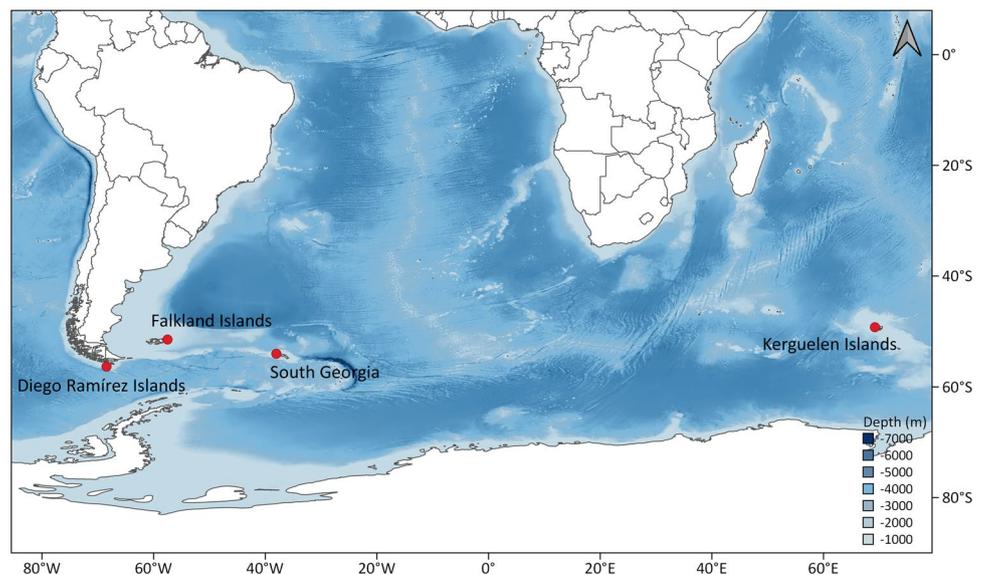


Fig. 2 a Bill morphology and measurements: 1 = superior unguicorn-maxillary unguis, 2 = inferior unguicorn-mandibular unguis, 3 = ramicorn, 4 = latericorn, 5 = nares, 6 = culmicorn and 7 = tomia-cutting edges. Landmarks (red dots) and semi-landmarks (green dots) used to describe the shape of b the profile and c the dorsal view of the bill. All pictures are of a blue petrel

Fig. 1 Location of the different breeding colonies of Antarctic prions, thin-billed prions and blue petrels sampled in this study



Bill shape analysis

Characterization and assessment of variability in bill shape were performed using geometric morphometric methods (Rohlf and Marcus 1993; Zelditch et al. 2004). A total of 10 landmarks (fixed homologous points) in dorsal pictures (Tokita et al. 2017; Trallero et al. 2019) and 11 landmarks and 3 semi-landmarks (mobile non-homologous points) in profile pictures (Navarro et al. 2009; Militão et al. 2014; Trallero et al. 2019) were used to define the overall shape of bill and nares (Fig. 2, Table 2). Landmarks and semi-landmarks coordinates were digitized and transformed into geometric data using the tpsDig2 v.2.31 (Rohlf 2017), creating a metric map for each individual. A Generalized Procrustes Analysis (GPA) was then applied, using tpsRelw v.1.70 (Rohlf 2019). GPA compares all the landmark configurations removing distortions not related to shape, translating all configurations to a common centroid position, scaling them to the unit centroid size and rotating them to minimise the distances between corresponding landmarks (Adams et al. 2004; Zelditch et al. 2004). Next, a consensus configuration was obtained by averaging the spatial coordinates of all landmarks using a thin-plate spline procedure. The comparison of each configuration with this consensus form allows the shape deformation variables (relative warps, RWs) to be extracted for each individual. Each RW

represents a specific set of morphological characteristics, and their comparison allows the potential variation in shape of analysed objects to be visualised (Rohlf and Marcus 1993; Zelditch et al. 2004). Thus, the values of RWs were plotted spatially (generating a morphospace) to compare individuals according to morphological features and axis orientation. Only the first two RWs were used to create morphospaces as they represented a sufficiently high percentage of total morphological variance (Table 3), for the profile (59.11%) and dorsal (71.63%) perspectives, respectively (Farré et al. 2016a; Trallero et al. 2019). The morphospaces were built using PAST v.3.26 (Paleontological Statistics software package, Hammer et al. 2001).

Table 3 Percentage explained for the first five relative warps (RW) in both dorsal and profile perspectives

| | RW1 | RW2 | RW3 | RW4 | RW5 |
|---------------------------|-------|-------|-------|-------|-------|
| Dorsal | | | | | |
| Percentage (%) | 45.10 | 26.53 | 9.41 | 6.76 | 3.14 |
| Cumulative percentage (%) | 45.10 | 71.63 | 81.05 | 87.81 | 90.94 |
| Profile | | | | | |
| Percentage (%) | 38.18 | 20.93 | 11.46 | 6.38 | 4.24 |
| Cumulative percentage (%) | 38.18 | 59.11 | 70.57 | 76.95 | 81.19 |

Table 2 Description of the landmarks and semi-landmarks used to define the shape of the profile and dorsal views of the bills of Antarctic prions, thin-billed prions and blue petrels (following Trallero et al. 2019)

| Profile | | Dorsal | |
|---------------|--|----------|--|
| Landmark | Description | Landmark | Description |
| 1 | Upper jaw, most distal tip of maxilla (<i>maxillary unguis</i>) | 1 | Upper jaw, most distal tip of maxilla (<i>maxillary unguis</i>) |
| 2 | Lower jaw, most distal tip of the mandibular zone (<i>mandibular unguis</i>) | 2 | Articulation between the upper and lower <i>ramicorn</i> (right side) |
| 3 | Anterior tip of the inferior <i>ramicorn</i> at the conjuncture with the inferior <i>unguicorn</i> | 3 | The most distal tip of the <i>latericorn</i> (right side) |
| 4 | Posterior tip of the lower <i>ramicorn</i> | 4 | Lower and posterior border of the nare, at the junction with the posterior point of the <i>latericorn</i> joint (right side) |
| 5 | Posterior tip of the <i>latericorn</i> | 5 | Upper and posterior border of the nare |
| 6 | Lower and posterior border of the nares, at the junction with the posterior point of the <i>latericorn</i> joint | 6 | Point of maximum curvature at the rostral end of the right nare |
| 7 | Upper and posterior border of the nares | 7 | Point of maximum curvature at the rostral end of the left nare |
| 8 | Point of maximum curvature of the superior and anterior border of the nare | 8 | Lower and posterior border of the nare, at the junction with the posterior point of the <i>latericorn</i> joint (left side) |
| 9 | Lower and anterior border, in the joint with the <i>latericorn</i> | 9 | The most distal tip of the <i>latericorn</i> (left side) |
| 10 | Articulation between the upper anterior border of the <i>culminicorn</i> and the posterior superior border of the maxillary zone | 10 | Articulation between the upper and lower <i>ramicorn</i> (left side) |
| 14 | Articulation between the upper and lower <i>ramicorn</i> | | |
| Semi-landmark | | | |
| 11, 12, 13 | Curvature of the maxillary nail, between landmarks 1 and 10 | | |

Statistical analysis

Bill size (maximum bill depth, bill depth at nares and culmen length) and shape (using the RW1 and RW2 values of the profile and dorsal views) were compared among species and populations using Kruskal–Wallis and Mann–Whitney *U* tests, with species and island group as fixed factors. Sex was not included as a factor because it was unknown for the samples from some sites. Moreover, the study species are considered to be sexually monomorphic (Warham 1990), the differences between sexes in bill size and shape of Antarctic prions and blue petrels are very slight (Trallero et al. 2019), there are no significant sex differences in foraging strategies (Quillfeldt et al. 2008; Phillips et al. 2011; Cherel et al. 2014), and we had no reason to expect biased sex ratios during sampling. Data were tested for normality (Shapiro–Wilk test) and

homogeneity of variances (Levene's test). These analyses were performed using R 3.5.0 (R Core Team 2018).

Results

Interspecific differences in bill morphology

There were significant differences in bill size (all measurements) and shape of both profile and dorsal views among the three species (Tables 4 and 5). This included clear interspecific differences in profile shape (Fig. 3). Species segregated along the horizontal axis (RW1, representing 38.18% of the total morphological variability) separating individuals by shape of nares, length of *culminicorn* and size of *maxillary unguis* (Fig. 3): specimens with more triangular nares, longer *culminicorn* and smaller *maxillary* and *mandibular*

Table 4 Comparison of bill size and shape variation measurements between Antarctic prions, thin-billed prions and blue petrels breeding at different island groups

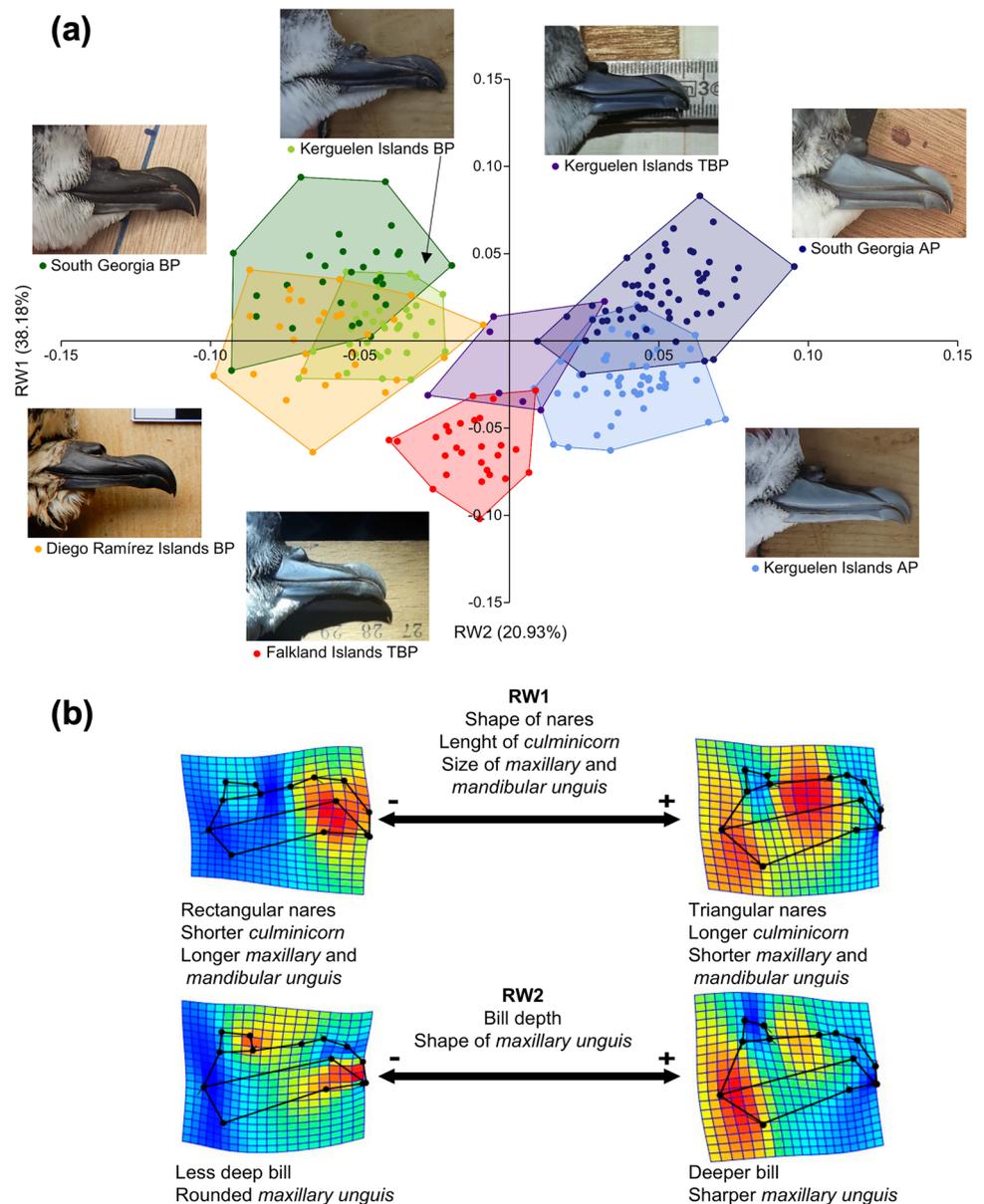
| | Antarctic prion | | Blue petrel | | | Thin-billed prion | |
|---------------------|--------------------------------------|-------------------------------------|---------------------------------------|---|---|--|--|
| | Kerguelen Islands | South Georgia | Kerguelen Islands | South Georgia | Diego Ramírez Islands | Kerguelen Islands | Falkland Islands |
| Maximum bill depth | 8.44 ± 0.39 (20) _{A1} | 12.42 ± 1.04 (53) _{A2} | 9.45 ± 0.40 (14) _{B1} | 10.12 ± 0.64 (27) _{B1,3} | 10.93 ± 0.46 (29) _{B3,4} | 12.00 ± 1.04 (7) _{A2,4} | 11.14 ± 0.42 (17) _{A2,3,4} |
| Bill depth at nares | | 9.13 ± 0.90 (53) _{A1} | | 7.51 ± 0.47 (28) _{B2} | 7.39 ± 0.47 (29) _{B2} | 8.64 ± 1.00 (7) _{B1} | 7.41 ± 0.35 (17) _{B2} |
| Culmen length | 26.91 ± 1.01 (20) _{A1,2} | 28.19 ± 1.16 (53) _{A1} | 26.08 ± 1.06 (14) _{B2,3} | 26.32 ± 1.10 (28) _{B2,4,5} | 25.21 ± 0.99 (29) _{B3,4,6} | 25.46 ± 1.30 (7) _{B2,6,7} | 25.10 ± 0.97 (17) _{B3,5,7} |
| Dorsal | | | | | | | |
| RW1 | − 0.01 ± 0.02 (54) _{A1} | 0.08 ± 0.02 (55) _{A2} | − 0.06 ± 0.03 (37) _{B3} | − 0.02 ± 0.03 (29) _{B1} | − 0.01 ± 0.02 (29) _{B1} | 0.01 ± 0.02 (7) _{B1,2} | − 0.03 ± 0.02 (23) _{B1,3} |
| RW2 | 0.04 ± 0.02 (54) _{A1} | 0.01 ± 0.02 (55) _{A2} | − 0.01 ± 0.03 (37) _{B2,3} | − 0.03 ± 0.02 (29) _{B3,4,5} | − 0.06 ± 0.02 (29) _{B4} | 0.01 ± 0.03 (7) _{C1,2,5} | 0.002 ± 0.016 (23) _{C2} |
| Profile | | | | | | | |
| RW1 | 0.04 ± 0.01 (54) _{A1} | 0.05 ± 0.02 (60) _{A1} | − 0.04 ± 0.01 (35) _{B2,3} | − 0.06 ± 0.02 (29) _{B2} | − 0.06 ± 0.02 (29) _{B2} | 0.001 ± 0.018 (7) _{C1,2,4} | − 0.01 ± 0.01 (27) _{C3,4} |
| RW2 | − 0.02 ± 0.02 (54) _{A1} | 0.03 ± 0.02 (60) _{A2,3} | 0.01 ± 0.02 (35) _{A2,4,5} | 0.04 ± 0.02 (29) _{A3} | − 0.0002 ± 0.0239 (29) _{A1,4} | − 0.01 ± 0.03 (7) _{B1,5,6} | − 0.06 ± 0.02 (27) _{B6} |

Values are mean ± standard deviation (sample size). Values with the same subscript indicate no significant difference between species (letters) or colonies (numbers) based on Mann–Whitney tests

Table 5 Summary of the Kruskal–Wallis tests examining variation in bill size and morphology (dorsal and profile) between Antarctic prions, thin-billed prions and blue petrels breeding at different island groups

| | Species | | Colony | | Species × colony | |
|---------------------|----------|----------|----------|----------|------------------|----------|
| | <i>H</i> | <i>p</i> | <i>H</i> | <i>p</i> | <i>H</i> | <i>p</i> |
| Maximum bill depth | 26.4 | <0.001 | 56.6 | <0.001 | 131.7 | <0.001 |
| Bill depth at nares | 75.3 | <0.001 | 40.2 | <0.001 | 84.6 | <0.001 |
| Culmen length | 82.3 | <0.001 | 68.9 | <0.001 | 99.5 | <0.001 |
| Dorsal-RW1 | 91.4 | <0.001 | 69.9 | <0.001 | 164.7 | <0.001 |
| Dorsal-RW2 | 103.8 | <0.001 | 91.9 | <0.001 | 155.1 | <0.001 |
| Profile-RW1 | 197.4 | <0.001 | 57.9 | <0.001 | 203.9 | <0.001 |
| Profile-RW2 | 69.7 | <0.001 | 141.3 | <0.001 | 160.0 | <0.001 |

Fig. 3 **a** Morphospace of the shape of the right profile of the bills of Antarctic prions (AP) from South Georgia and Kerguelen Islands, blue petrels (BP) from South Georgia, Kerguelen and Diego Ramírez Islands, and thin-billed prions (TBP) from Kerguelen and Falkland Islands. **b** Descriptions of the meaning of the relative warps (RW1 and RW2), corresponding to the horizontal and vertical axes of profile morphospace (red/orange and blue/green indicate higher and lower shape variation, respectively)

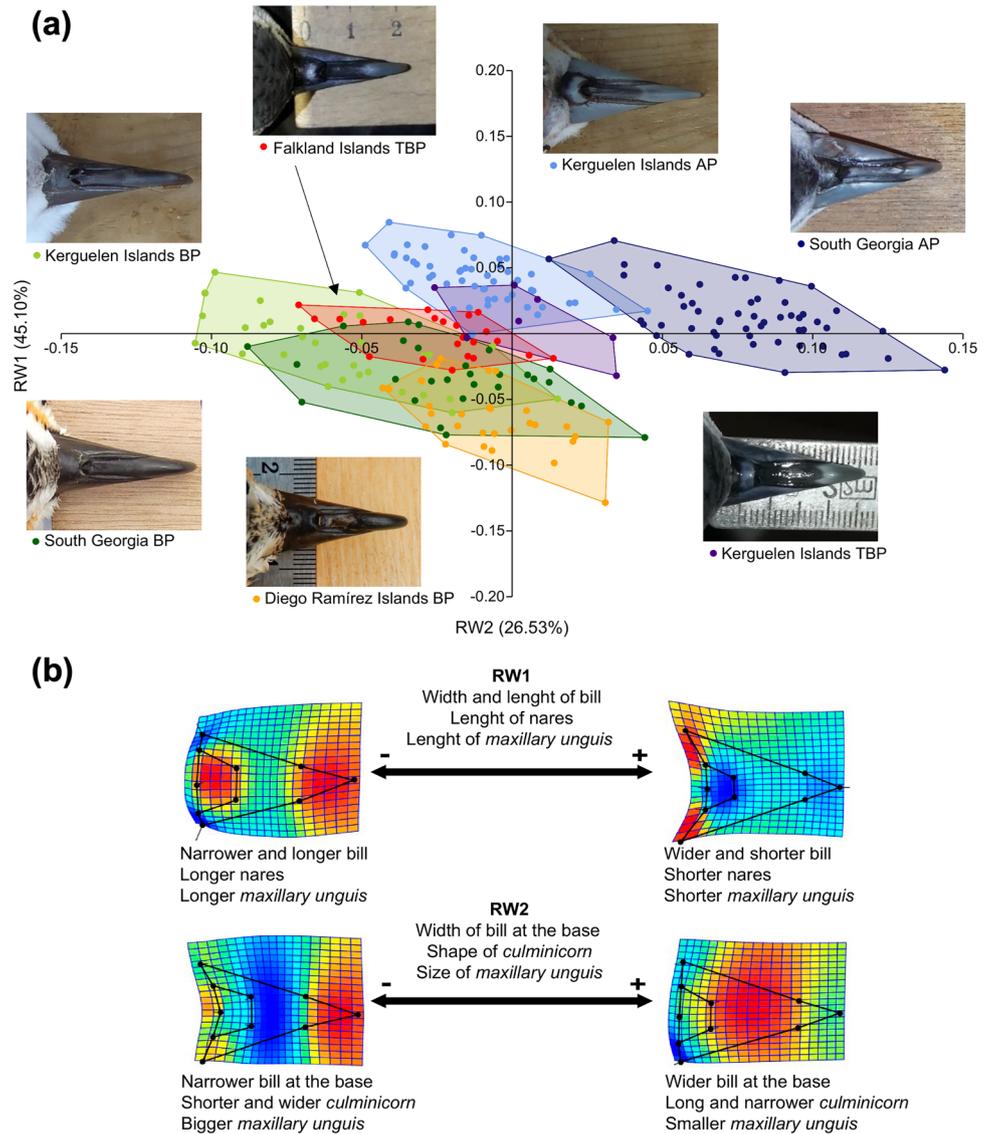


unguis showed positive values (Antarctic prions); specimens with more rectangular nares, shorter *culminicorn* and proportionally bigger *maxillary* and *mandibular unguis* (blue petrels) showed negative values; and thin-billed prions showed intermediate (near to zero) values. The vertical axis (RW2, 20.93% of the total morphological variation) differentiated individuals by bill depth, and shape of *maxillary unguis* (Fig. 3): most of the blue petrels and Antarctic prions had deeper bill and sharper *maxillary unguis*, with higher values and located towards the positive extreme, and those with less deep bills and more rounded *maxillary unguis* showed lower values in the negative extreme (thin-billed prions).

Differences in bill shape among species were also observed in the dorsal perspective (Fig. 4), although less

so than in the profile view. The horizontal axis (RW1) explained a high proportion of the total morphological variability (45.10%), grouping individuals by width and length of bill, length of nares and length of *maxillary unguis* (Fig. 4): birds with wider and shorter bills, shorter nares and shorter *maxillary unguis* tended to the positive extreme (Antarctic prions), and those with narrower and longer bills, longer nares and longer *maxillary unguis* to the negative extreme (blue petrels and thin-billed prions). The vertical axis (RW2, 26.53% of the total morphological variability) differentiated specimens by width of bill base, shape of *culminicorn* and size of *maxillary unguis* (Fig. 4): birds with wider bill base, longer and narrower *culminicorn* and smaller *maxillary unguis* were positioned towards the positive extreme (most Antarctic prions) and those with narrower bill base,

Fig. 4 **a** Morphospace of the shape of the dorsal view of the bills of Antarctic prions (AP) from South Georgia and Kerguelen Islands, blue petrels (BP) from South Georgia, Kerguelen and Diego Ramírez Islands, and thin-billed prions (TBP) from Kerguelen and Falkland Islands. **b** Descriptions of the meaning of the relative warps (RW1 and RW2), corresponding to the horizontal and vertical axes of dorsal morphospace (red/orange and blue/green indicate higher and lower shape variation, respectively)



shorter and wider *culminicorn* and bigger *maxillary unguis* had more negative RW2 values (mostly blue petrels). Thin-billed prions showed intermediate (near to zero) values.

Differences in bill morphology between populations

There were significant differences in bill size and in both profile and dorsal-view bill shape between populations of Antarctic prions and blue petrels at different island groups (Tables 4 and 5). Antarctic prions from South Georgia had a bigger maximum bill depth than those breeding at Kerguelen (Tables 4 and 5), and blue petrels from Diego Ramírez had bigger maximum bill depth than those from Kerguelen (Tables 4 and 5). Thin-billed prions from Kerguelen had a bigger bill depth at nares than conspecifics from Falkland (Tables 4 and 5). In profile view, there were differences between populations of blue petrels and Antarctic prions

(Fig. 3). Between-populations morphological variation was only significant in the vertical axis (Tables 4 and 5). Both Antarctic prions and blue petrels from South Georgia had deeper bills and sharper *maxillary unguis* (higher RW2 values) than birds from other conspecific populations (Fig. 3).

Dorsal shape variability between populations was more apparent for Antarctic prions than blue petrels. Most birds from South Georgia and Diego Ramírez (blue petrel only) had wider and shorter bills, as well as shorter nares and *maxillary unguis*, than conspecifics at Kerguelen (higher RW1 values, Fig. 4). Most Antarctic prions and blue petrels from Kerguelen had wider bills at the base, longer and narrower *culminicorn* and smaller *maxillary unguis* (higher RW2 values, Fig. 4) than conspecifics at Diego Ramírez (blue petrels) and South Georgia (Antarctic prions). No differences were found in both profile and dorsal views, between the two populations of thin-billed prions (Tables 4 and 5).

Discussion

Using geometric morphometrics, we found significant differences among species and populations (island groups) in bill morphology of three planktivorous petrels. Specifically, Antarctic prions have more robust and shorter bills with shorter nares, while both blue petrels and thin-billed prions have slenderer and elongated bills, with longer nares. The Antarctic prions from Kerguelen have longer and narrower bills, and longer nares, than conspecifics from South Georgia. Overall, blue petrels from South Georgia and Diego Ramírez Islands had wider and shorter bills, with shorter nares, than conspecifics from Kerguelen Islands. Even though they have overall similar bill shape, thin-billed prions from Kerguelen had bigger bill depth at nares, than individuals from Falkland.

As the main function of the bill in seabirds is for foraging, niche differentiation could presumably be the main driver of the interspecific and between-populations segregation in bill shape found in the present study. Antarctic prions have smaller but more robust bills than blue petrels and thin-billed prions. Antarctic prions feed mainly on crustaceans, including small copepods (see diet review in Table 1) and use a hydroplaning, surface-filtration technique to capture very large numbers of these abundant but small prey (Croxall and Prince 1980; Harper 1987; Warham 1990). These strategies consist of sitting on the water, or swimming with the head below the surface and filtering seawater through the palatal lamellae (a specialized adaptation for filter-feeding) that line the interior edge of the upper mandible (Prince 1980; Warham 1990). We hypothesise that a wide and deep bill is particularly adapted to this feeding strategy because it allows filtering of a greater volume of water, thus maximizing the number of small copepods that can be ingested at one time. Blue petrels and thin-billed prions, on the other hand, have narrower and longer bills that lack palatal lamellae. Although they also feed mostly on crustaceans, copepods are rare or absent, and they consume a higher percentage of larger prey (small fish and squid); this applies particularly to thin-billed prions during incubation (Quillfeldt et al. 2010), compared with Antarctic prions (Table 1). The foraging strategy of blue petrels mainly involves dipping while in flight and selection of single, large prey items (Croxall and Prince 1980; Prince 1980). Their long and narrow bills are more well adapted for quick movements and catching, and may thus allow them to seize and tear quicker, more slippery and larger prey (fish or squid) that cannot be ingested whole (Harper 1987; Warham 1990).

The morphological segregation of bill morphology observed between populations of Antarctic prions and blue petrels from Kerguelen and South Georgia might

be also related to prey selection. At South Georgia, Antarctic prions consume on large numbers of small copepods, along with Antarctic krill (Table 1), and the short but deeper bills are potentially better adapted for filter-feeding (Croxall and Prince 1980; Prince 1980; Warham 1990; Cherel et al. 2002b). In contrast, the diet of Antarctic prions at Kerguelen is mainly composed of hyperiid amphipods, primarily *T. gaudichaudii*, which are larger than copepods and are caught mostly in pelagic waters (Table 1). This would explain why the bills of Antarctic prions at Kerguelen are longer and narrower, thus more adapted for the capture of single prey items. Blue petrels from South Georgia feed mainly on Antarctic krill and small myctophids (length range: ≈ 35 – 55 mm, Cherel et al. 2002a; Table 1). At Kerguelen, besides crustaceans and myctophids, the diet of blue petrels also includes a high percentage of larger prey such as squid, and fish *P. gracilis* (mean length: ≈ 283 mm, Cherel et al. 2002a) (Table 1). Hence, the long and narrow bills of blue petrels at this site are also consistent with the requirement to seize and tear larger individual prey items. Although there are no published studies of the diet of blue petrels at Diego Ramírez, stomachs of adults contained lots of crustaceans (Euphausiids and Amphipods), followed by remains of small fish and cephalopod beaks (Suazo, unpubl. data). Therefore, we predict according to the similarity in bill morphology that their diet is more similar to conspecifics from South Georgia, rather than Kerguelen. Even though dietary proportions of crustaceans, fish and cephalopods differ between both populations of thin-billed prions, no variation in bill morphology was detected. Since they feed on a higher percentage of cephalopods, along with lower intake of crustaceans and myctophids, individuals from Falkland were expected to have narrower and longer bills than conspecifics from Kerguelen (this is corroborated by significant differences in measurements of bill depth at the nares, between the two colonies). As in the other two species, bill structures showing these morphologic features could be better adapted to catch larger and quicker prey, such as the squid *G. antarcticus*. However, the main species composing thin-billed prions' diet in both sites are similar, and thus dietary proportions might not be sufficient to cause significant morphological variation in the bill, in this case. Also, it is important to notice that Kerguelen's sample size ($n = 7$) is much lower than Falkland's ($n = 27$), which could lead to biased results when comparing the two colonies. Hence, further studies are necessary to properly identify and assess differences in bill shape of thin-billed prions, among different areas.

In conclusion, our results reveal key interspecific and geographic differences in bill shape and size of three small petrels, which seem likely to reflect variation in prey selection and foraging style. Our study also highlights the

usefulness of geometric morphometric methods for investigating the bill morphology of seabirds. Further studies linking bill shape and foraging strategies (including quantitative analysis of association between bill morphology and diet), or even accounting for the phylogenetic relatedness among species, are needed to better identify the main ecological drivers that lead to morphological variation of biological structures in seabirds.

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Availability of data and material All data are included into the manuscript supplements.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

Ethics approval Work on South Georgia was approved by the Animal Welfare and Ethical Review Body (AWERB) of the British Antarctic Survey and was carried out under permit from the Government of South Georgia and the Sandwich Islands. Work on New Island was approved by the Falkland Islands Government (Environmental Office). Kerguelen data were supported by the French Polar Institute Paul Emile Victor. Work on Diego Ramírez Islands was supported by Armada de Chile (Chilean Navy, 3rd Naval Zone).

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