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

3

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20

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24 **Abstract**

25 Morphological variation in biological structures may be driven by genetic and  
26 environmental factors, such as inter and intraspecific competition for resources. In  
27 seabirds, although the bill is also involved in vocalization, olfaction, sexual selection  
28 and defence, the main drivers of high morphological plasticity in bill size and shape  
29 appear to relate primarily to diet and thus to niche differentiation. Here, we combined  
30 geometric morphometrics and comparisons of linear measurements as a precise tool for  
31 measuring shape variation in anatomical features, to investigate the differences among  
32 species and populations (island groups) in bill shape of three abundant planktivorous  
33 petrels (Antarctic prion *Pachyptila desolata*, blue petrel *Halobaena caerulea* and thin-  
34 billed prion *Pachyptila belcheri*). Fieldwork was carried out in South Georgia (54°0'S,  
35 38°3'W), Falkland Islands (51°42'S, 57°51'W), Diego Ramírez Islands (56°31'S,  
36 68°44'W) and Kerguelen Islands (49°20'S, 69°20'E), across 2010-2021. As expected,  
37 the bills of Antarctic prions were more robust and shorter, appropriate for filtering large  
38 amounts of small prey. Blue petrels and thin-billed prions had narrower and longer bills,  
39 effective for catching and tearing large single prey. Also, Antarctic prions and blue  
40 petrels from Kerguelen had longer and narrower bills than conspecifics from other  
41 colonies, which could potentially be explained by geographic variation in diet. In  
42 conclusion, prey availability and diversity appear to be important factors influencing  
43 variation in bill morphology. This study highlights the utility of geometric  
44 morphometrics for investigating bill shape variation in seabirds. Nevertheless, further  
45 studies are needed to better understand selective pressures leading to morphological  
46 displacement of biological structures.

47

## 48 **Introduction**

49 Morphological variation is known to be shaped by abiotic and biotic conditions, and  
50 their interaction. For instance, genes provide the potential for a particular phenotype,  
51 but environmental factors determine how this potential is expressed through selective  
52 pressures (Grant and Grant 1989; Aldrich and James 1991). In seabirds, selective  
53 pressures can be related to environmental conditions, predation, disease, and  
54 interspecific and intraspecific competition for resources such as food or nest sites  
55 (Buckley and Buckley 1980; Warham 1996). Suitable breeding sites are limited in  
56 number and hence multiple species of seabirds often breed in sympatry (Warham 1996;  
57 Brooke 2004). As seabirds are often very abundant, and foraging ranges subject to the  
58 central-place constraint during breeding (i.e., the need to return to incubate eggs or feed  
59 chicks), interspecific and intraspecific competition around colonies is particularly  
60 intense (Lewis et al. 2001; Phillips et al. 2005; Wakefield et al. 2014). Seabirds have  
61 therefore evolved diverse ecological strategies which allow coexistence, including  
62 segregation of foraging areas, behaviour or diet (Quillfeldt et al. 2013; Navarro et al.  
63 2013; Corman et al. 2016), as well as allochrony to reduce overlap in the periods of  
64 higher demand for prey, including chick-rearing and moulting (Cherel et al. 2016; Jones  
65 et al. 2020). Selective pressures differ between regions and thus morphological variation  
66 might reflect adaptation to local conditions in different populations (i.e., breeding at  
67 different island groups) of the same species (Mayr and Diamond 2001; Bull et al. 2004;  
68 Bull 2006).

69 Common examples of variation among birds in specific morphological traits include  
70 the shape and size of feeding structures such as the bill. This is widely established, for  
71 example, in different species of Darwin's finches (Coerebinae), in which bill  
72 morphology is associated with interspecific variability in foraging strategies (Boag and

73 Grant 1981; Kleindorfer et al. 2006; Foster et al. 2008). Similar patterns occur in  
74 boobies (*Sula* spp.) in the Pacific, and little penguins (*Eudyptula minor*) in south  
75 Australia, in which wing and bill size differ between colonies in relation to prey  
76 selection and competition with sympatric species, and with variation in environmental  
77 conditions, respectively (Colombelli-Négrel 2016; Van Oordt et al. 2018). In seabirds,  
78 the bill is of great ecological and biological importance since it provides essential  
79 functions related to food intake, vocalization, sexual selection or defensive and  
80 territorial behaviour (Warham 1996; Nebel 2005; Gémard et al. 2019). Given its  
81 versatile role, the bill is subject to strong selective forces and it shows wide  
82 morphological plasticity and divergence (Schluter 2000; Van Oordt et al. 2018). Many  
83 studies have pointed out the association between bill shape and size, and diet and niche  
84 differentiation (Nebel et al. 2005; Bull 2006; Trallero et al. 2019), presumably driven by  
85 interspecific competition and natural selection (Grémillet et al. 2004; Navarro et al.  
86 2013; Corman et al. 2016).

87 In spite of sometimes wide geographic separation between colonies, breeding  
88 populations of seabirds often show limited genetic structure (Moum and Árnason 2001;  
89 Wojczulanis-Jakubas et al. 2014). This applies to Antarctic prions (*Pachyptila desolata*)  
90 and blue petrels (*Halobaena caerulea*) breeding at South Georgia and Kerguelen  
91 Islands, even though the island groups are far apart and the populations exploit different  
92 trophic niches (Quillfeldt et al. 2017). Therefore, morphological variation among  
93 individuals and populations in the bill might be related to environmental factors such as  
94 relative availability of different prey (Croxall and Prince 1980). Based on previous  
95 studies, the diet of Antarctic prions at South Georgia is composed mainly of small  
96 copepods and Antarctic krill *Euphausia superba*, followed by the amphipod *Themisto*  
97 *gaudichaudii*, small fish and cephalopods (Prince 1980; Croxall et al. 1997; Reid et al.

98 1997). At Kerguelen, although crustaceans are also important, Antarctic prion prey  
99 mainly on *T. gaudichaudii*, and only rarely on Antarctic krill and copepods (Cherel et  
100 al. 2002b). Blue petrels at South Georgia feed mostly on crustaceans and small  
101 myctophids, whereas conspecifics from Kerguelen also catch larger fish such as  
102 *Paradiplospinus gracilis* and consume substantial numbers of cephalopods (Prince  
103 1980; Cherel et al. 2002a). The targeting of distinct prey could therefore drive  
104 morphological differences between these colonies. Cherel et al. (2002b) suggested that  
105 while other crustaceans can be caught individually, large numbers of small copepods  
106 might be ingested at once by Antarctic prions through filter feeding. Moreover, Prince  
107 (1980) suggested that long and narrow bills in blue petrels could be indicative of surface  
108 dipping, and tearing of large single prey. Accordingly, the bill, as the anatomical  
109 structure most directly related to diet, might be the key to detecting phenotypical  
110 variation within these genetically similar populations.

111 Geometric morphometric analyses represents a precise tool for measuring shape  
112 variation in anatomical features (Adams et al. 2013), providing insights into  
113 relationships between morphological structures and ecological strategies (Adams 1999;  
114 Zelditch et al. 2004; Farré et al. 2016b), including in seabirds (Foster et al. 2008;  
115 Navarro et al. 2009; Berns and Adams 2010; Trallero et al. 2019). With this approach, it  
116 is possible to accurately compare biological form in statistical terms, while accounting  
117 for the non-shape variation (size, orientation, deformation etc.) (Adams et al. 2004;  
118 Zelditch et al. 2004). In a previous study (Trallero et al. 2019), we quantified  
119 differences among species and sexes in bill morphology of Antarctic prions, blue  
120 petrels, and two species of diving petrels (*Pelecanoides* spp.) all breeding at South  
121 Georgia, South Atlantic. Here, we extend this by investigating the differences in bill  
122 shape among populations of three abundant planktivorous petrels (Antarctic prion, blue

123 petrel and thin-billed prion *Pachyptila belcheri*) which have circumpolar distributions in  
124 the Southern Ocean. Although diet proportions are similar in terms of prey classes, the  
125 three species differs in terms of the main crustacean species consumed (Prince 1980;  
126 Cherel et al. 2002a,b) which might explain the striking spatial and ecological  
127 segregation among species and populations (Quillfeldt et al. 2013, 2015; Navarro et al.  
128 2013, 2015). Hence, our initial hypothesis was that these differences in foraging  
129 ecology would be reflected in bill-character displacement. While species differences  
130 have been described with traditional methods, geometric morphometric analyses can  
131 reveal subtler contrasts and offers a precise tool to analyse less obvious differences, as  
132 may be found between populations.

133

## 134 **Material and Methods**

### 135 *Study species*

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

145

### 146 *Study sites*

147 Fieldwork was conducted in breeding colonies at four sub-Antarctic island groups  
148 >1000 km apart (Fig. 1): Bird Island, South Georgia (54°0'S, 38°3'W), New Island,  
149 Falkland Islands (Malvinas) (51°42'S, 57°51'W), Gonzalo Island, Diego Ramírez  
150 Islands (56°31'S, 68°44'W) and Île Verte, Kerguelen Islands (49°20'S, 69°20'E).  
151 Antarctic krill are particularly abundant around and to the south of South Georgia  
152 (Atkinson et al. 2001). Prey availability for seabirds is high in the waters surrounding  
153 the Falkland Islands, which are characterised by low temperatures, strong winds and  
154 turbulent waters (Armstrong and Forbes 1997). At Diego Ramírez, temperatures are low  
155 and there are strong westerly winds and high annual rainfall (Schlatter & Riveros,  
156 1997). The Kerguelen Islands are also in a region characterized by low temperatures and  
157 high winds, with strong upwellings (Zhou et al. 2014). Estimated breeding populations  
158 in each island group are as follows: Antarctic prion, South Georgia (22 million pairs);  
159 blue petrel, South Georgia (70 000 pairs); Antarctic prion, Kerguelen (2-3 million  
160 pairs); blue petrel, Kerguelen (100-200,000 pairs); thin-billed prion, New Island,  
161 Falkland Islands (Malvinas) (2 million pairs); blue petrel, Diego Ramírez (1.35 million  
162 pairs) (Prince and Croxall 1983; Weimerskirch et al. 1989; Schlatter and Riveros 1997;  
163 Catry et al. 2003; Barbraud and Delord 2006; Lawton et al. 2006).

164

#### 165 *Sampling and morphological data acquisition*

166 During the breeding period, a total of 60 Antarctic prions and 29 blue petrels were  
167 sampled at Bird Island (November 2010 – February 2011); 54 Antarctic prions and 37  
168 blue petrels at Île Verte (December 2018 – January 2019), 29 blue petrels at Gonzalo  
169 Island (November 2020 – January 2021) and 27 thin-billed prions at New Island  
170 (February 2019). For each individual, digital pictures were taken of the right profile and  
171 dorsal view of the bill using a compact digital camera in a consistent orientation: the bill



172 was supported using a wooden board with a ruler underneath for scale, and the camera  
173 lens was always perpendicular to the bill surface. Any pictures that were not  
174 standardized in this way were excluded from morphological analyses. In addition, three  
175 biometric measurements were taken in the field: maximum bill depth, bill depth at nares  
176 and culmen length as shown in Trallero et al. (2019). All measurements were made  
177 using digital callipers ( $\pm 0.1$  mm) (Fig. 2).

178

### 179 *Bill shape analysis*

180 Characterization and assessment of variability in bill shape were performed using  
181 geometric morphometric methods (Rohlf and Marcus 1993; Zelditch et al. 2004). A  
182 total of 10 landmarks (fixed homologous points) in dorsal pictures (Tokita et al. 2017;  
183 Trallero et al. 2019) and 11 landmarks and 3 semilandmarks (mobile non-homologous  
184 points) in profile pictures (Navarro et al. 2009; Militão et al. 2014; Trallero et al. 2019)  
185 were used to define the overall shape of bill and nares (Fig. 2, Table 2). Landmarks and  
186 semilandmarks coordinates were digitized and transformed into geometric data using  
187 the tpsDig2 v.2.31 (Rohlf 2017), creating a metric map for each individual. A  
188 Generalized Procrustes Analysis (GPA) was then applied, using tpsRelw v.1.70 (Rohlf  
189 2019). GPA compares all the landmark configurations removing distortions not related  
190 to shape, translating all configurations to a common centroid position, scaling them to  
191 the unit centroid size and rotating them to minimise the distances between  
192 corresponding landmarks (Adams et al. 2004; Zelditch et al. 2004). Next, a consensus  
193 configuration was obtained by averaging the spatial coordinates of all landmarks using a  
194 thin-plate spline procedure. The comparison of each configuration with this consensus  
195 form allows the shape deformation variables (relative warps, RWs) to be extracted for  
196 each individual. Each RW represents a specific set of morphological characteristics, and

197 their comparison allows the potential variation in shape of analysed objects to be  
198 visualised (Rohlf and Marcus 1993; Zelditch et al. 2004). Thus, the values of RWs were  
199 plotted spatially (generating a morphospace) to compare individuals according to  
200 morphological features and axis orientation. Only the first two RWs were used to create  
201 morphospaces as they represented a sufficiently high percentage of total morphological  
202 variance (Table 3), for the profile (60.27%) and dorsal (72.07%) perspectives,  
203 respectively (Farré et al. 2016a; Trallero et al. 2019). The morphospaces were built  
204 using PAST v.3.26 (Paleontological Statistics software package, Hammer et al. 2001).

205

#### 206 *Statistical analysis*

207 Bill size (maximum bill depth, bill depth at nares and culmen length) and shape  
208 (using the RW1 and RW2 values of the profile and dorsal views) were compared among  
209 species and populations using Kruskal-Wallis and Mann-Whitney U tests, with species  
210 and island group as fixed factors. Sex was not included as a factor because it was  
211 unknown for the samples from some sites. Moreover, the study species are considered  
212 to be sexually monomorphic (Warham 1990), the differences between sexes in bill size  
213 and shape of Antarctic prions and blue petrels are very slight (Trallero et al. 2019), there  
214 are no significant sex differences in foraging strategies (Quillfeldt et al. 2008; Phillips et  
215 al. 2011; Cherel et al. 2014), and we had no reason to expect biased sex ratios during  
216 sampling. Data were tested for normality (Shapiro-Wilk test) and homogeneity of  
217 variances (Levene's test). These analyses were performed using R 3.5.0 (R Core Team  
218 2018).

219

## 220 **Results**

### 221 *Interspecific differences in bill morphology*

222 There were significant differences in bill size (all measurements) and shape of both  
223 profile and dorsal views among the three species (Tables 4 and 5). This included clear  
224 interspecific differences in profile shape (Fig. 3). Species segregated along the  
225 horizontal axis (RW1, representing 39.12% of the total morphological variability)  
226 separating individuals by shape of nares, length of *culminicorn* and size of *maxillary*  
227 *unguis* (Fig. 3): specimens with more triangular nares, longer *culminicorn* and smaller  
228 *maxillary* and *mandibular unguis* showed positive values (Antarctic prions); specimens  
229 with more rectangular nares, shorter *culminicorn* and proportionally bigger *maxillary*  
230 and *mandibular unguis* (blue petrels) showed negative values; and thin-billed prions  
231 showed intermediate (near to zero) values. The vertical axis (RW2, 21.15% of the total  
232 morphological variation) differentiated individuals by bill depth, and shape of *maxillary*  
233 *unguis* (Fig. 3): most of the blue petrels and Antarctic prions had deeper bill and sharper  
234 *maxillary unguis*, with higher values and located towards the positive extreme, and  
235 those with less deep bills and more rounded *maxillary unguis* showed lower values in  
236 the negative extreme (thin-billed prions).

237 Differences in bill shape among species were also observed in the dorsal perspective  
238 (Fig. 4), although less so than in the profile view. The horizontal axis (RW1) explained  
239 a high proportion of the total morphological variability (45.52%), grouping individuals  
240 by width and length of bill, length of nares and length of *maxillary unguis* (Fig. 4): birds  
241 with wider and shorter bills, shorter nares and shorter *maxillary unguis* tended to the  
242 positive extreme (Antarctic prions), and those with narrower and longer bills, longer  
243 nares and longer *maxillary unguis* to the negative extreme (blue petrels and thin-billed  
244 prions). The vertical axis (RW2, 26.55% of the total morphological variability)  
245 differentiated specimens by width of bill basis, shape of *culminicorn* and size of  
246 *maxillary unguis* (Fig. 4): birds with wider bill basis, longer and narrower *culminicorn*

247 and smaller *maxillary unguis* were positioned towards the positive extreme (most  
248 Antarctic prions) and those with narrower bill basis, shorter and wider *culminicorn* and  
249 bigger *maxillary unguis* had more negative RW2 values (mostly blue petrels). Thin-  
250 billed prions showed intermediate (near to zero) values.

#### 251 *Differences in bill morphology between populations*

252 There were significant differences in bill size and in both profile and dorsal-view bill  
253 shape between populations of Antarctic prions and blue petrels at different island  
254 groups (Tables 4 and 5). Antarctic prions and blue petrels from South Georgia had a  
255 bigger maximum bill depth than those breeding at Kerguelen (Tables 4 and 5), and blue  
256 petrels from Diego Ramírez had bigger maximum bill depth than those from South  
257 Georgia and Kerguelen (Tables 4 and 5). Antarctic prions from South Georgia had  
258 longer culmens than at Kerguelen, and blue petrels at Diego Ramírez had shorter  
259 culmens than at South Georgia and Kerguelen (Tables 4 and 5). In profile view, there  
260 were differences among populations of the sympatric species (blue petrel and Antarctic  
261 prion) (Fig. 3). Between-population morphological variation was significant in both  
262 axes (Tables 4 and 5). Antarctic prions from Kerguelen had more rectangular nares,  
263 shorter *culminicorn* and a bigger *maxillary* and *mandibular unguis* than at South  
264 Georgia (lower RW1 values, Fig. 3). Blue petrels from Kerguelen (higher RW1 values)  
265 had slightly more triangular nares, longer *culminicorn* and smaller *maxillary* and  
266 *mandibular unguis* than at South Georgia and Diego Ramírez (Fig. 3). Also, both  
267 Antarctic prions and blue petrels from South Georgia had deeper bills and sharper  
268 *maxillary unguis* (higher RW2 values) than birds from other conspecific populations  
269 (Fig. 3).

270 Dorsal shape variability between populations was more apparent for Antarctic prions  
271 than blue petrels. Most birds from South Georgia and Diego Ramírez (blue petrel only)

272 had wider and shorter bills, as well as shorter nares and *maxillary unguis*, than  
273 conspecifics at Kerguelen (higher RW1 values, Fig. 4). Most Antarctic prions and blue  
274 petrels from Kerguelen had wider bills at the base, longer and narrower *culminicorn* and  
275 smaller *maxillary unguis* (higher RW2 values, Fig. 4) than conspecifics at Diego  
276 Ramírez (blue petrels) and South Georgia.

## 277 **Discussion**

278 Using geometric morphometrics, we found significant differences among species  
279 and populations (island groups) in bill morphology of three planktivorous petrels.  
280 Specifically, Antarctic prions have more robust and shorter bills with shorter nares,  
281 while both blue petrels and thin-billed prions have slenderer and elongated bills, with  
282 longer nares. The Antarctic prions from Kerguelen have longer and narrower bills, and  
283 longer nares, than conspecifics from South Georgia. Overall, blue petrels from South  
284 Georgia and Diego Ramírez Islands had wider and shorter bills, with shorter nares, than  
285 conspecifics from Kerguelen Islands.

286 As the main function of the bill in seabirds is for foraging, niche differentiation  
287 could presumably be the main driver of the interspecific and between-population  
288 segregation in bill shape found in the present study. Antarctic prions have smaller but  
289 more robust bills than blue petrels and thin-billed prions. Antarctic prions feed mainly  
290 on crustaceans, including small copepods (see diet review in Table 1) and use a  
291 hydroplaning, surface-filtration technique to capture very large numbers of these  
292 abundant but small prey (Croxall and Prince 1980; Harper 1987; Warham 1990). These  
293 strategies consist of sitting on the water, or swimming with the head below the surface  
294 and filtering seawater through the palatal lamellae (a specialized adaptation for filter-  
295 feeding on small copepods) that line the interior edge of the upper mandible (Prince  
296 1980; Warham 1990). We hypothesise that a wide and deep bill is particularly adapted

297 to this feeding strategy because it allows filtering of a greater volume of water, thus  
298 maximizing the number of small copepods that can be ingested at one time. Blue petrels  
299 and thin-billed prions, on the other hand, have narrower and longer bills that lack palatal  
300 lamellae. Although they also feed mostly on crustaceans, copepods are rare or absent,  
301 and they consume a higher percentage of small fish and squid; this applies particularly  
302 to thin-billed prions during incubation (Quillfeldt et al. 2010), compared with Antarctic  
303 prions (Table 1). The foraging strategy of blue petrels mainly involves dipping while in  
304 flight and selection of single, large prey items (Croxall and Prince 1980; Prince 1980).  
305 Their long and narrow bills are more well adapted for quick movements and catching,  
306 and may thus allow them to seize and tear quicker, more slippery and larger prey (fish  
307 or squid) that cannot be ingested whole (Harper 1987; Warham 1990).

308 The morphological segregation of bill morphology observed between populations  
309 from Kerguelen and South Georgia might be also related to prey selection. At South  
310 Georgia, Antarctic prions consume on large numbers of small copepods, along with  
311 Antarctic krill (Table 1), and the short but deeper bills are potentially better adapted for  
312 filter-feeding (Croxall and Prince 1980; Prince 1980; Warham 1990; Cherel et al.  
313 2002b). In contrast, the diet of Antarctic prions at Kerguelen is mainly composed of  
314 hyperiid amphipods, primarily *T. gaudichaudii*, which are larger than copepods and are  
315 caught mostly in pelagic waters (Table 1). This would explain why the bills of Antarctic  
316 prions at Kerguelen are longer and narrower, thus more adapted for the capture of single  
317 prey items. Blue petrels from South Georgia feed mainly on Antarctic krill and small  
318 myctophids (length range:  $\approx$ 35-55 mm, Cherel et al. 2002a; Table 1). At Kerguelen,  
319 besides crustaceans and myctophids, the diet of blue petrels also includes a high  
320 percentage of larger prey such as squid, and fish *P. gracilis* (mean length:  $\approx$ 283 mm,  
321 Cherel et al. 2002a) (Table 1). Hence, the long and narrow bills of blue petrels at this

322 site are also consistent with the requirement to seize and tear larger individual prey  
323 items. Although there are no published studies of the diet of blue petrels at Diego  
324 Ramírez, stomachs of adults contained lots of crustaceans (Euphausiids and  
325 Amphipods), followed by remains of small fish and cephalopod beaks (Suazo, unpubl.  
326 data). Therefore, we predict according to the similarity in bill morphology that their diet  
327 is more similar to conspecifics from South Georgia, rather than Kerguelen.

328 In conclusion, our results reveal key interspecific and geographic differences in bill  
329 shape and size of four small petrels, which seem likely to reflect variation in prey  
330 selection and foraging style. Our study also highlights the usefulness of geometric  
331 morphometric methods for investigating the bill morphology of seabirds. Further studies  
332 linking bill shape and foraging strategies are needed to better identify the main  
333 ecological drivers that lead to morphological displacement of biological structures in  
334 seabirds.

335

### 336 **Compliance with Ethical Standards**

337 Conflicts of interest/Competing interests: The authors declare that they have no conflicts of  
338 interest.

339 Ethics approval: Work on South Georgia was approved by the Animal Welfare and Ethical  
340 Review Body (AWERB) of the British Antarctic Survey and was carried out under permit from  
341 the Government of South Georgia and the Sandwich Islands. Work on New Island was  
342 approved by the Falkland Islands Government (Environmental Office). Kerguelen data were  
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361 **Code availability:** Not applicable

362 **Consent to participate:** Not applicable

363 **Consent for publication:** Not applicable

364



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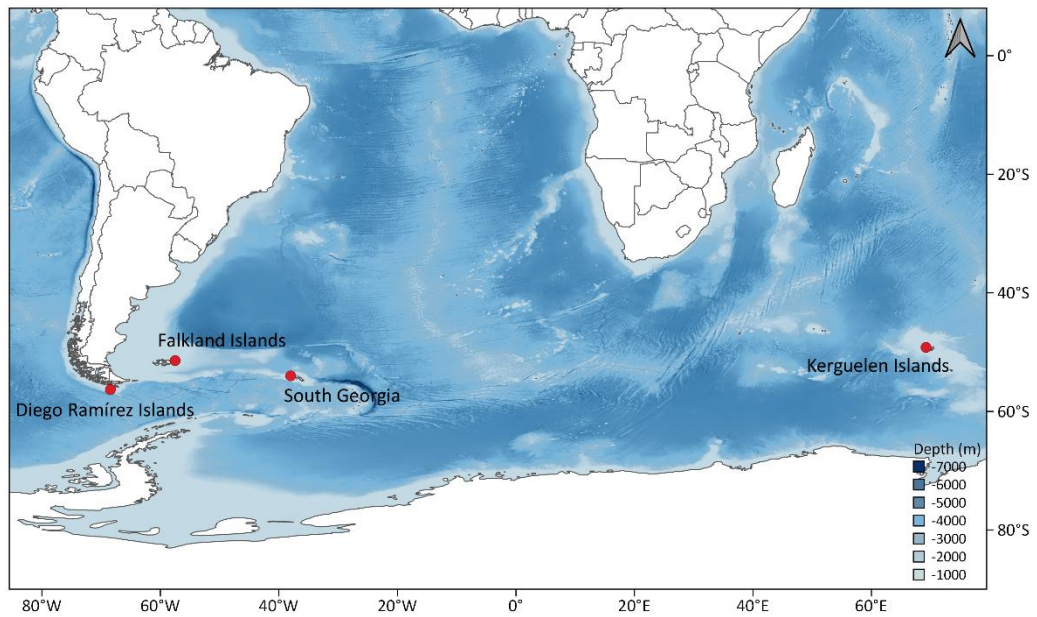
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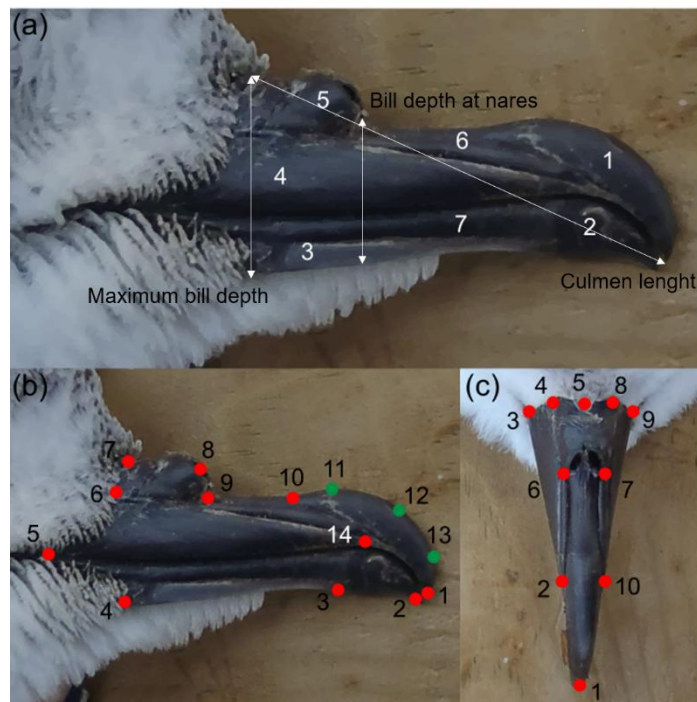
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545 **Fig. 1** Location of the different breeding colonies of Antarctic prions, thin-billed prions and  
 546 blue petrels sampled in this study

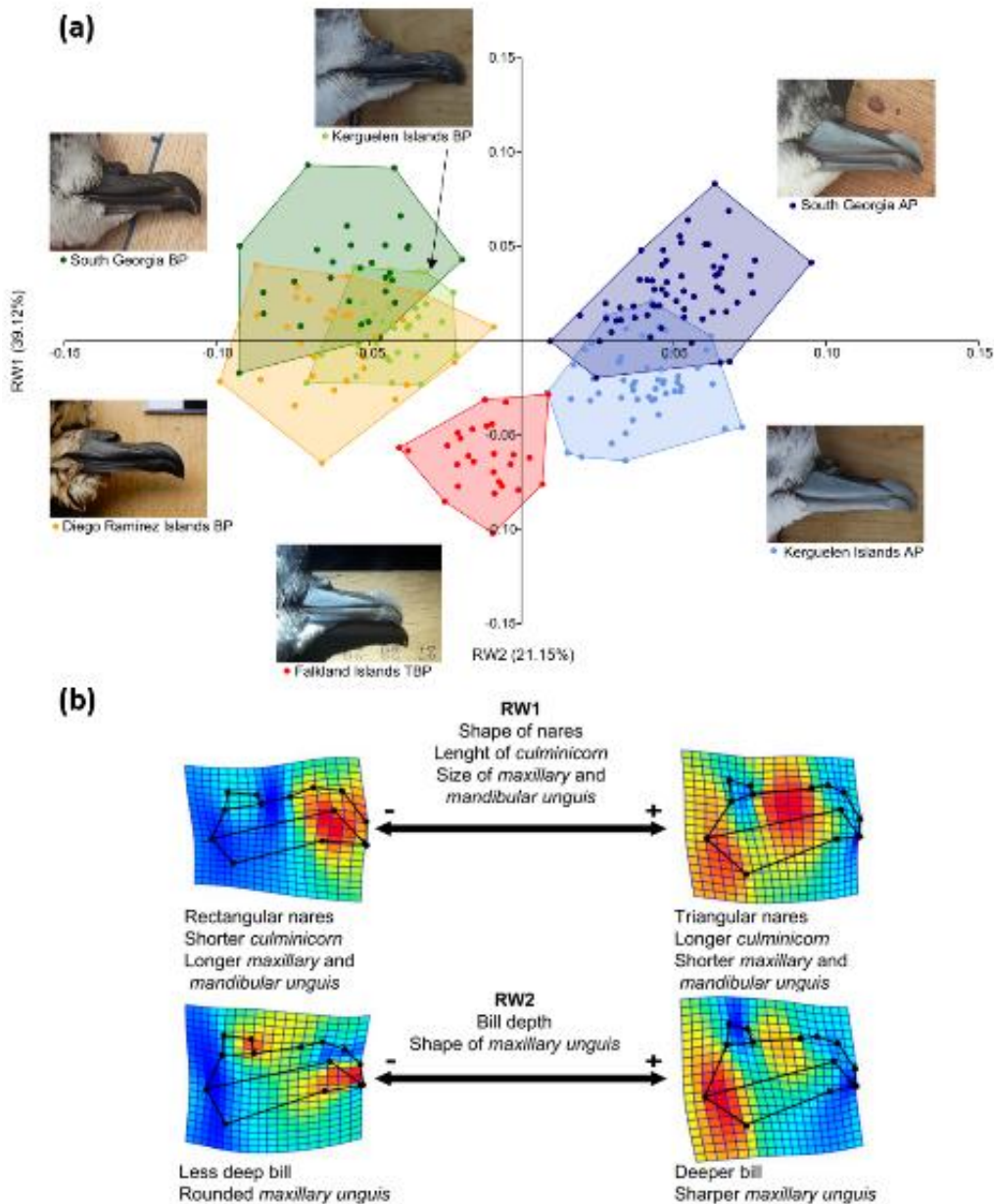
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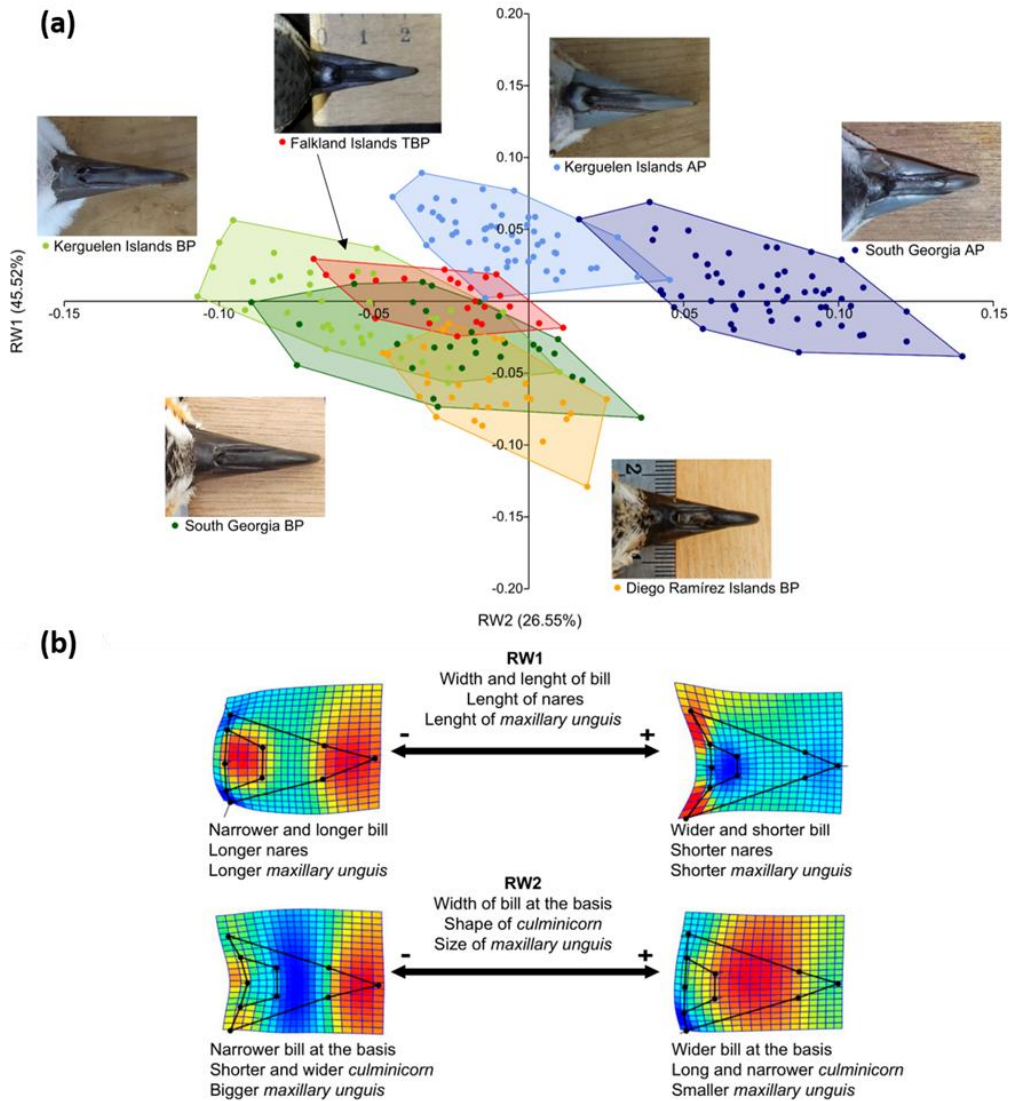
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 556 **Fig. 2** (a) Bill morphology and measurements: 1 = *superior unguicorn-maxillary unguis*, 2 =  
 557 *inferior unguicorn-mandibular unguis*, 3 = *ramicorn*, 4 = *latericorn*, 5 = *nares*, 6 = *culminicorn*  
 558 and 7 = *tomia-cutting edges*. Landmarks (red dots) and semilandmarks (green dots) used to



559 describe the shape of (b) the profile, and (c) the dorsal view of the bill. All pictures are of a blue  
 560 petrel



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



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

574 **Tables**575 **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 Falkland Islands.

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

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

577

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

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

580 2019).

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>		
Semilandmark			
11, 12, 13	Curvature of the maxillary nail, between landmarks 1 and 10		

581

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

	RW1	RW2	RW3	RW4	RW5
Dorsal					
Percentage (%)	45.52	26.55	9.24	6.75	2.96
Cumulative percentage (%)	45.52	72.07	81.31	88.07	91.02
Profile					
Percentage (%)	39.12	21.15	10.73	6.46	4.11
Cumulative percentage (%)	39.12	60.27	71.00	77.46	81.57

582

583

584 **Table 4.** Comparison of bill size and shape variation measurements between Antarctic prions, thin-billed prions and blue petrels breeding at different island groups. Values  
585 are mean  $\pm$  standard deviation (sample size). Values with the same subscript indicate no significant difference between species (letters) or colonies (numbers) based on Mann-  
586 Whitney tests.

	Antarctic prion		Blue petrel			Thin-billed prion
	Kerguelen Islands	South Georgia	Kerguelen Islands	South Georgia	Diego Ramírez Islands	Falkland Islands
Maximum bill depth	8.44 $\pm$ 0.39 (20) <sub>A1</sub>	12.42 $\pm$ 1.04 (53) <sub>A2</sub>	9.45 $\pm$ 0.40 (14) <sub>B3</sub>	10.12 $\pm$ 0.64 (27) <sub>B4</sub>	10.93 $\pm$ 0.46 (29) <sub>B5</sub>	7.41 $\pm$ 0.35 (17) <sub>C6</sub>
Bill depth at nares		9.13 $\pm$ 0.90 (53) <sub>A1</sub>		7.51 $\pm$ 0.47 (28) <sub>B2</sub>	7.39 $\pm$ 0.47 (29) <sub>B2</sub>	
Culmen length	26.91 $\pm$ 1.01 (20) <sub>A1</sub>	28.19 $\pm$ 1.16 (53) <sub>A2</sub>	26.08 $\pm$ 1.06 (14) <sub>B3</sub>	26.32 $\pm$ 1.10 (28) <sub>B1,3</sub>	25.21 $\pm$ 0.99 (29) <sub>B4</sub>	25.10 $\pm$ 0.97 (17) <sub>C4</sub>
Dorsal						
RW1	-0.01 $\pm$ 0.02 (54) <sub>A1</sub>	0.08 $\pm$ 0.02 (55) <sub>A2</sub>	-0.06 $\pm$ 0.03 (37) <sub>B3</sub>	-0.02 $\pm$ 0.03 (29) <sub>B4</sub>	-0.01 $\pm$ 0.02 (29) <sub>B1,4</sub>	-0.03 $\pm$ 0.02 (23) <sub>B4</sub>
RW2	0.04 $\pm$ 0.02 (54) <sub>A1</sub>	0.01 $\pm$ 0.02 (55) <sub>A2</sub>	-0.01 $\pm$ 0.03 (37) <sub>B3</sub>	-0.03 $\pm$ 0.02 (29) <sub>B4</sub>	-0.06 $\pm$ 0.02 (29) <sub>B5</sub>	0.003 $\pm$ 0.016 (23) <sub>C2,3</sub>
Profile						
RW1	0.04 $\pm$ 0.01 (54) <sub>A1</sub>	0.05 $\pm$ 0.02 (60) <sub>A2</sub>	-0.04 $\pm$ 0.01 (35) <sub>B3</sub>	-0.06 $\pm$ 0.02 (29) <sub>B4</sub>	-0.06 $\pm$ 0.02 (29) <sub>B4</sub>	-0.01 $\pm$ 0.01 (27) <sub>C5</sub>
RW2	-0.02 $\pm$ 0.02 (54) <sub>A1</sub>	0.03 $\pm$ 0.02 (60) <sub>A2</sub>	0.01 $\pm$ 0.02 (35) <sub>B3</sub>	0.04 $\pm$ 0.02 (29) <sub>B4</sub>	-0.001 $\pm$ 0.024 (29) <sub>B3</sub>	-0.06 $\pm$ 0.02 (27) <sub>C5</sub>

587

**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.

	<b>Species</b>		<b>Colony</b>		<b>Species*colony</b>	
	<b>H</b>	<b><i>p</i></b>	<b>H</b>	<b><i>p</i></b>	<b>H</b>	<b><i>p</i></b>
Maximum bill depth	58.2	<0.001	103.8	<0.001	138.0	<0.001
Bill depth at nares	70.2	<0.001	26.2	<0.001	96.4	<0.001
Culmen length	79.4	<0.001	68.0	<0.001	96.4	<0.001
Dorsal-RW1	93.8	<0.001	70.7	<0.001	160.2	<0.001
Dorsal-RW2	101.0	<0.001	92.2	<0.001	152.4	<0.001
Profile-RW1	189.3	<0.001	56.2	<0.001	195.9	<0.001
Profile-RW2	70.7	<0.001	139.4	<0.001	157.3	<0.001