1　**Ecological segregation of two superabundant, morphologically similar,**

2　**sister seabird taxa breeding in sympatry**

3

4　Christopher W. Jones[1*], Richard A. Phillips[2], W. James Grecian[3] and Peter G. Ryan[1]

5

6　[1]FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of

7　Cape Town, Rondebosch, 7701, South Africa

8　*Corresponding author: chrisj22123@gmail.com

9　[2] British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley

10　Road, Cambridge CB3 0ET, U.K.

11　[3] Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St

12　Andrews KY16 8LB, U.K.

13

14 **ABSTRACT**

15 Prions *Pachyptila* are the most abundant seabirds in the Southern Ocean and comprise two

16 main groups: those with and without bill lamellae to filter zooplankton. With few exceptions,

17 each breeding location supports at most one species from each of these groups. However,

18 Gough Island supports two morphologically very similar, filter-feeding species: broad-billed

19 *P. vittata* and MacGillivray's prions *P. macgillivrayi*. To understand how these two species

20 co-occur in sympatry, we compared the foraging ranges, habitat selectivity, trophic

21 segregation and moult schedules of these species using combined geolocation-immersion

22 loggers. After breeding, both species showed a well-defined westward migration prior to

23 moulting. Moult lasted 11 to 19 weeks and was significantly longer in MacGillivray's than

24 broad-billed prions. Moulting birds occurred in specific areas within the Argentine Basin,

25 with little overlap between the two species. Habitat analysis revealed species-specific

26 preferences, in particular sea surface temperature. Activity patterns also differed;

27 MacGillivray's prions spent more time in flight, which indicates a more active foraging

28 strategy, relying less on filter feeding. Stable isotope ratios (δ^{15}N) in flight feathers were

29 greater in MacGillivray's prion, which is consistent with its less specialized bill morphology

30 resulting in feeding at a higher trophic level. Inter-specific spatial segregation was observed

31 for most of the tracking period, in large part because broad-billed prions breed roughly 3

32 months earlier than MacGillivray's prions. At Tristan da Cunha, 250 km farther north, where

33 only broad-billed prions breed, they departed, moulted and returned significantly later (15-17

34 days) than conspecifics from Gough Island, providing evidence for character displacement in

35 sympatry with MacGillivray's prion.

36

37 Keywords: biologging, geolocation, character displacement, stable isotopes, moult,

38 allochrony, foraging ecology

INTRODUCTION

Spatial segregation is a key factor to reduce competition for food among seabirds (Furness and Birkhead 1984; Chesson 2000; Lewis et al. 2001). However, where there are few breeding sites, the main drivers of interspecific ecological segregation in seabirds may be differences in prey preferences, at-sea activity budgets or in the timing of breeding and moulting (Cherel et al. 2016; Whitehead et al. 2016; Taylor and Friesen 2017). In large parts of the Southern Ocean, there are very few islands where seabirds can breed. For example, in the South Atlantic Ocean, Tristan da Cunha group (37°S) and Gough Island (40°S) are the only islands between the Falklands (51°S) and tropical islands around 20°S (Trindade, Martim Vaz, St Helena and Ascension). This makes the four islands of the Tristan-Gough group the only breeding option for species foraging in temperate and sub-Antarctic waters in the central South Atlantic Ocean. As a result, these temperate South Atlantic islands support remarkable numbers of several seabird species, mainly Procellariiformes (petrels, shearwaters and albatrosses) (Ryan 2007). The procellariiforms are among the longest ranging seabirds, and have several adaptations that permit them to efficiently utilize distant foraging areas (Phillips and Hamer 1999; Weimerskirch et al. 2000).

In birds, breeding, migration, and moult all increase energy demands. When no longer restricted to operate as central-place foragers by breeding duties, many seabirds migrate to more productive foraging zones in order to moult and build up body condition for the next breeding attempt (Phillips et al. 2006; Grecian et al. 2016a). Resource availability and decisions made during the non-breeding period therefore affect population dynamics, including survival and subsequent breeding success (Grosbois and Thompson 2005; Schroeder et al. 2009). However, information on the non-breeding period, including the location and habitat characteristics of core foraging and moulting, and at-sea activity patterns are lacking for many small species of seabirds.

The prions (*Pachyptila* spp.) are the most abundant seabirds in the Southern Ocean. Their taxonomy is still debated, but most authorities recognise 6-7 species (Marchant and Higgins 1990; Brooke 2004). They are similar in plumage and general structure, making them very difficult to identify at sea (Onley and Scofield 2007; Shirihai 2007), and as a result their foraging distributions are poorly known. The species differ mainly in bill structure, which shows increasing specialisation from the narrow bills of the slender-billed prion *P. belcheri* and the fairy prion complex *P. turtur/crassirostris*, to the broad, lamellae-fringed bills adapted for filtering small crustaceans and other zooplankton, found in the so-called 'whalebirds' (Warham 1990). As such, the prions provide a useful group for investigating

73 niche partitioning and community structure (Bretagnolle et al. 1990; Cherel et al. 2002;
74 Quillfeldt et al. 2013).

75   The seemingly unlikely finding that two very morphologically similar species of prion
76 co-exist in large numbers at the same breeding island (Ryan et al. 2014, Jones 2018) provides
77 the basis for this study. Generally, prions breeding in sympatry tend to differ in bill structure,
78 allowing them to occupy different niches by reducing dietary overlap. For example, at islands
79 around New Zealand, broad-billed prions *P. vittata* (bill width: 20-24.5 mm) breed
80 sympatrically with fairy prions (bill width: 10-12 mm). Similarly at the Prince Edward and
81 Crozet island groups, there are breeding Salvin's prion *P. salvini* (bill width: 14-19 mm) and
82 fairy prions (Bretagnolle et al. 1990; Marchant and Higgins 1990). Until recently, the only
83 island group where two species of whalebirds (i.e. prions with filtering lamellae) were known
84 to breed was the Crozet Islands, where small numbers of Antarctic prions *P. desolata* (bill
85 width: 12-16 mm) breed alongside much larger numbers of Salvin's prions (Bretagnolle et al.
86 1990). Antarctic Prions also breed with slender-billed prions (bill width: 9-12 mm) at the
87 Kerguelen archipelago (Quillfeldt et al. 2015b; Cherel et al. 2016), and in both cases there is
88 allochrony, i.e., temporal segregation in the time of breeding and moult (Bretagnolle et al.
89 1990; Cherel et al. 2016). Thus the co-occurrence of hundreds of thousands of breeding
90 broad-billed and MacGillivray's *P. macgillivrayi* (bill width: 15.5-20.5 mm) prions at Gough
91 Island (Birdlife International 2017) is unusual and begs further investigation.

92   Recent technological advances have reduced the size, mass and cost of bird-borne
93 dataloggers, allowing an increasing number of studies to examine the spatial distribution and
94 activity patterns of the smaller petrels (Procellariidae), including prions (Navarro et al. 2013;
95 2015; Quillfeldt et al. 2013; 2015a; 2015b; Cherel et al. 2016; Grecian et al. 2016b).
96 Geolocation and feather stable isotope data from previous studies in the southwest Atlantic
97 have found evidence for spatial segregation among seabirds (Cherel et al. 2006; Quillfeldt et
98 al. 2008; Quillfeldt et al. 2013; Cherel et al. 2014; Phillips et al. 2009). The two prion species
99 breeding in sympatry at the Kerguelen archipelago are similar in size and possibly certain
100 feeding methods (Cherel et al. 2002) and segregate at large spatial scales during the non-
101 breeding period (Quillfeldt et al. 2015b; Cherel et al. 2016). However, the two prion species
102 that breed sympatrically on Gough Island are more similar morphologically than other prion
103 species compared in previous tracking studies, and the degree of niche segregation is
104 unknown.

105   We examine the factors that may explain how two closely-related and
106 morphologically-similar prion species are able breed in sympatry at high densities. We

107   deployed geolocators (Global Location Sensor or GLS loggers) and sampled feathers to

108   investigate the movements, activity patterns (time spent in flight and on the water), habitat

109   preferences and isotopic niche of the two species in sympatry, and compared these data with

110   birds from Tristan da Cunha, 250 km farther north, where only broad-billed prions breed

111   (Ryan et al. 2014). We also report differences in bill morphology between the two species,

112   given the implications for prey selection and hence trophic level. The comparison between

113   the two species is pertinent for understanding niche partitioning and ecological segregation

114   between abundant, closely related seabirds.

115

116   **METHODS**

117   Fieldwork was carried out at the main island of Tristan da Cunha (hereafter Tristan; 37.07°S;

118   12.32°W) and Nightingale Island (approx. 30 km to the south-southwest) where only broad-

119   billed prions breed, and at Gough Island (40.32°S; 9.94°W) where broad-billed and

120   MacGillivray's prions breed sympatrically. Breeding is highly synchronous within species,

121   but MacGillivray's prions breeds c. 3 months later; broad-billed prions lay from late August

122   to early September and chicks fledge in December, whereas MacGillivray's prions lay from

123   late November to early December and chicks fledge in February-March (Ryan et al. 2014).

124   Both species return to their nest sites after breeding, around February-March for broad-billed

125   prions (Ryan 2007) and July-August for MacGillivray's prions (Jones 2018). Information on

126   their moult phenology of prions is scarce (Marchant and Higgins 1990). Adult prions undergo

127   a complete moult of their flight feathers, but the timing of moult within the non-breeding

128   period varies among species. Most species have a rapid moult shortly after breeding, which is

129   associated with a period of reduced flight activity (Cherel et al. 2016). Primary feathers are

130   replaced from the innermost (P1) to the outermost (P10) (Bridge 2006), with up to 4 inner

131   primaries and 2-3outer primaries replaced at the same time (PGR unpubl data). Observations

132   of adults in fresh plumage when they return to the colony a few months after breeding

133   indicate that broad-billed prions replace all primary, secondary and tail feathers during the

134   initial post-breeding exodus (Ryan 2007).

135   In order to investigate the relationships between trophic level, other aspects of

136   foraging strategies and bill morphology, the number of palatal lamellae was counted with a

137   dissecting microscope from birds killed by brown skuas *Catharacta antarctica* on Gough

138   Island, and compared with Salvin's prions from Marion Island. Bill width and culmen length

139   were measured using Vernier callipers to the nearest 0.1 mm (following Ryan et al. 2014).

140

Geolocators

Combined geolocator-immersion loggers (model C65; Migrate Technology Ltd., Cambridge)
weighing approximately 1 g (< 1% of the average body mass for both species, ~150-230 g)
were deployed on a plastic leg ring, and a numbered steel ring was put on the other leg. At
Gough Island, loggers were deployed on 18 broad-billed prions breeding in burrows at 250 m
above sea level and in a small cave in the sea cliffs near the meteorological station from 19-
21 September 2014. Fifteen MacGillivray's prions breeding in 'Prion Cave' (50 m elevation)
were tagged during incubation from 25 November–3 December 2014. At Tristan, loggers
were deployed on 15 broad-billed prions attending chicks in a cave accessible only from the
sea under the Hillpiece on 4 November 2014. Birds were captured by hand, their nests
marked and only on Gough Island was breeding performance monitored in conjunction with a
sample of control nests (birds not equipped with loggers). Breeding sites were revisited and
most devices retrieved in the following breeding season, with some loggers from
MacGillivray's prion being retrieved prematurely during their pre-breeding return and thus
were not tracked for a whole year (**Table 1**).

Stable isotope analysis

Small portions of primary feathers were collected from logger-equipped birds at recapture in
2015. In addition, feather samples were collected in September-October 2013 from 24 birds
of each species found dead on Gough Island, and from 20 broad-billed prions found dead on
Nightingale Island. These were fully grown (i.e. not fledglings), killed by skuas before or
during the breeding season. In each case, approximately 10 mm was cut from the tip of
primary feather P1 (GLS birds) or P2 (dead birds), and similar-sized sections of the basal part
of the inner vane of primaries P5 and P9 were collected in order to gather sequential isotopic
information over primary moult. Only P1 was collected from one of the individuals from
which a logger was retrieved at Tristan. Feather samples were placed in plastic bags and
stored frozen until analysis.

Feather sample preparation and isotopic analysis were performed at the Stable Light
Isotope Unit, University of Cape Town, South Africa. Each feather sample was cleaned of
surface lipids and contaminants using 2:1 chloroform: methanol solution for 2 min followed
by two successive methanol rinses and then by two distilled water rinses (a few seconds each
rinse). Feather samples were then oven dried at 40°C for 48 hours and homogenized by
cutting into small fragments. Sub-samples (~0.4 mg) were weighed in tin cups with a micro
balance (Sartorius M2P). Carbon and nitrogen isotope ratios were determined using

175   established methods, by combusting samples in a Flash 2000 organic elemental analyzer and

176   passing gasses through a Delta V Plus isotope ratio mass spectrometer via a Conflo IV gas

177   control unit (Thermo Scientific). Conventional notation was used when expressing isotopic

178   signatures ($\delta X = [R_{sample}/R_{standard}) - 1] \times 1000$) where X is ^{13}C or ^{15}N, R is the corresponding

179   ratio ^{13}C/^{12}C or ^{15}N/^{14}N and $R_{standard}$ is Vienna Pee-Dee Belemnite and atmospheric N_2 for

180   δ^{13}C and δ^{15}N, respectively. Replicate measures of internal laboratory standards were used to

181   correct for any instrument error. Indicated measurement errors ($\pm$ 1 SD) of standards were as

182   follows: Merck gel - δ^{13}C = 0.17‰, δ^{15}N = 0.07‰, valine - δ^{13}C =0.18‰, δ^{15}N =0.11‰ and

183   seal bone - δ^{13}C = 0.19‰, δ^{15}N = 0.06‰. Internal laboratory standards used for replicate

184   measurement were calibrated against International Atomic Energy Agency standards.

185

186   **Data processing and analysis**

187   Tracking data covered the period September 2014 to September 2015 for broad-billed prions

188   and December 2014 to November 2015 for MacGillivray's prions (i.e. one annual cycle per

189   species). Geolocators provide two position estimates per day based on light levels; positions

190   have an associated error of approximately 186 $\pm$ 114 km (Phillips et al. 2004). Light data

191   were processed using Intiproc v1.03 software (Migrate Technology Ltd.) by checking for the

192   integrity of light curves and marking dawn and dusk times; latitude was estimated from day

193   length and longitude from the time of local mid-day relative to Greenwich Mean Time. A sun

194   elevation angle of -6° was used, based on positions obtained during calibration of the loggers

195   at the colony before and after each deployment. All estimated locations were examined in

196   QGIS v3.6 (Free Software Foundation, Boston) and any erroneous positions, either associated

197   with interference to light curves at dawn or dusk, or within 2-3 weeks of the equinoxes when

198   latitudes are unreliable, were excluded from further analyses. The unfiltered data were used

199   to obtain information about longitudinal movements, as return migration in some individuals

200   occurred around the equinoxes. After processing, 7011 and 4128 locations were retained for

201   broad-billed and MacGillivray's prions, respectively (approximately 80% of the original

202   location estimates).

203   The loggers tested for saltwater immersion every 6 s. The number of positive tests

204   was recorded for each 5-min period, providing a value that ranged from 0 (continuously dry)

205   to 50 (continuously wet). Each 5-min period was categorised as daylight or darkness using

206   sunset and sunrise times estimated from the thresholds in light curves recorded by the logger.

207   Using established methods (Phillips et al. 2007b; Catry et al. 2009; Grecian et al. 2016b), the

208   activity data were integrated with a custom script using R v. 3.5.0 (R Core Team 2018) that

209 provided summaries of the daily proportion of time spent flying during daylight and darkness,

210 and the total time spent per day (consecutive light and dark period) in flight and on the water.

211 The duration and number of flight bouts per day were also calculated; where flight bouts

212 were defined as any continuous sequence of 5-min periods in which the logger was

213 completely dry (i.e. 0 values). This method is likely to underestimate the number of flight

214 bouts, as birds may engage in several short flights within 5 minutes. However, Phalan et al.

215 (2007) found a close correlation between number of bouts derived from lower and higher

216 resolution loggers, indicating that bouts are adequate as proxies of activity

217   Prions are sexually monomorphic and feeding behaviour is not linked to sex

218 (Quillfeldt et al. 2013; Cherel et al. 2016), so data from males and females were pooled. Data

219 were split into breeding, non-breeding and pre-laying exodus periods (**Table 2**). The non-

220 breeding period was considered to be the period from the date that an individual moved > 500

221 km from the colony with a clear pattern of outward movement, to the first date that an

222 individual spent in a nesting burrow upon returning to the breeding colony, based on light and

223 activity data (Grecian et al. 2016b). The pre-laying exodus was defined as the time between

224 the last day in a burrow during the pre-breeding occupation of burrows and the first day in a

225 burrow prior to laying. The non-breeding period was divided into moulting and non-moulting

226 periods based on immersion data. Prions have reduced flight ability during moult, and start

227 and end dates of moult for each tracked individual were determined from the marked

228 decrease in flight activity at its onset, and the sharp increase when moult presumably was

229 more or less complete (Cherel et al. 2016). At-sea activity characteristics were compared

230 between species and between daylight and darkness (**Table S1**).

231   Foraging distributions were inferred from 90% (general use) and 50% (core)

232 utilization distributions (UDs) for each individual using kernel analysis with a fixed

233 smoothing parameter of 200 km (Phillips et al. 2006). UDs were also generated at the species

234 level for various stages of the annual cycle (breeding, moulting, non-moulting, pre-laying

235 exodus, etc.). Kernel analyses were performed in a Lambert equal-area azimuthal projection

236 centred on the core range (45ºS and 20ºW) using QGIS v3.6 and the Heatmap plugin.

237 Overlap in monthly foraging distribution between species was estimated using

238 Bhattacharyya's affinity (BA) where 0 equates to no overlap and 1 to complete overlap in

239 UDs. We estimated a null distribution of BA values by randomly reassigning species among

240 the tracked individuals 10000 times and calculated p-values as the proportion of random

241 assignment BA values that were smaller than the observed BA estimate. To test the degree of

242 spatial overlap in the absence of allochrony we repeated this process with a three month lag.

243

Environmental data

Habitat analysis followed the methods described by Grecian et al. (2016b). Bathymetry data were extracted at 1 minute resolution from the ETOPO1 database (Amante and Eakins 2009) and global monthly chlorophyll a (CHL) and monthly sea surface temperature (SST, 11 μ night-time) composite data at 4 km^2 resolution were extracted from the MODIS instrument on the Aqua (EOS PM) satellite (http://oceancolor.gsfc.nasa.gov/). Distance to seamounts was determined using the Global Seamount Database (Wessel 2001). Distance to breeding colony was also included as preference is a function of availability (Matthiopoulos 2003). All data were projected in a custom Lambert Azimuthal Equal Area projection centred on 45°S and 20°W.

An availability approach was used to examine habitat preference, which compared presences (from the geolocation data) with pseudo-absences generated randomly from across the species range at a 5:1 absence to presence ratio. To incorporate the error associated with geolocation, 50 random points were generated around each presence or pseudo-absence from a bivariate Gaussian distribution with a mean and standard deviation that approximated geolocation error (Phillips et al. 2004). The mean of each environmental variable from the 50 random points was used in subsequent analyses (Grecian et al. 2016b). The relationship between prion presence-absence and environmental covariates was examined using binomial generalized additive mixed models (GAMMSs) fitted with the package mgcv (Wood 2006) in R v. 3.5.0 (R Core Team 2018). Model estimates were assessed on the exponential scale due to the use of pseudo-absences (Boyce & McDonald 1999). Distance to colony, depth, SST, CHL and distance to seamount were included as covariates in the global model, and cubic regression splines fitted with a maximum of 5 knots; superfluous knots were penalized during model fitting. CHL was $\log_{10}$ transformed prior to inclusion. An individual-level random effect was included as a spline term (Pedersen et al. 2019). Each covariate was first fitted with species as an interaction, and then compared against a model without the species interaction. Model selection was based on Akaike's Information Criterion (AIC), with species interaction dropped if its inclusion did not improve the model by more than 2 ΔAIC relative to the lowest AIC. Variance inflation factors revealed no multicollinearity between covariates (VIFs < 3) and variograms of model residuals did not reveal any problems with spatial autocorrelation in final models.

Statistical Analysis

Data on timing of movements, activity patterns and stable isotope ratios were all normally distributed and parametric tests were used. Univariate statistical tests were conducted using XLSTAT v2018.1 (Addinsoft SARL, Paris). Data are shown as means ± SD unless otherwise indicated.

RESULTS

Thirteen devices (39%) were recovered from broad-billed prions: 9 from Gough (50% of those deployed) and 4 from Tristan (27%), and 8 devices (53%) were recovered from MacGillivray's prions at Gough (Table 1). Hatching success in 2014 of equipped birds at Gough Island (46% overall; 7 of 15 MacGillivray's prions and 8 of 18 broad-billed prions) was similar to control birds (41%, n=44 MacGillivray's prions). No chicks fledged from any study nests on Gough Island due to predation by introduced house mice *Mus musculus* (Dilley et al. 2015). No data on breeding performance was available at Tristan because the study site was very difficult to access.

Table 1 Details of geolocator-immersion logger deployments, recovery rates and feather sampling of broad-billed and Macgillivray's prions at Tristan da Cunha and Gough Island from 2013 to 2015. Some Macgillivray's prions were recaptured before the pre-laying exodus

Species	Loggers		Tracks				Primary feathers collected	
	Deployed	Retrieved	Breeding	Moult	Non-Breeding	Pre-laying	Tracked	Untracked
	n	n (%)	n	n	n	n	n	n
Broad-billed prion (Tristan)	12	4 (33)	4	4	4	4	4	20
Broad-billed prion (Gough)	18	9 (50)	9	9	9	9	9	24
Macgillivray's prion	15	8 (53)	8	8	8	3	8	24

Breeding and migration schedule

The annual cycle of the equipped birds was in accordance with the known breeding and migration schedules of the two species (**Table 2**). Post-breeding departure dates of adult broad-billed prions were from late October to November, and arrival was in July. Birds from Tristan departed and returned on average 15 and 17 days later, respectively, than conspecifics at Gough Island. MacGillivray's prions left the colony in late January to early February, on average 91 days later than broad-billed prions from Gough Island. Breeding failure of all equipped individuals from Gough Island is likely to have advanced their departure date from the colony. Both species returned to burrows, or, in one case, at least to waters around the colony, for short periods in the immediate post-breeding period. Prolonged dark periods in the light data indicate that 12 of 13 broad-billed prions spent 1–7 days in burrows at the colony from 2 February to 18 March at Gough Island and 27 February to 10 April at Tristan. One broad-billed prion from Gough Island apparently did not spend a day ashore in a burrow but did return to the vicinity of the island, possibly coming ashore at night. All eight MacGillivray's prions spent 1–7 days in burrows from 30 June to 16 September. The length of the non-breeding period did not differ significantly between species or populations (**Table 2**). After returning to their respective colonies, all three MacGillivray's prions that were tracked for a year, and 12 of 13 (92%) broad-billed prions that returned to breed in 2015, engaged in a pre-laying exodus. Broad-billed prions from Tristan returned to the colony and started their pre-laying trip significantly later than conspecifics from Gough Island; however the onset of breeding did not differ because the birds from Tristan had shorter pre-laying trips (**Table 2**). The length of the pre-laying exodus did not differ significantly between MacGillivray's and broad-billed prions from Tristan, although this may be an artefact of the small sample size for MacGillivray's prions.

314 **Table 2** Summary of the main features of the annual cycle of broad-billed (BBP) and

315 MacGillivray's prions (MP) tracked from Gough and Tristan da Cunha in 2014-2015. Values

316 are means ± SD. Values not sharing the same superscript letter are significantly different at *p*

317 < 0.05 (ANOVA, posthoc Tukey's HSD multiple comparison tests)

318

	BBP Gough	BBP Tristan	MP Gough	ANOVA results
Non-breeding period	**n=9**	**n=4**	**n=8**	
Departure date	29 Oct 2014 ± 11[a]	13 Nov 2014 ± 10[b]	28 Jan 2015 ± 7[c]	$F_{2,18}$=203.1, p<0.001
Return date	10 Jul 2015 ± 7[a]	27 Jul 2015 ± 17[b]	12 Oct 2015 ± 8[c]	$F_{2,18}$=211.0, p<0.001
Duration (days)	254 ± 15	256 ± 23	257 ± 15	$F_{2,18}$=0.08, p=0.924
Total distance (km)	36872 ± 3238	37833 ± 6411	41679 ± 8930	$F_{2,18}$=1.1, p=0.352
Max. distance from colony (km)	2957 ± 396[a]	3126 ± 254[ab]	3468 ± 87[b]	$F_{2,18}$=6.7, p=0.007
Travel speed (km.day^{-1})	145 ± 13	147 ± 12	161 ± 25	$F_{2,18}$=1.8, p=0.199
Moulting period	**n=9**	**n=4**	**n=8**	
Start date	09 Nov 2014 ± 4[a]	27 Nov 2014 ± 10[b]	04 Feb 2015 ± 7[c]	$F_{2,18}$=400.7, p<0.001
End date	12 Feb 2015 ± 11[a]	03 Mar 2015 ± 4[b]	30 May 2015 ± 13[c]	$F_{2,18}$=212.5, p<0.001
Duration (days)	95 ± 8[a]	96 ± 8[a]	115 ± 10	$F_{2,18}$=11.4, p=0.001
Latitude centroid (S°)	39.4 ± 0.8[a]	40.3 ± 0.3[a]	44.6 ± 0.8[b]	$F_{2,18}$=108.9, p<0.001
Longitude centroid (W°)	25.4 ± 19.8[a]	36.5 ± 5.4[ab]	43.2 ± 2.5[b]	$F_{2,18}$=3.8, p=0.043
Post-moult colony visit	**n=9**	**n=4**	**n=8**	
Return date	22 Feb 2015 ± 15[a]	10 Mar 2015 ± 11[a]	23 Jul 2015 ± 16[b]	$F_{2,18}$=250.3, p<0.001
Departure date	11 Mar 2015 ± 14[a]	30 Mar 2015 ± 15[a]	31 Aug 2015 ± 14[b]	$F_{2,18}$=352.3, p<0.001
Total duration (days)	17 ± 19	20 ± 18	40 ± 24	$F_{2,18}$=2.7, p=0.094
Time in burrow (days)	3 ± 3	3 ± 2	5 ± 2	$F_{2,18}$=1.4, p=0.268
Pre-breeding period	**n=8**	**n=4**	**n=3**	
Pre-breeding arrival date	10 Jul 2015 ± 7[a]	27 Jul 2015 ± 17[b]	12 Oct 2015 ± 8[c]	$F_{2,18}$=211.0, p<0.001
Pre-laying exodus departure	28 Aug 2015 ± 9[a]	21 Aug 2015 ± 7[b]	04 Nov 2015 ± 2[c]	$F_{2,12}$=190.7, p<0.001
In burrow (days)	4 ± 3	6 ± 2	6 ± 5	$F_{2,13}$=1.1, p=0.350
Pre-lay exodus duration (days)	30 ± 16[a]	18 ± 4[ab]	21 ± 6[b]	$F_{2,13}$=4.6, p=0.032
Return from pre-laying exodus	01 Sep 2015 ± 9[a]	08 Sep 2015 ± 7[a]	26 Nov 2015 ± 3[b]	$F_{2,13}$=128.9, p<0.001

Spatial distribution

The two species showed a high degree of spatial segregation at sea, with the observed BA being significantly lower than the null expectation for most months of the year (**Fig. S1, Table 3**). Overlap was highest in June and October (BA = 0.66, p = 0.05 and BA = 0.77, p = 0.09, respectively). June is when MacGillivray's prions have completed moult and are returning to the colony and broad-billed prions depart the colony after their short post-moult visit. October is when both species are near their breeding colonies during the pre-breeding or breeding phases (**Table 3**). However, there was less evidence of spatial segregation when distributions were compared in the absence of temporal segregation; the observed BA was significantly higher than the null expectation for most months (**Fig. 1, Table 3**). This indicates that the two species would overlap in space for most of their annual cycles if they did not segregate their annual phenology.
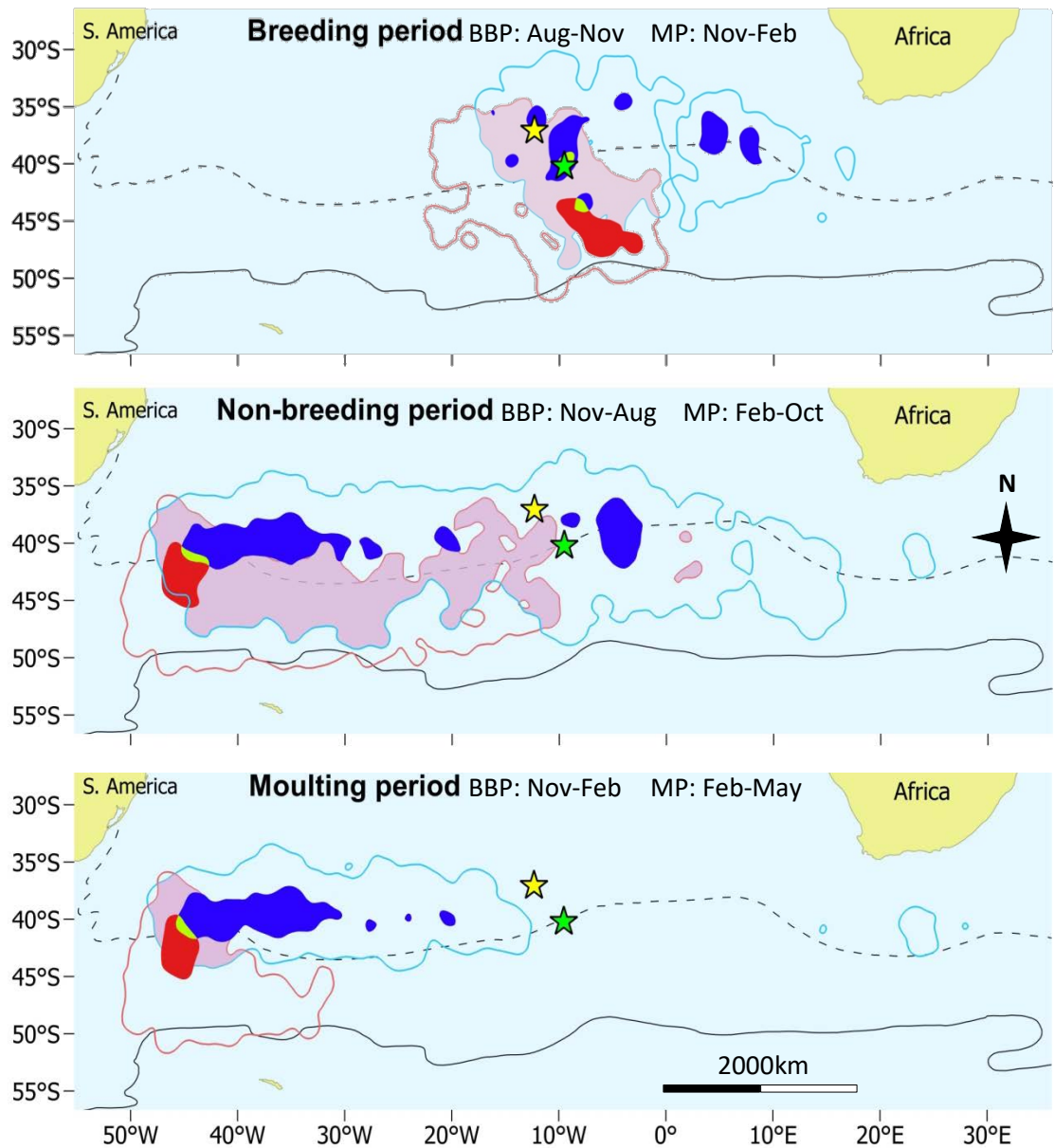
Breeding period

Both species mostly remained within 1000–1500 km of their colonies during their breeding seasons. Breeding broad-billed prions mostly remained in the vicinity of Tristan da Cunha and Gough Island or foraged in sub-tropical waters north-east of the islands toward South Africa, whereas MacGillivray's prions tended to forage farther south in sub-Antarctic waters. However, in the absence of temporal segregation, spatial overlap was high (**Fig. 1**).

Non-breeding period

Both species showed a well-defined outward migration (the period between departure from the colony and the start of moult), lasting 11 ± 9 days for broad-billed prions and 7 ± 7 days for MacGillivray's prions. All individuals of both species migrated west, except one broad-billed prion from Gough Island which migrated southeast. The ranges of two species largely overlapped in the absence of temporal segregation (**Fig. 1**), although MacGillivray's prions moved farther west and marginally farther south than broad-billed prions (**Fig. 1**). Neither species displayed a rapid, directed return migration to their breeding ground in late winter, instead returning to the vicinity of the breeding islands over several weeks.

Fig. 1 Utilisation distributions (UDs) of broad-billed (BBP, blue) and MacGillivray's prions (MP, red) tracked in 2014/15 during the breeding, non-breeding and moult periods in relation to the Sub-tropical Front (dashed line) and Antarctic Polar Front (solid line). The solid fill is the 50% UD (core area), and the outer polygons are the 90% UD (area of general use). Purple and green shades are the species overlap at the 90% and 50% UD, respectively. Yellow star = Tristan da Cunha; green star = Gough Island

357 **Table 3** Estimated monthly spatial overlap (Bhattacharyya's affinity, BA) in kernel
358 utilisation distributions between broad-billed and MacGillivray's prions tracked using
359 geolocators from Tristan da Cunha and Gough Island in 2014 to 2015, showing both the
360 observed overlap, and the overlap if there were no difference in the timing of the annual cycle
361 (broad-billed prions lagged by 3 months). *P*: the proportion of randomised overlaps that were
362 smaller than the observed overlap

| Month	Observed spatial overlap		Lagged spatial overlap	
	BA	*P*	BA	*P*
January	0.295	0	0.231	0
February	0.446	0	0.339	0
March	0	0	0.348	0.03
April	0.212	0	0.719	0.722
May	0.640	0.005	0.712	0.991
June	0.660	0.049	0.534	0.183
July	0.267	0	0.751	0.894
August	0.517	0	0.390	0.518
September	0.336	0	0.531	0.973
October	0.772	0.091	0.458	0.316
November	0.475	0.001	0.411	0
December	0.162	0	0.368	0.098

363

364 **Timing and location of moult**
365 Throughout the tracking period, broad-billed prions spent $43.2 \pm 5.5\%$ and MacGillivray's
366 prions $46.1 \pm 5.1\%$ of time in flight per day. However, in the early post-breeding period, both
367 species showed a sharp decline in the proportion of each day spent in flight, presumably
368 coinciding with the onset of primary moult (**Fig. 2**). During moult, the proportion of time in
369 flight per day decreased to $19.7 \pm 3.0\%$ and $23.5 \pm 4.7\%$ for broad-billed and MacGillivray's
370 prions, respectively. The duration of moult was similar for broad-billed prions from Gough
371 Island (95 ± 8 days) and Tristan (96 ± 8 days), but the former started moult 2.5 weeks earlier
372 (9 November ± 4 days vs. 27 November ± 10 days; **Table 2**). MacGillivray's prions started
373 moult 2-3 months later (4 February ± 7 days), and took on average 20 days longer (115 ± 10
374 days, **Table 2**). Broad-billed prions reoccupied burrows 8 ± 8 days after moult ended,

375   whereas MacGillivray's prions spent substantially more time at sea before they returned to
376   their nests for the non-breeding season visit (53 ± 12 days).
377   Broad-billed prions moulted mostly in subtropical waters, whereas MacGillivray's
378   prions moulted farther south and west in sub-Antarctic waters (**Fig. 1**, **Table 2**). Spatial
379   segregation was more pronounced during moult than the remainder of the non-breeding
380   period (**Fig. 1**).
381
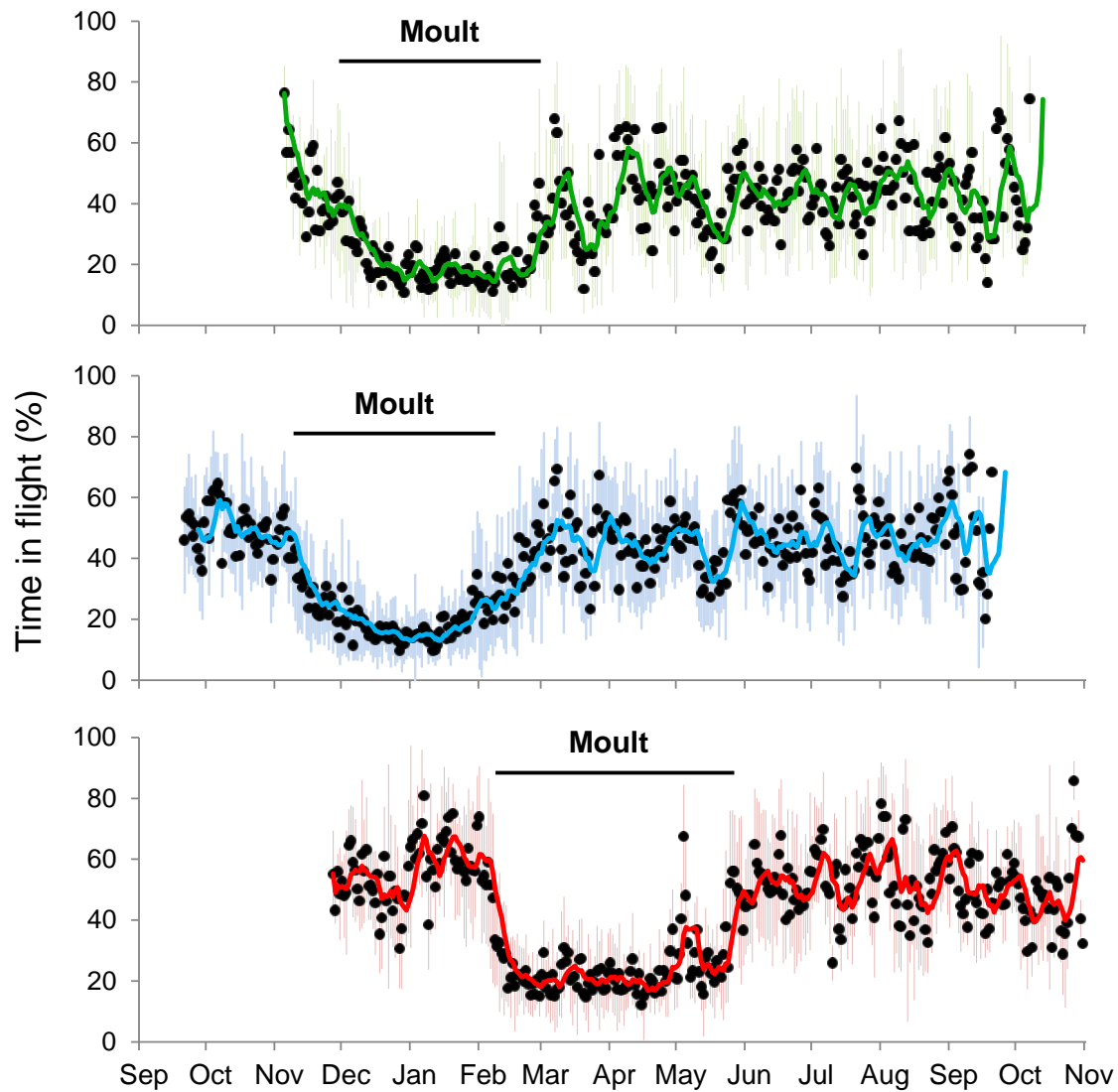
382
383   **Fig. 2** Time spent in flight (%) over the annual cycle based on immersion data from broad-
384   billed prions from Tristan (green) and Gough (blue), and MacGillivray's prions (red) tracked
385   in 2014 to 2015. Trend line is the 7-day running average. Values are daily means ± SD
386

Activity patterns

There were no significant differences in activity patterns between broad-billed prions tracked from Gough Island and Tristan (**Table S1**). During the breeding period, MacGillivray's prions spent a greater proportion of time in flight overall (**Table S1**) and significantly more time flying (13.5 ± 1.0 h) than sitting on the water (10.5 ± 1.0 h; t-test t_{14}=6.4, p<0.001), whereas broad-billed prions spent equal time flying (11.9 ± 1.5 h) and on the water (12.1 ± 1.5 h; t-test, t_{22}=-0.6, p=0.524). However, the mean number of flight bouts per day or average bout duration did not differ significantly between the two species (**Table S1**). Both species spent proportionately similar time in flight during daylight and darkness (**Table S1**; t-test, BBP: t_{22}=-1.9, p=0.069; MP: t_{14}=-2.0, p=0.075).

During the non-breeding period, there were few inter-specific differences in time on the water, and only flight time and number of flight bouts during the day were significantly higher in MacGillivray's prions than broad-billed prions (**Table S1**). This pattern was broadly mirrored in the moult period, which represented ~35% of the non-breeding period (**Tables 2 and S1**). The decrease in flight time during moult was apparent during daylight and at night, but unlike in the breeding and non-moulting periods, both species appeared to spend proportionately more time on the water at night (**Table S1**). After moulting there were greater activity differences between the species; MacGillivray's prions spent more time in flight (overall, and in daylight and night) mainly due to a greater number of flight bouts, because flight bout duration did not differ significantly. Activity patterns in general were also broadly similar to those exhibited during the breeding period (**Table S1**).

Activity patterns of broad-billed prions did not change significantly from the post-moult non-breeding period to the pre-laying exodus and breeding periods (ANOVA, $F_{(4, 58)}$ =65.9, p=0.194). There were too few data for MacGillivray's prions (n=3) to make a meaningful comparison between the two species. Nonetheless, none of the activity parameters differed significantly between the two species during this period (**Table S1**). The few MacGillivray's prions sampled spent significantly less time in flight compared to breeding and post-moult non-breeding periods (ANOVA, $F_{(4, 30)}$ =73.9, p<0.001).

**Stable isotope ratios and bill morphology**

Isotopic data were obtained from 262 primary feathers from 88 individuals: 58 primaries from 21 tracked birds and 204 measurements from 68 other birds (**Table S2**). Considering the respective timing of moult for each species (see **Table 2**), P1 from MacGillivray's prions and P9 from broad-billed prions are replaced at roughly the same time (February). There was no

significant difference between $\delta^{13}C$ and $\delta^{15}N$ in P1 in MacGillivray's prions and P9 in broad-billed prions, in either the tracked or dead birds. There was a significant difference between dead birds sampled in 2013 and tracked birds sampled in 2015 in $\delta^{13}C$ for P5 in both species (t-test, BBP: t_{17}=-2.6, p=0.037; MP: t_{14}=3.4, p<0.001) and P1/P2 in broad-billed prions (t_{24}=-4.4, p<0.001). No differences were observed in $\delta^{15}N$ values between tracked birds and dead adults in either species (all p>0.05). Variability was low when comparing broad-billed prions from Nightingale and Gough Island (**Table S2; Fig. 3**). In addition, there was no significant difference in the $\delta15N$ values of feathers from equipped and control birds (killed by skuas) (**Table S2**). P1/2 and P5 of MacGillivray's prions had consistently higher $\delta^{15}N$ than those of broad-billed prions (**Table S2; Fig. 3**). Both species replaced primaries in subtropical to sub-Antarctic waters, characterised by $\delta^{13}C$ values between -19‰ to -16‰, which agrees with the tracking data (Phillips et al. 2009).

The number of palatal lamellae was significantly greater in broad-billed prions than MacGillivray's prions, and lowest in Salvin's prions (**Table S3**), with the number of lamellae increasing with bill width and culmen length (**Fig. S2**).
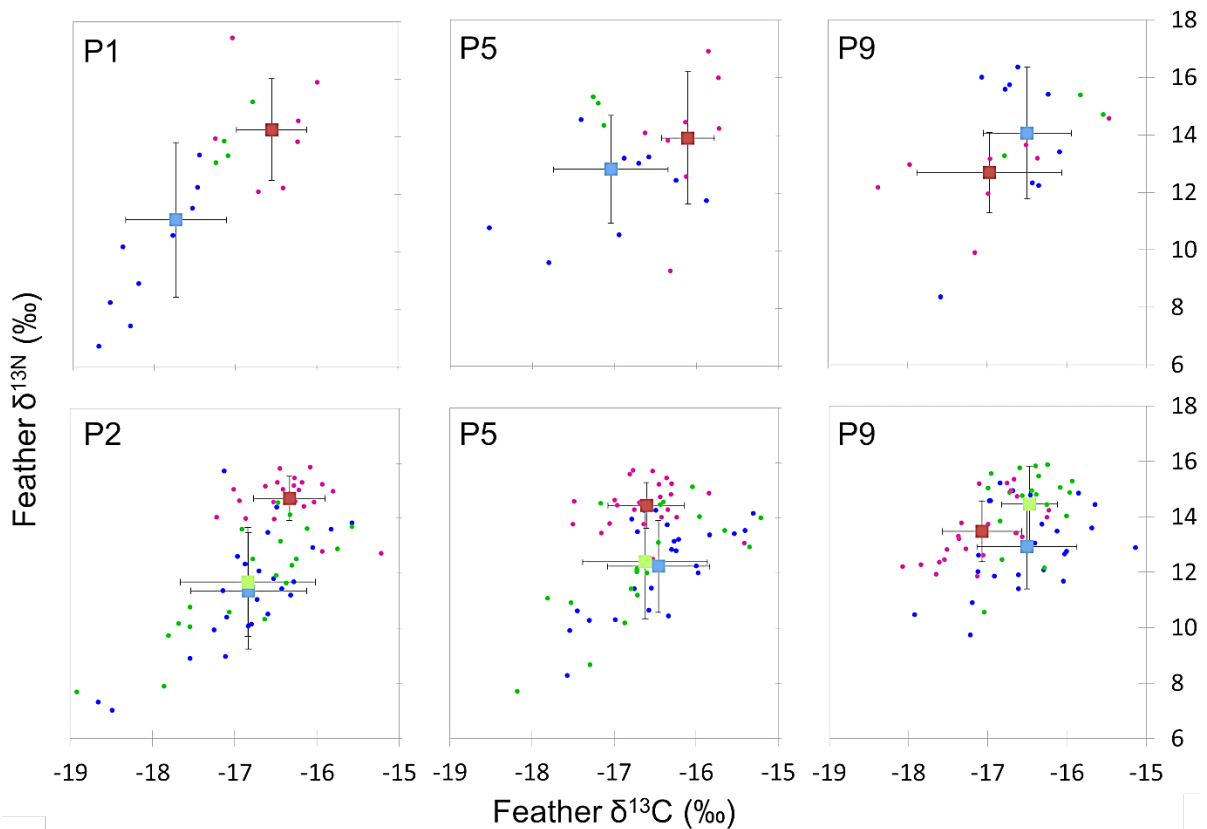
Fig. 3 Stable isotope ratios $\delta^{13}C$ and $\delta^{15}N$ in primary feathers (P1/2, P5, P9) of broad-billed prions from Gough (blue), Tristan/Nightingale (green) and MacGillivray's prions (red) that

440   were tracked in 2015 (top row) and dead prions collected in 2013 (bottom row). Dots are

441   individuals and squares with whiskers are group means ± SD for each species (top row) and

442   population (bottom row)

443

444   **Habitat preferences**

445   Habitat preferences during the non-breeding season differed between MacGillivray's and

446   broad-billed prions; the top-ranking model retained a species interaction for distance from the

447   breeding colony, chlorophyll *a*, distance to seamount and sea surface temperature, but not for

448   water depth (**Table S4**). Both species showed a preference for waters around 5000 m deep

449   (**Fig. 4**), and utilised areas within 1000 km from the breeding colonies and around 2500 km

450   from the breeding colonies. Both species showed a preference for areas of increased

451   productivity, but MacGillivray's were less likely to occur in areas of low CHL. Neither

452   species showed a preference for waters close to seamounts, but MacGillivray's were more

453   likely than broad-billed prions to occur further from seamounts. Broad-billed prions tended to

454   occur in waters of intermediate temperatures (10-20°C), while MacGillivray's prions showed

455   a preference for cooler waters (<10°C) and warmer waters (>20°C).

456

457
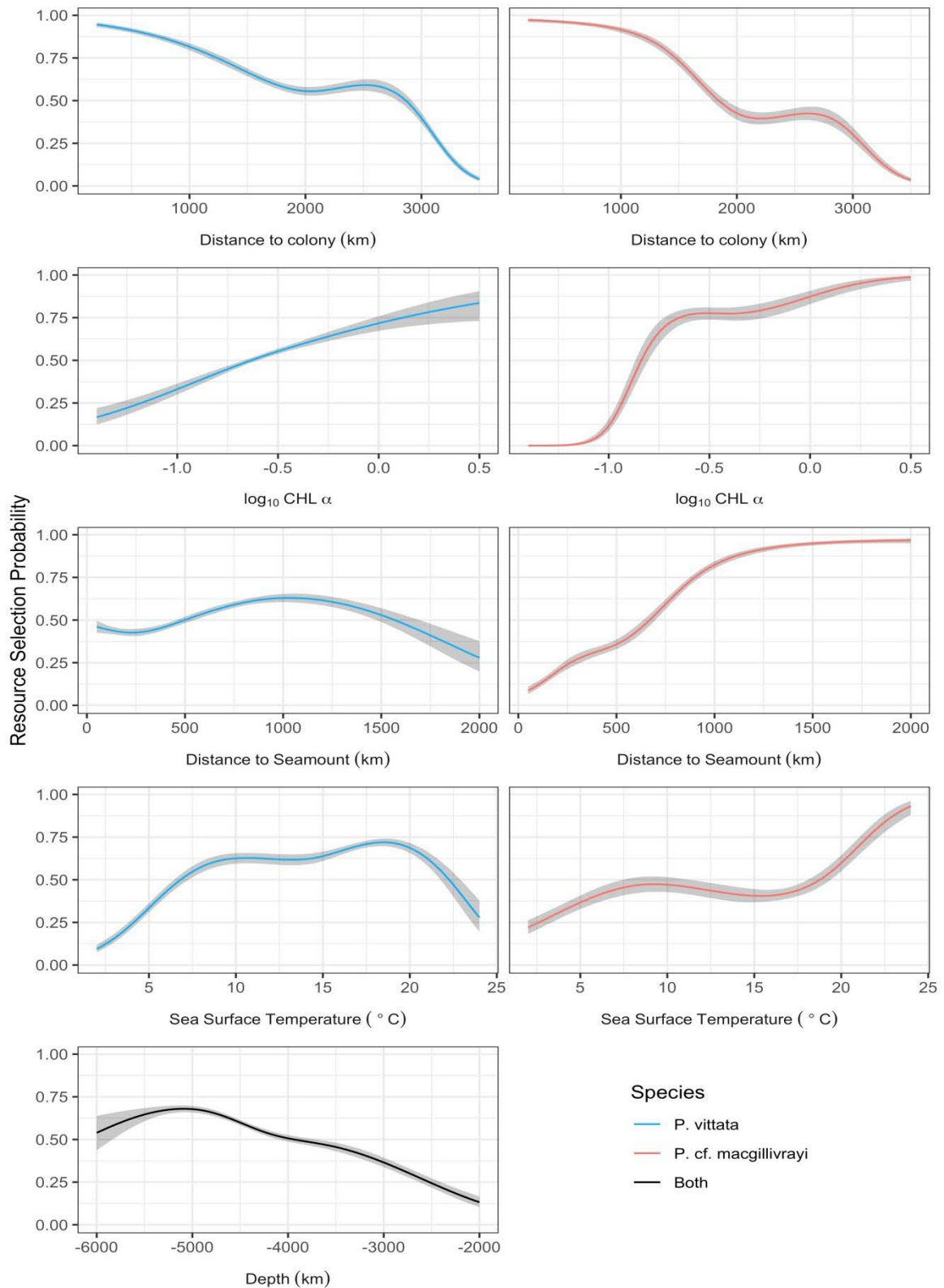
Fig. 4 Model estimated resource selection probability functions for broad-billed (blue) and MacGillivray's (red) prions. Solid line shows the mean estimated relationship and darker grey shaded area shows 95% confidence intervals

461

Discussion

Gough Island is seemingly unique in having two highly abundant, morphologically very similar prion species breeding together in similar proportions (Jones 2018). By combining tracking and stable isotope analyses we revealed the foraging strategies and ecological segregation of these prion species across different stages of their annual cycles. In addition, the analysis of activity data provided novel insights into the timing of moult. The relatively low logger recovery rate was attributable to a combination of complex burrow structure, which made it difficult to locate and access nest chambers at Gough, and logistical constraints that restricted the number of visits to the study site at Tristan da Cunha. However, sample sizes were nevertheless similar to tracking studies of this type (Phillips et al. 2007b; Navarro et al. 2013; 2015; Quillfeldt et al. 2013). The logger weighed <1% of body mass, which is well below the level (c. 3%) generally thought to affect flight ability (Phillips et al. 2003; Bodey et al. 2018). It is unlikely therefore that the behaviour of tracked individuals was compromised. Moreover, the similarity in feather isotope ratios of the tracked birds and a larger sample of birds sampled opportunistically (including in other years) indicate that tracked birds used the same water masses and maintained a similar diet during the moulting period as the wider population.

The tracked prions showed periods of marked reduction in flight activity, consistent with intense flight feather moult. Cherel et al. (2016) confirmed moult took place in the immediate post-breeding period in blue petrels *Halobaena caerulea* by matching at-sea activity data with observations of birds at colonies with fresh flight feathers, and subsequently inferred the timing of moult using activity data for Antarctic *P. desolata* and thin-billed prions. *P. belcheri* also undergoes a rapid post-breeding moult, but Antarctic prions migrate initially to sub-tropical waters and then have a more protracted moult which ends just before they return to their colonies. Neither species returns to the colony during the non-breeding period, and therefore only the blue petrel has a schedule similar to broad-billed and MacGillivray's prions.

Non-breeding MacGillivray's prions mainly occurred far west of Gough Island within the Argentine Basin in sub-Antarctic and mixed sub-Antarctic and sub-tropical waters between the Antarctic Polar Front (APF) and the Sub-tropical Convergence (STC). Zones within this oceanic region are productive because of eddies created where the warm waters of the south-flowing Brazil Current meet the northern extent of the Falklands Current (Phillips et al. 2007b; Baylis et al. 2019). In contrast, broad-billed prions occupied waters to the north and east of the core range of MacGillivray's prions, north of the sub-tropical convergence.

The tracked broad-billed prions had a wider longitudinal range than MacGillivray's prions, showing some movement to the south-east Atlantic, to broadly the same productive area used by other seabird species in previous tracking studies (Quillfeldt et al. 2013; 2015a; Cherel et al. 2016).

Analysis of the GLS light data indicated broad-billed prions from Tristan departed from and arrived at the breeding colony significantly later than conspecifics at Gough Island. The departure of broad-billed prions from Gough Island is close in timing with the return of MacGillivray's prions at the start of their breeding season, and hence there is little overlap at the colony. This high degree of allochrony could be a result of character displacement, a characteristic seen in sister species in seabird communities at other sites (Brown et al. 2015; Taylor and Friesen 2017). Similar differences exist in the timing of all activities between the two populations, at every stage of the annual cycle and not only the start and end of breeding (**Table 2**). Although there was a high degree of spatial segregation at sea between the two species, this was largely due to allochrony and spatial overlap was greater when distribution was compared in the absence of temporal segregation (**Fig. 1 and Table 3**). Previous studies of small petrels that breed sympatrically have found them to be spatially segregated at large scales, particularly during the nonbreeding period (Quillfeldt et al. 2013; 2015b; Navarro et al. 2013; 2015; Cherel et al. 2016). However in these cases, allochrony was not as distinct as the two prion species on Gough Island.

Seabirds use a variety of mechanisms to alleviate inter-specific competition, including specific foraging areas (Frere et al. 2008; Navarro et al. 2009; Wilson 2010), diving depths (Masello et al. 2010; Wilson 2010), prey (Weiss et al. 2009), show otherwise divergent foraging patterns (Wilson 2010) or allochrony (Croxall and Prince 1980; Friesen et al. 2017). However, it is often difficult to determine whether these mechanisms that permit similar species to coexist result from competitive exclusion or habitat specialization. Character displacement is one of the definitive predictions of competitive exclusion (Grant 1994) and there are few examples of character displacement as neat as the two prion species at Gough Island. This study shows that they only partially segregate in several aspects of their ecology, with some similarity in foraging strategies suggested from activity patterns of flight and landings (**Fig. 2**), trophic level (inferred from feather $\delta^{15}N$ isotopic signatures, **Fig. 3**), and habitat preference (**Fig. 4**). Thus, temporal segregation allows coexistence of these prion species by reducing competition for resources and some of the differences in foraging distribution may merely be an artefact of resource seasonality.

529   Habitat mainly differed only terms of sea surface temperature and allochrony may be

530   main factor underlying the differences in habitat use. Seasonality of resources and

531   productivity in the Southern Ocean are well documented (Pakhomov and McQuaid 1996;

532   Llido et al. 2005; Bost et al. 2009). MacGillivray's prions start moulting on average 2.5

533   months later than broad-billed prions, during early winter, so may have to spend more time

534   searching for food. The longer duration of moult in MacGillivray's prions also suggests that

535   resources may be more limited at this time. The growth rate of primary feathers are probably

536   very similar in both species (Bridge 2006), suggesting that broad-billed prions had a more

537   intense moult (i.e. replaced more feathers at once) and were able to meet the energetic

538   demands of replacing these feathers even when flying ability was compromised (Cherel et al.

539   2016). The longer moult period in MacGillivray's prions probably results from moulting

540   fewer feathers at once, which is consistent with the greater proportion of time that they spend

541   in flight (**Fig. 2, Table S1**).

542   The two prion species at Gough Island are similar in size and presumably feeding

543   methods (Klages and Cooper 1992; Ryan et al. 2014). Given that the spacing between palatal

544   lamellae did not differ significantly between species (**Table S3**, Klages and Cooper 1992),

545   both likely feed on similar-sized copepods. The slightly narrower bill of MacGillivray's

546   prions has fewer palatal lamellae on average, and is likely less efficient at filtering and more

547   efficient for surface-picking. This is consistent with the greater time spent in flight by

548   MacGillivray's prions, perhaps searching for larger prey. Among the 'whalebirds', bill width

549   generally decreases with latitude, so the fact that MacGillivray's prion forages slightly farther

550   south is consistent with a slightly smaller bill and its presence only at Gough Island, not

551   250km north at Tristan da Cunha. However, there does not appear to be a relationship

552   between bill width and trophic level when comparing isotopic data from Antarctic and

553   slender-billed prions breeding at the Kerguelen archipelago (**Table S5**). There does however

554   appear to be a relationship between trophic level and duration of moult. $\delta^{15}N$ is higher in

555   prion species that take longer to moult. Cherel et al. (2016) suggest that by spending more

556   time on water, Antarctic and slender-billed prions might use an opportunistic sit-and-wait

557   foraging strategy, picking out low trophic prey items in highly productive foraging areas. By

558   comparison, broad-billed prions occupy a higher trophic level maybe because with their

559   larger lamellae, they are unable to be as selective, and MacGillivray's prions occupies the

560   highest trophic level of these four prion species by adopting a strategy involving either

561   picking out prey or filter-feeding. However, broad-billed and MacGillivray's prions are better

562   adapted to filter feed than Antarctic and slender-billed prions (the latter lacks lamellae

563 entirely), and should be more efficient at feeding while sitting on the water. Therefore the

564 shorter moult of the smaller billed species suggests they have more predictable food supply

565 despite their more selective foraging technique.

566   In conclusion, the two morphologically similar sympatric prion species achieve near

567 complete ecological segregation through temporal separation in the timing of breeding and

568 moulting. This study furthers our understanding of how morphologically similar species

569 coexist at high abundances. In addition, the tracking data identify key foraging areas and

570 habitat preferences of these species, which is important for marine spatial planning, allowing

571 informed decisions regarding the mitigation of climate-driven or other anthropogenic impacts

572 on zooplankton predators (Grecian et al. 2016b).

573

574 **COMPLIANCE WITH ETHICAL STANDARDS**

575 The authors declare that they have no conflicts of interest. Field procedures and animal

576 manipulations were approved by the Animal Ethics Committees of the British Antarctic

577 Survey and University of Cape Town.

578

579 **ACKNOWLEDGEMENTS**

591

REFERENCES

Amante C, Eakins BW (2009) ETOPO1 1 Arc-Minute Global Relief Model: Procedures,
     Data Sources and Analysis. NOAA Technical Memorandum NESDIS NGDC-24
     http://www.ngdc.noaa.gov/mgg/global/relief/ETOPO1/docs/ETOPO1

Baylis, AMM, Tierney M, Orben RA, Warwick-Evans V, Wakefield E, Grecian WJ, et al.
     (2019) Important At-Sea Areas of Colonial Breeding Marine Predators on the
     Southern Patagonian Shelf. Scientific Reports 9:8517

Bearhop S, Waldron S, Votier SC, Furness RW (2002) Factors that influence assimilation
     rates and fractionation of nitrogen and carbon stable isotopes in avian blood and
     feathers. Physiol Biochem Zool 75:451–458

BirdLife International (2017) *Pachyptila macgillivrayi*. (amended version published in 2016)
     The IUCN Red List of Threatened Species 2017: e.T104062579A112126747

Bodey TW, Cleasby IR, Bell F, Parr N, Schultz A, Votier SC, et al. (2018). A
     phylogenetically controlled meta-analysis of biologging device effects on birds:
     Deleterious effects and a call for more standardized reporting of study data. Methods
     Ecol Evol 9, 946–955. doi:10.1111/2041-210X.12934

Bost CA, Cotté C, Bailleul F, Cherel Y, Charrassin JB, Guinet C, Ainley DG, Weimerskirch
     H (2009) The importance of oceanographic fronts to marine birds and mammals of
     the southern oceans. ICES J Mar Sci 78:363–376

Boyce MS, McDonald LL (1999) Relating populations to habitats using resource selection
     functions. Trend Ecol & Evo 14(7): 268–272

Bretagnolle V, Zotier R, Jouventin P (1990) Comparative population biology of four prions
     (genus *Pachyptila*) from the Indian Ocean and consequences for their taxonomic
     status. Auk 107:305–316

Bridge ES (2006) Influences of morphology and behaviour on wing-moult strategies in
     seabirds. Mar Ornithol 34:7–19

Brooke M (2004) Albatrosses and petrels across the world. Oxford University Press, Oxford.

Brown RM, Techow NMSM, Wood AG, Phillips RA (2015) Hybridization and back-crossing
     in giant petrels (*Macronectes giganteus and M. halli*) at Bird Island South Georgia,
     and a summary of hyrbridization in seabirds. PLoS ONE 10:e0121688

Catry T, Ramos JA, LeCorre M, Phillips RA (2009) Movements, at- sea distribution and
     behaviour of a tropical pelagic seabird: the wedge-tailed shearwater in the western
     Indian Ocean. Mar Ecol Prog Ser 391:231–242

Cherel Y, Bocher P, de Broyer P, Hobson KA (2002) Food and feeding ecology of the sympatric thin-billed *Pachyptila belcheri* and Antarctic *P. desolata* prions at Iles Kerguelen, Southern Indian Ocean. Mar Ecol Prog Ser 228:263–281

Cherel Y, Phillips RA, Hobson KA, McGill R (2006) Stable isotope evidence of diverse species-specific and individual wintering strategies in seabirds. Biol Lett 2:301–303

Cherel Y, Connan M, Jaeger A, Richard P (2014) Seabird year-round and historical feeding ecology: blood and feather δ^{13}C and δ^{15}N values document foraging plasticity of small sympatric petrels. Mar Ecol Prog Ser 505:267–280

Cherel Y, Quillfeldt P, Delord K, Weimerskirch H (2016) Combination of at-sea activity, geolocation and feather stable isotopes documents where and when seabirds moult. Front Ecol Evol 4:3

Chesson P (2000) Mechanisms of maintenance of species diversity. Annu Rev Ecol Syst 31:343–366

Croxall JP, Prince PA (1980) Food, feeding ecology and ecological segregation of seabirds at South Georgia. Biol J Linnean Soc 14:103–131

Dilley BJ, Davies D, Bond AL, Ryan PG (2015) Effects of mouse predation on burrowing petrel chicks at Gough Island. Antarct Sci 27:543–553

Frere E, Quintana F, Gandini P, Wilson RP (2008) Foraging behaviour and habitat partitioning of two sympatric cormorants in Patagonia, Argentina. Ibis 150:558–564

Furness RW, Birkhead TR (1984) Seabird colony distributions suggest competition for food supplies during the breeding season. Nature 311:655–656

Grant PR (1994) Ecological character displacement. Science 266:746-747

Grecian WJ, Witt MJ, Attrill MJ, Bearhop S, Becker PH, Egevang C, Furness RW, Godley B J, González-Solís J, Grémillet D, Kopp M, Lescroël A, Matthiopoulos J, Patrick SC, Peter HU, Phillips RA, Stenhouse IJ, Votier SC (2016a) Seabird diversity hotspot linked to ocean productivity in the Canary Current Large Marine Ecosystem. Biol Lett 12:20160024

Grecian WJ, Taylor GA, Loh G, McGill RAR, Miskelly CM, Phillips RA, Thompson DR, Furness RW (2016b) Contrasting migratory responses of two closely-related seabirds to long-term climate change. Mar Ecol Prog Ser 559:231–242

Grosbois V, Thompson PM (2005) North Atlantic climate variation influences survival in adult fulmars. Oikos 109:273–290

657   Hedd A, Montevecchi WA, Phillips RA, Fifield DA (2014) Seasonal sexual segregation by

658   monomorphic sooty shearwaters *Puffinus griseus* reflects different reproductive roles

659   during the pre-laying period. PLoS ONE 9:e85572

660   Hobson KA, Clark RG (1993) Turnover of $\delta^{13}C$ in cellular and plasma fractions of blood:

661   implications for non-destructive sampling in avian dietary studies. Auk 110:638–641

662   Jaeger A, Lecomte VJ, Weimerskirch H, Richard P, Cherel Y (2010) Seabird satellite

663   tracking validates the use of latitudinal isoscapes to depict predators' foraging areas

664   in the Southern Ocean. Rapid Commun Mass Spectrom 24:3456–3460

665   Jones CWP (2018) Comparative ecology of *Pachyptila* species breeding sympatrically at

666   Gough Island. MSc dissertation, University of Cape Town

667   Klages NTW, Cooper J (1992) Bill morphology and diet of a filter-feeding seabird: the

668   broad-billed prion *Pachyptila vittata* at South Atlantic Gough Island. J Zool

669   227:385–396

670   Lewis S, Sherratt TN, Hamer KC, Wanless S (2001) Evidence of Intra-Specific Competition

671   for Food in a Pelagic Seabird. Nature 412:816–819

672   Llido J, Garçon V, Lutjiharms JRE, Sudre J (2005) Event-scale blooms drive enhanced

673   primary productivity at the Subtropical Convergence. Geophys Res Lett 32:L5611

674   Marchant S, Higgins PJ (1990) Handbook of Australian, New Zealand and Antarctic birds.

675   vol. 1 Ratites to Ducks. Oxford University Press, Melbourne

676   Masello JF, Mundry R, Poisbleau M, Demongin L, Voigt CC, Wikelski M, Quillfeldt P

677   (2010) Diving seabirds share foraging space and time within and among species.

678   Ecosphere 1:19

679   Navarro J, Forero MG, González-Solís J, Igual JM, Bécares J, Hobson KA (2009) Foraging

680   segregation between two closely related shearwaters breeding in sympatry. Biol Lett

681   5:545–548

682   Navarro J, Votier SC, Aguzzi J, Chiesa JJ, Forero MG, Phillips RA (2013) Ecological

683   segregation in space, time and trophic niche of sympatric planktivorous petrels. PLoS

684   ONE 8:e62897

685   Navarro J, Cardador L, Brown R, Phillips RA (2015) Spatial distribution and ecological

686   niches of non-breeding planktivorous petrels. Sci Rep 5:12164

687   Onley D, Scofield P (2007) Field guide to the albatrosses, petrels and shearwaters of the

688   world. Christopher Helm, London

689   Pakhomov EA, McQuaid CD (1996) Distribution of surface zooplankton and seabirds across

690   the Southern Ocean. Polar Biol 16:271–286

Pedersen EJ, Miller DL, Simpson GL, Ross N (2019) Hierarchical generalized additive
models in ecology: an introduction with mgcv. PeerJ 7:e6876
https://doi.org/10.7717/peerj.6876

Phalan B, Phillips RA, Silk JR, Afanasyev V, Fukuda A, Fox J, Catry P, Higuchi H, Croxall
JP (2007) Foraging behaviour of four albatross species by night and day. Mar Ecol
Prog Ser 340:271–286

Phillips RA, Hamer KC (1999) Lipid reserves, fasting capability and the evolution of nestling
obesity in procellariiform seabirds. Proc R Soc Lond [Biol] 266:1329–1334

Phillips RA, Xavier JC, Croxall JP (2003) Effects of satellite transmitters on albatrosses and
petrels. Auk 120:1082–1090

Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Briggs DR (2004) Accuracy of geolocation
estimates for flying seabirds. Mar Ecol Prog Ser 266:265–272

Phillips RA, Silk JR, Croxall JP, Afanasyev V (2006) Year-round distribution of white-
chinned petrels from South Georgia: relationships with oceanography and fisheries.
Biol Conserv 129:336–347

Phillips RA, Croxall JP, Silk JRD, Briggs DR (2007) Foraging ecology of albatrosses and
petrels from South Georgia: two decades of insights from tracking technologies.
Aquat Conserv Mar Freshw Ecosyst 17:S6–S21

Phillips RA, Bearhop S, McGill RAR, Dawson DA (2009) Stable isotopes reveal individual
variation in migration strategies and habitat preferences in a suite of seabirds during
the nonbreeding period. Oecologia 160:795–806

Quillfeldt P, McGill RAR, Masello JF, Weiss F, Strange IJ, Brickle P, Furness RW (2008)
Stable isotope analysis reveals sexual and environmental variability and individual
consistency in foraging of thin-billed prions. Mar Ecol Prog Ser 373:137–148

Quillfeldt P, Masello JF, Navarro J, Phillips RA (2013) Year-round spatial segregation of two
small petrel species in the South Atlantic. J Biogeogr 40:430–441

Quillfeldt P, Cherel Y, Masello JF, Delord K, McGill RA, Furness RW, Moodley Y,
Weimerskirch H (2015a) Half a world apart? Overlap in nonbreeding distributions of
Atlantic and Indian Ocean thin-billed prions. PLoS ONE 10:e0125007

Quillfeldt P, Cherel Y, Delord K, Weimerkirch H (2015b) Cool, cold or colder? Spatial
segregation of prions and blue petrels is explained by differences in preferred sea
surface temperatures. Biol Lett 11:20141090

R Core Team (2016) R: a language and environment for statistical computing. R Foundation
for Statistical Computing, Vienna

725   Ryan PG (2007) Field guide to the animals and plants of Tristan da Cunha and Gough Island.
726   Pisces Publications, Newbury

727   Ryan PG, Bourgeois K, Dromzeé S, Dilley BJ (2014) The occurrence of two bill morphs of
728   prions *Pachyptila vittata* on Gough Island. Polar Biol 37:727–735.

729   Schroeder ID, Sydeman WJ, Sarkar N, Thompson SA, Bograd SJ, Schwing FB (2009) Winter
730   pre-conditioning of seabird phenology in the California Current. Mar Ecol Prog Ser
731   393:211–223

732   Taylor RS, Friesen VL (2017) The role of allochrony in speciation. Mol Ecol 26:3330–3342

733   Tranquilla LAM, Montevecchi WA, Hedd A, Fifield DA, Burke CM, Smith PA, Regular PM,
734   Robertson GJ, Gaston AJ, Phillips RA (2013) Multiple-colony winter habitat use by
735   murres *Uria* spp. in the Northwest Atlantic Ocean: implications for marine risk
736   assessment. Mar Ecol Prog Ser 472:287–303

737   Warham J (1990) The petrels: their ecology and breeding systems. Academic Press, London

738   Weimerskirch H, Guionnet T, Martin J, Shaffer SA, Costa DP (2000) Fast and fuel-efficient?
739   Optimal use of wind by flying albatrosses. Proc R Soc Lond [Biol] 267:1869–1874

740   Weiss F, Furness RW, McGill RAR, Strange IJ, Masello JF, Quillfeldt P (2009) Trophic
741   segregation of Falkland Islands seabirds: insights from stable isotope analysis. Polar
742   Biol 32:1753–1763

743   Wessel P (2001) Global distribution of seamounts inferred from gridded Geosat/ERS 1
744   altimetry. J Geophys Res 106:19431–19441

745   Whitehead TO, Kato A, Ropert-Coudert Y, Ryan PG (2016) Habitat use and diving
746   behaviour of macaroni *Eudyptes chrysolophus* and eastern rockhopper *E. chrysocome*
747   *filholi* penguins during the critical pre-moult period. Mar Biol 163:19

748   Wilson RP (2010) Resource partitioning and niche hypervolume overlap in free-living
749   pygoscelid penguins. Funct Ecol 24:646–657

750   Wood SN (2006) Generalized additive models: an introduction with R. Chapman and
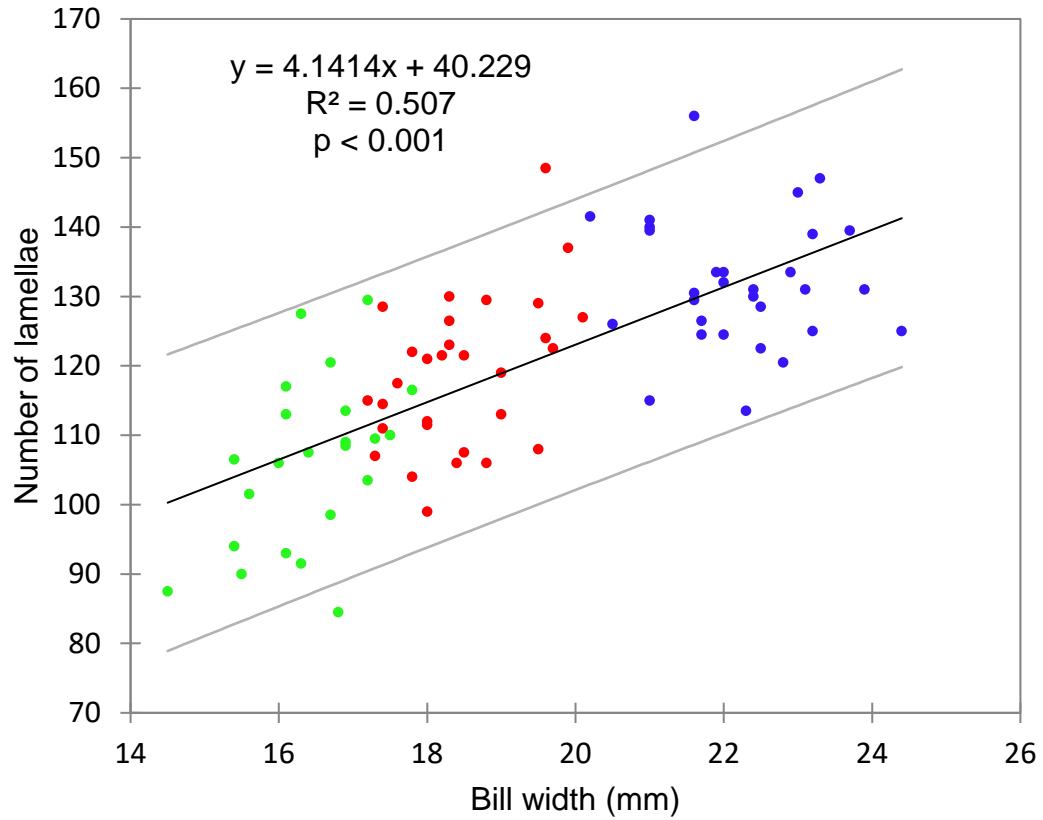751   Hall/CRC, London

752

Supplementary Material
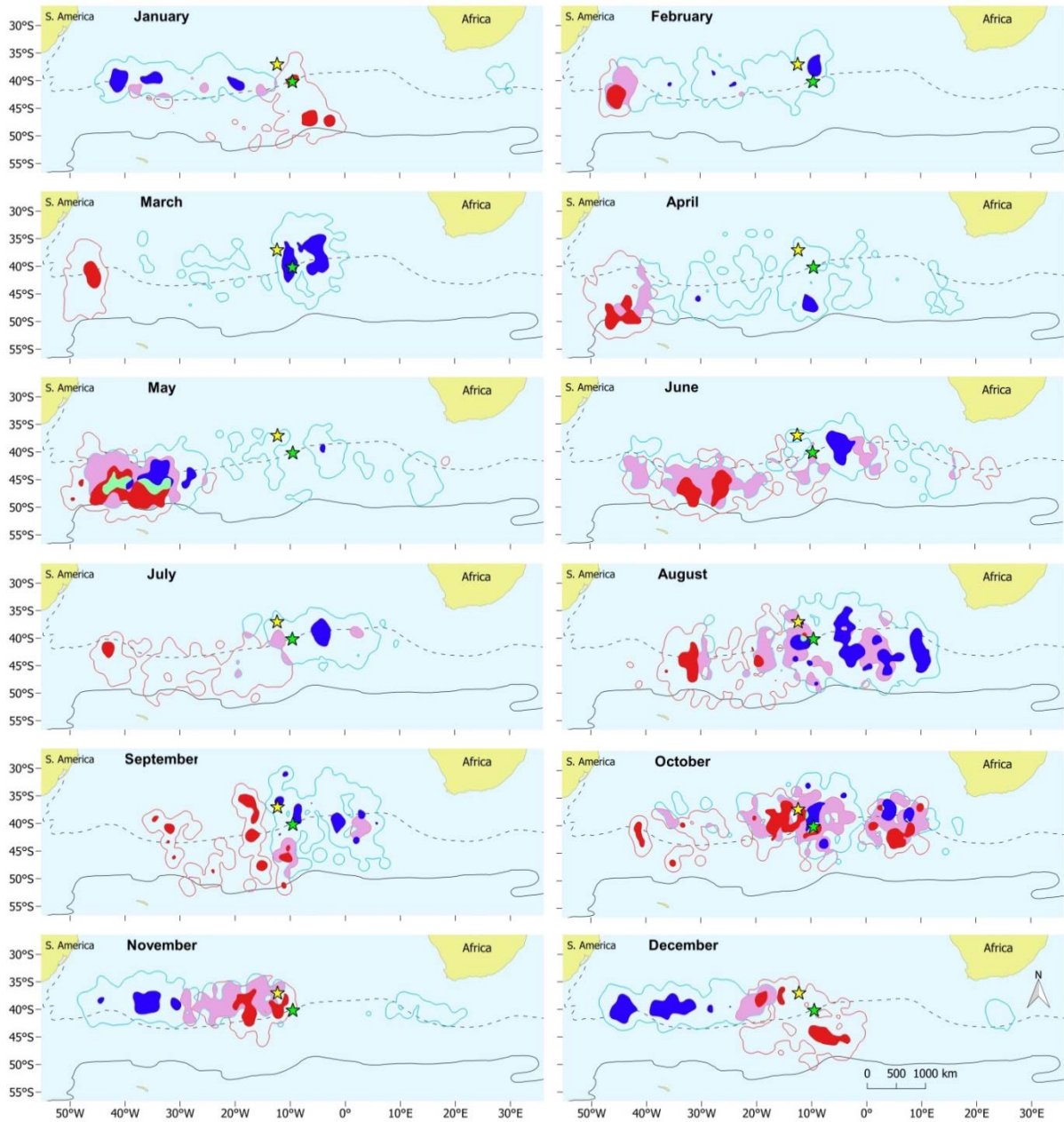
Fig. S1 Monthly utilisation distributions (UDs) of broad-billed (blue) and MacGillivray's prions (red) from Tristan and Gough in relation to the Sub-tropical Front (dashed line) and Antarctic Polar Front (solid line). Conventions as Fig. 1

$$y = 4.1414x + 40.229$$
$$R^2 = 0.507$$
$$p < 0.001$$

760

Fig. S2 Comparison of the relationships between bill width (mm) and average number of palatal lamellae in Salvin's (green), MacGillivray's (red) and broad-billed prions (blue). Regression parameters for all species combined are given with 95% prediction limits (grey lines)

765

Table S1 At-sea activities during various periods of broad-billed (BBP) and MacGillivray's prions (MP) tracked from Tristan da Cunha and Gough Islands in 2014 to 2015. Values are means ± SD. Values not sharing the same superscript letter are significantly different at the 0.05 level

	Gough BBP	Tristan BBP	All BBP	MP	ANOVA results
Breeding Period	**n=9**	**n=3**	**n=12**	**n=8**	
Flight time (%)	51.3 ± 4.3^{ab}	43.0 ± 7.4^{a}	49.2 ± 6.1^{a}	56.4 ± 4.0^{b}	$F_{3,\,28}=5.5$, p=0.004
Flight time (h.d^{-1})	12.4 ± 1.0^{ab}	10.3 ± 1.8^{a}	11.9 ± 1.5^{a}	13.5 ± 1.0^{b}	$F_{3,\,28}=5.3$, p=0.005
Flight time during daylight (%)	48.3 ± 4.9^{ab}	42.5 ± 7.0^{a}	46.9 ± 5.8^{a}	54.3 ± 3.6^{b}	$F_{3,\,28}=5.1$, p=0.006
Flight time at night (%)	54.6 ± 4.9^{ab}	44.0 ± 7.7^{a}	52.0 ± 7.2^{a}	60.7 ± 8.3^{b}	$F_{3,\,28}=4.9$, p=0.007
Daily flight bouts (n)	7.7 ± 1.6	6.0 ± 2.6	7.3 ± 1.9	8.2 ± 0.8	$F_{3,\,28}=1.2$, p=0.312
Flight bout duration (min)	63.4 ± 8.5	54.8 ± 7.5	61.3 ± 8.8	53.8 ± 5.2	$F_{3,\,28}=2.7$, p=0.064
Non-Breeding Period	**n=9**	**n=4**	**n=13**	**n=8**	
Flight time (%)	35.6 ± 3.7	34.1 ± 4.9	35.1 ± 4.0	39.4 ± 3.1	$F_{3,\,30}=2.6$, p=0.070
Flight time (h.d^{-1})	8.5 ± 0.9	8.2 ± 1.2	8.4 ± 1.0	9.4 ± 0.7	$F_{3,\,30}=2.6$, p=0.070
Flight time during daylight (%)	33.9 ± 3.9^{a}	33.2 ± 5.5^{a}	33.7 ± 4.2^{a}	40.8 ± 1.5^{b}	$F_{3,\,30}=7.0$, p=0.001
Flight time at night (%)	35.8 ± 4.4	34.1 ± 4.2	35.3 ± 4.2	37.5 ± 4.7	$F_{3,\,30}=0.7$, p=0.572
Daily flight bouts (n)	5.9 ± 1.0^{a}	6.0 ± 0.7^{ab}	5.9 ± 0.9^{a}	7.2 ± 0.6^{b}	$F_{3,\,30}=4.6$, p=0.009
Flight bout duration (min)	55.4 ± 6.4	50.0 ± 1.9	53.7 ± 5.9	50.3 ± 3.8	$F_{3,\,30}=1.8$, p=0.176
Moulting Period	**n=9**	**n=4**	**n=13**	**n=8**	
Flight time (%)	19.3 ± 3.1	20.6 ± 2.8	19.7 ± 3.0	23.5 ± 4.7	$F_{3,\,30}=2.6$, p=0.069
Flight time (h.d^{-1})	4.6 ± 0.8	5.0 ± 0.7	4.7 ± 0.7	5.7 ± 1.1	$F_{3,\,30}=2.7$, p=0.066
Flight time during daylight (%)	23.1 ± 4.1^{a}	23.1 ± 3.4^{a}	23.1 ± 3.8^{a}	30.2 ± 4.7^{b}	$F_{3,\,30}=6.1$, p=0.002
Flight time at night (%)	12.2 ± 3.3	15.9 ± 2.0	13.3 ± 3.4	16.4 ± 5.4	$F_{3,\,30}=2.2$, p=0.109
Daily flight bouts (n)	3.8 ± 0.9	4.4 ± 0.6	4.0 ± 0.8	4.7 ± 1.1	$F_{3,\,30}=2.1$, p=0.119
Flight bout duration (min)	44.6 ± 4.1	40.1 ± 1.2	43.2 ± 4.0	45.1 ± 5.4	$F_{3,\,30}=1.4$, p=0.254
Non-Moulting Period	**n=9**	**n=4**	**n=13**	**n=8**	
Flight time (%)	45.6 ± 5.3^{a}	42.5 ± 5.6^{a}	44.6 ± 5.3^{a}	52.9 ± 2.9^{b}	$F_{3,\,30}=6.3$, p=0.002
Flight time (h.d^{-1})	10.9 ± 1.3^{a}	10.2 ± 1.3^{a}	10.7 ± 1.3^{a}	12.7 ± 0.7^{b}	$F_{3,\,30}=6.3$, p=0.002
Flight time during daylight (%)	40.4 ± 5.6^{a}	39.6 ± 6.5^{a}	40.1 ± 5.6^{a}	49.9 ± 2.1^{b}	$F_{3,\,30}=7.3$, p=0.001
Flight time at night (%)	50.4 ± 5.3^{ab}	45.2 ± 4.9^{a}	48.8 ± 5.6^{a}	55.7 ± 5.4^{b}	$F_{3,\,30}=4.2$, p=0.013
Daily flight bouts (n)	7.3 ± 1.7^{a}	6.9 ± 0.9^{a}	7.2 ± 1.5^{a}	9.2 ± 0.8^{b}	$F_{3,\,30}=4.4$, p=0.011
Flight bout duration (min)	59.0 ± 7.9	53.8 ± 2.0	57.4 ± 7.0	52.5 ± 4.4	$F_{3,\,30}=1.8$, p=0.176
Pre-Lay Exodus	**n=8**	**n=4**	**n=12**	**n=3**	
Flight time (%)	45.5 ± 5.1	43.5 ± 10.3	44.8 ± 6.8	35.8 ± 9.2	$F_{3,\,23}=1.5$, p=0.245
Flight time (h.d^{-1})	10.9 ± 1.2	10.4 ± 2.5	10.7 ± 1.6	8.6 ± 2.2	$F_{3,\,23}=1.5$, p=0.246
Flight time during daylight (%)	41.2 ± 5.4	45.9 ± 8.3	42.8 ± 6.5	37.0 ± 9.9	$F_{3,\,23}=1.1$, p=0.382
Flight time at night (%)	49.1 ± 6.2	41.0 ± 13.7	46.4 ± 9.6	34.0 ± 8.7	$F_{3,\,23}=2.2$, p=0.111
Daily flight bouts (n)	7.1 ± 1.3	8.4 ± 1.9	7.6 ± 1.5	7.6 ± 1.9	$F_{3,\,23}=0.6$, p=0.615
Flight bout duration (min)	56.4 ± 7.3	46.8 ± 5.2	53.2 ± 8.0	49.6 ± 7.5	$F_{3,\,23}=1.7$, p=0.198

771 **Table S2.** $\delta^{15}N$ and $\delta^{13}C$ values from primary feathers (P1/2, P5, P9) of broad-billed and

772 MacGillivray's prions, grown during the non-breeding period, collected from tracked birds

773 from Tristan and Gough in 2015 and dead birds from Nightingale and Gough in 2013. Values

774 are means ± SD

775

Species	Population	2015 (GLS)			2013 (dead)		
		Feather	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	Feather	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
Broad-billed prion	Gough	P1 (n=9)	9.9 ± 2.2	-18.0 ± 0.5	P2 (n=24)	11.4 ± 2.1	-16.8 ± 0.7
		P5 (n=9)	12.1 ± 1.6	-17.0 ± 0.8	P5 (n=24)	12.2 ± 1.7	-16.5 ± 0.6
		P9 (n=9)	13.9 ± 2.6	-16.6 ± 0.5	P9 (n=24)	12.9 ± 1.5	-16.5 ± 0.6
	Tristan/ Nightingale	P1 (n=4)	13.9 ± 0.9	-17.1 ± 0.2	P2 (n=20)	11.7 ± 2.0	-16.8 ± 0.8
		P5 (n=3)	14.9 ± 0.5	-17.2 ± 0.1	P5 (n=20)	12.4 ± 2.1	-16.6 ± 0.8
		P9 (n=3)	14.5 ± 1.1	-16.0 ± 0.7	P9 (n=20)	14.4 ± 1.4	-16.5 ± 0.3
	Pooled	P1 (n=13)	11.1 ± 2.7	-17.7 ± 0.6	P2 (n=44)	11.5 ± 2.0	-16.8 ± 0.8
		P5 (n=12)	12.8 ± 1.9	-17.0 ± 0.7	P5 (n=44)	12.3 ± 1.8	-16.5 ± 0.7
		P9 (n=12)	14.1 ± 2.3	-16.5 ± 0.6	P9 (n=44)	13.6 ± 1.6	-16.5 ± 0.5
MacGillivray's prion	Gough	P1 (n=8)	14.2 ± 1.7	-16.6 ± 0.4	P2 (n=24)	14.7 ± 0.8	-16.5 ± 0.8
		P5 (n=8)	13.9 ± 2.3	-16.1 ± 0.3	P5 (n=24)	14.5 ± 0.8	-16.6 ± 0.5
		P9 (n=8)	12.7 ± 1.4	-17.0 ± 0.9	P9 (n=24)	13.5 ± 1.1	-17.1 ± 0.5

776 **Table S3** Comparative bill morphology of the three largest filter-feeding prion species. The

777 number of palatal lamellae represents the average number counted on the left and right sides

778 of the bill. Values are means ± SD. Values not sharing the same superscript letter are

779 significantly different at the 0.05 level (ANOVA, with posthoc Newman–Keuls tests)

	Broad-billed (n = 30)	MacGillivray's (n = 30)	Salvin's (n = 23)	ANOVA results
Bill width (mm)	22.2 ± 1.0^a	18.5 ± 0.8^b	16.4 ± 0.8^c	$F_{2, 82}=287.8, p<0.001$
Bill length (mm)	34.2 ± 1.3^a	33.3 ± 1.4^b	30.1 ± 1.7^c	$F_{2, 82}=56.7, p<0.001$
No. of lamellae	132 ± 9^a	119 ± 10^b	106 ± 12^c	$F_{2, 82}=38.0, p<0.001$
Lamellae.mm^{-1}	3.3 ± 0.3	3.4 ± 0.2	3.4 ± 0.2	$F_{2, 82}= 0.4, p=0.692$

780

781 **Table S4** Model selection table examining differences between broad-billed and

782 MacGillivray's prions in preference for distance to colony (DIS), depth (DEP), chlorophyll *a*

783 (CHL), sea surface temperature (SST) and distance to seamount (SEA). Terms in bold

784 indicate the model includes a species-level interaction for that covariate. All models include

785 an individual-level random effect. Adj-R^2 of best-supported model = 0.36

|	Parameters	d.f.	AIC	ΔAIC
1	**DIS** + DEP + **CHL** + **SST** + **SEA**	55.28	7821	0
2	**DIS** + **DEP** + **CHL** + **SST** + **SEA**	59.25	7823	2.52
3	DIS + **DEP** + **CHL** + **SST** + **SEA**	54.98	7879	58.36
4	**DIS** + **DEP** + **CHL** + SST + **SEA**	56.09	7936	115.40
5	**DIS** + **DEP** + CHL + **SST** + **SEA**	52.29	7945	124.01
6	**DIS** + **DEP** + **CHL** + **SST** + SEA	52.88	8054	232.47

786
787
788
789
790
791
792
793

794

795   **Table S5** Summary of flight patterns and trophic level (δ^{15}N) in comparison with bill

796   morphology and duration of moult. Data for Antarctic prion *P. desolata* and slender-billed

797   prion *P. belcheri* are from Cherel et al. (2016). Species limits are given for bill width and

798   other values are means ± SD

799

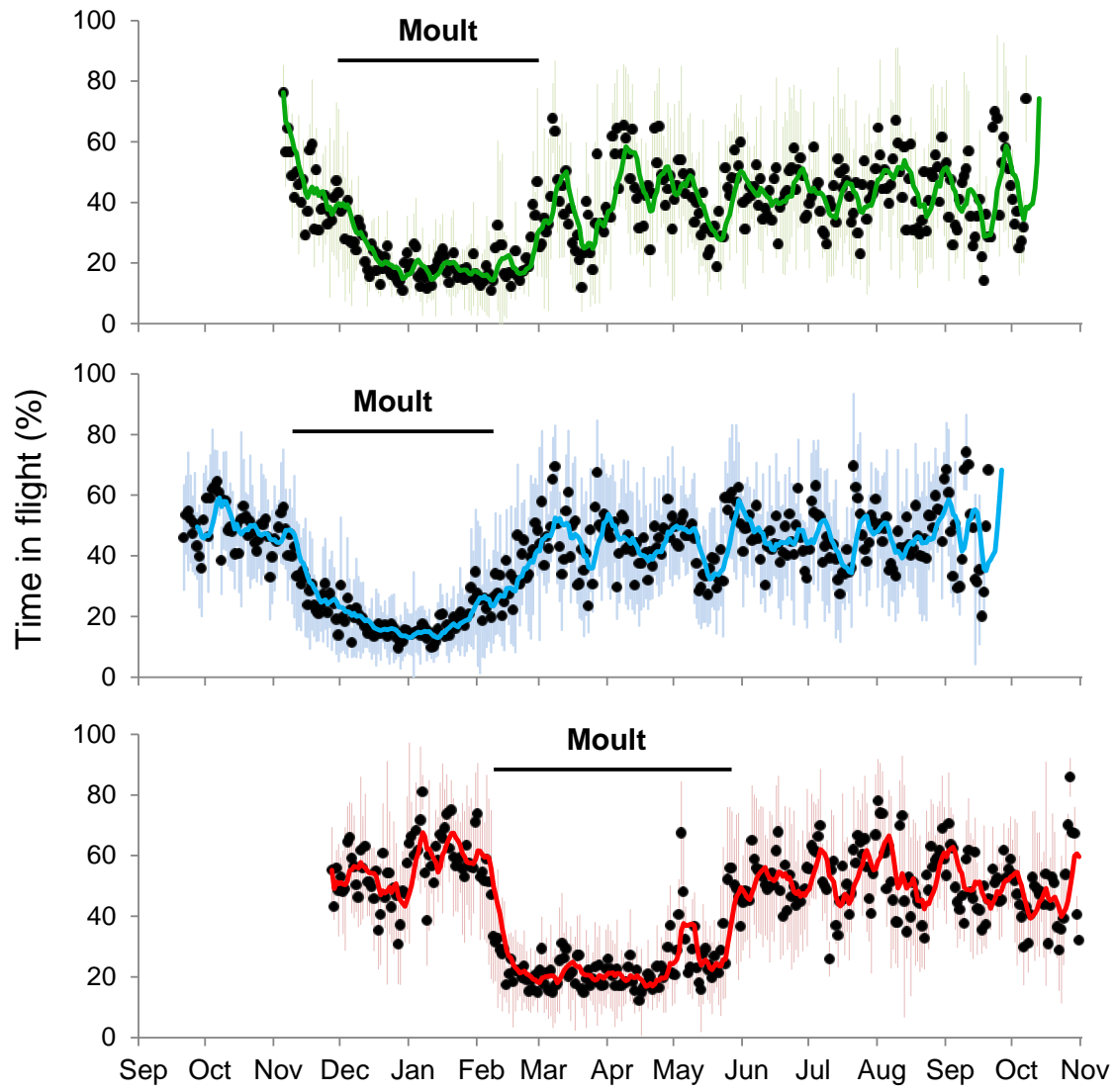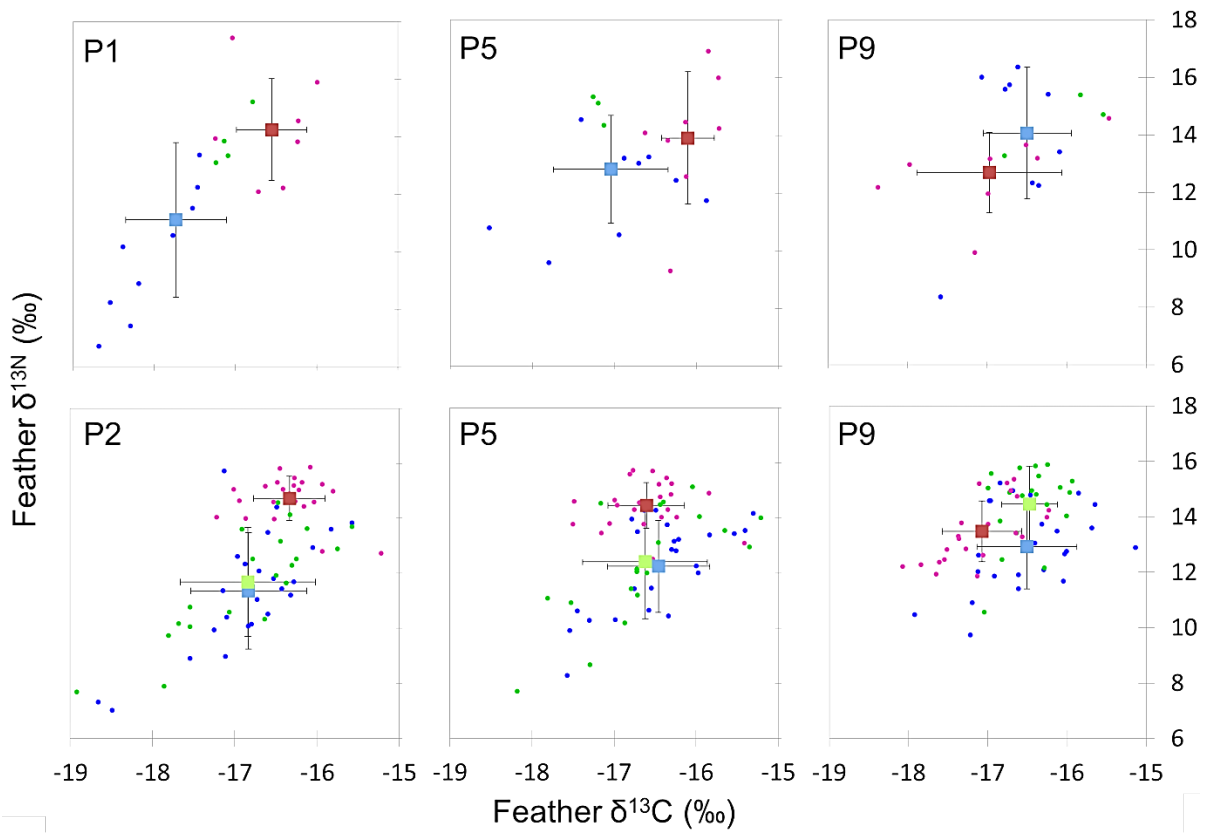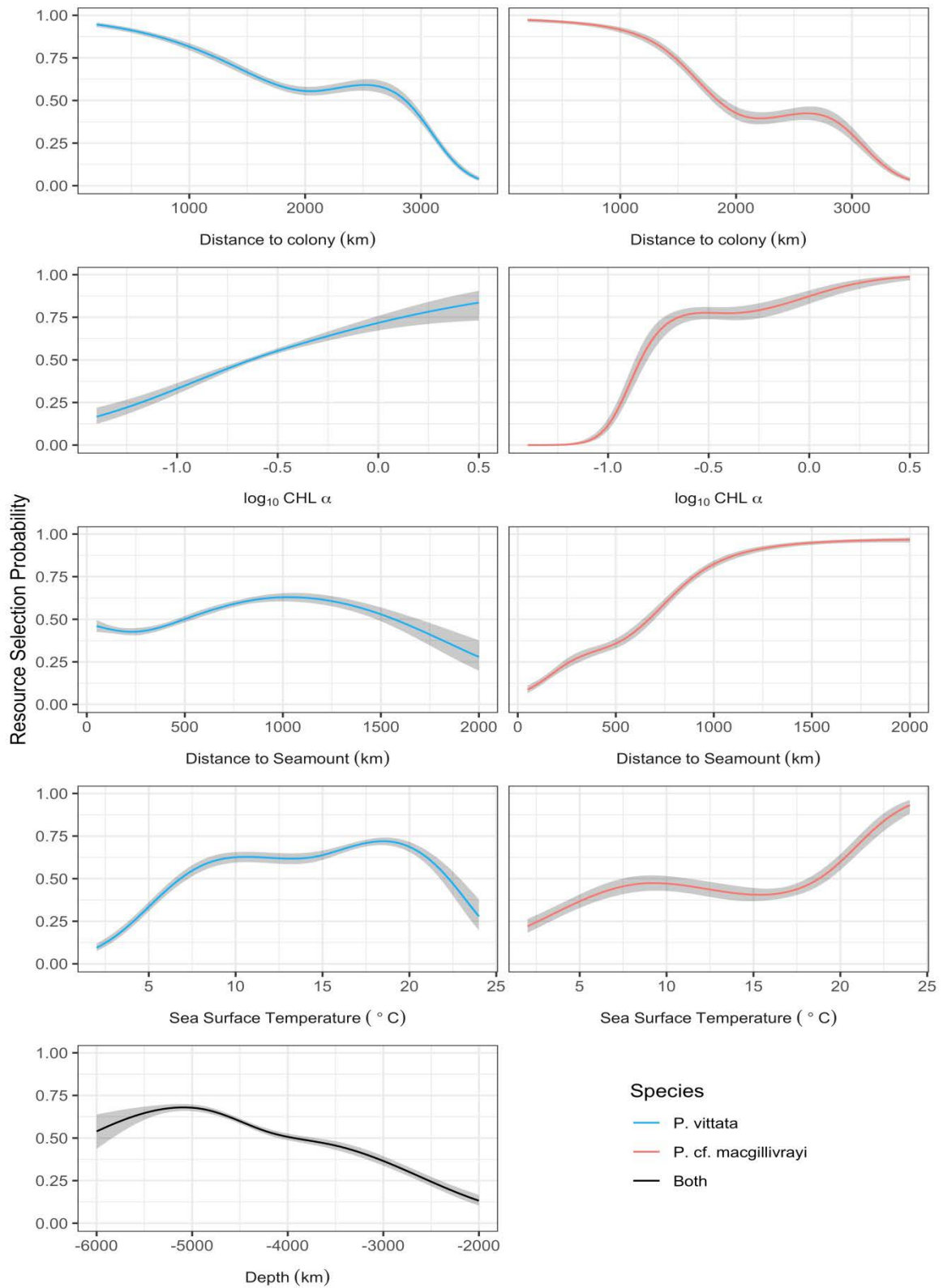| Prion Species	Bill width (mm)	Moult duration (days)	Flight time (%)		δ^{15}N (‰)
			Non-moulting	Moulting	
Broad-billed	20 - 24.5	95 ± 8	44 ± 6	20 ± 3	12.6 ± 2.0
MacGillivray's	15.5 - 20.5	115 ± 10	53 ± 3	24 ± 5	13.9 ± 1.4
Antarctic	12 - 16	109 ± 13	28 ± 7	17 ± 9	11.4 ± 2.0
Slender-billed	9 - 12	83 ± 13	24 ± 3	5 ± 2	8.8 ± 0.4

800

801
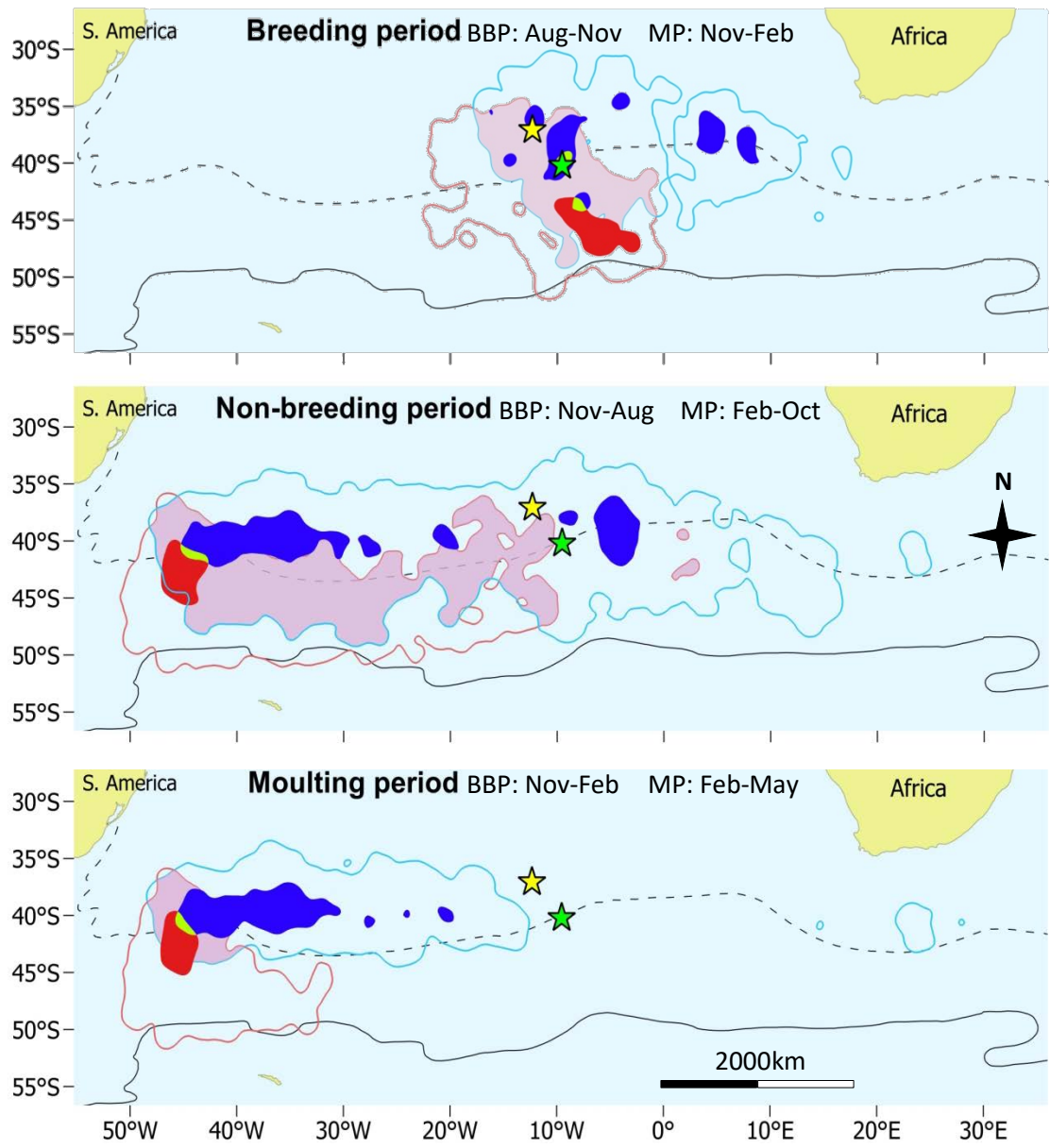
802

803   **Fig. 1**

804

805

806   **Fig. 2**

807

808

809

Fig. 3

811

812

Fig. 4

813

814

815