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Animal behaviour

Cool, cold or colder? Spatial segregation of prions and blue petrels is explained by differences in preferred sea surface temperatures

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The Southern Ocean provides one of the largest environmental gradients on Earth that lacks geographical barriers, and small but highly mobile petrels living there may offer fine models of evolution of diversity along environmental gradients. Using geolocation devices, we investigated the winter distribution of closely related petrel species breeding sympatrically in the southern Indian Ocean, and applied ecological niche models to compare environmental conditions in the habitat used. We show that thin-billed prions (*Pachyptila belcheri*), Antarctic prions (*Pachyptila desolata*) and blue petrels (*Halobaena caerulea*) from the Kerguelen archipelago in the southern Indian Ocean segregate latitudinally, sea surface temperature being the most important variable separating the distribution of the species. Antarctic prions spent the winter north of the Polar Front in temperate waters, whereas blue petrels were found south of the Polar Front in Antarctic waters. Thin-billed prions preferred intermediate latitudes and temperatures. Stable isotope values of feathers reflected this near complete niche separation across an ecological gradient that spans large scales, and suggest evolutionary isolation by environment. In pelagic seabirds that exploit large areas of ocean, spatial niche partitioning may not only facilitate coexistence among ecologically similar species, but may also have driven their evolution in the absence of geographical barriers.

1. Introduction

Individual movements and behaviour are inextricably linked to habitat characteristics, which determine the distribution and availability of trophic resources. In the oceans, the more productive areas are often in cold-water or upwelling regions where higher nutrient availability sustains productive food webs. Seabird species often breed in large communities and target productive areas within their foraging range, leading to intense competition for resources [1] and reduced foraging efficiency [2]. Seabirds can avoid interspecific competition at least partially by ecological segregation in foraging areas [3,4], diving depths [4,5] or diet choice [6,7]. However, little is known from pelagic birds during the non-breeding season, when seabirds forage over much larger spatial scales. Among the most abundant small seabirds worldwide, prions (*Pachyptila* spp.) and closely related blue petrels (*Halobaena caerulea*) inhabit the open waters of the Southern Ocean. As these small petrels are very similar in size, foraging techniques and diet during the breeding season, it has been suggested that they may be suitable model species in the context of niche partitioning and community assembly rules [8,9]. In the southwest Atlantic Ocean, thin-billed and Antarctic prions had divergent patterns of migration, resulting in nearly complete spatial segregation (0–5% overlap by month, [10]). Consistent foraging in different water

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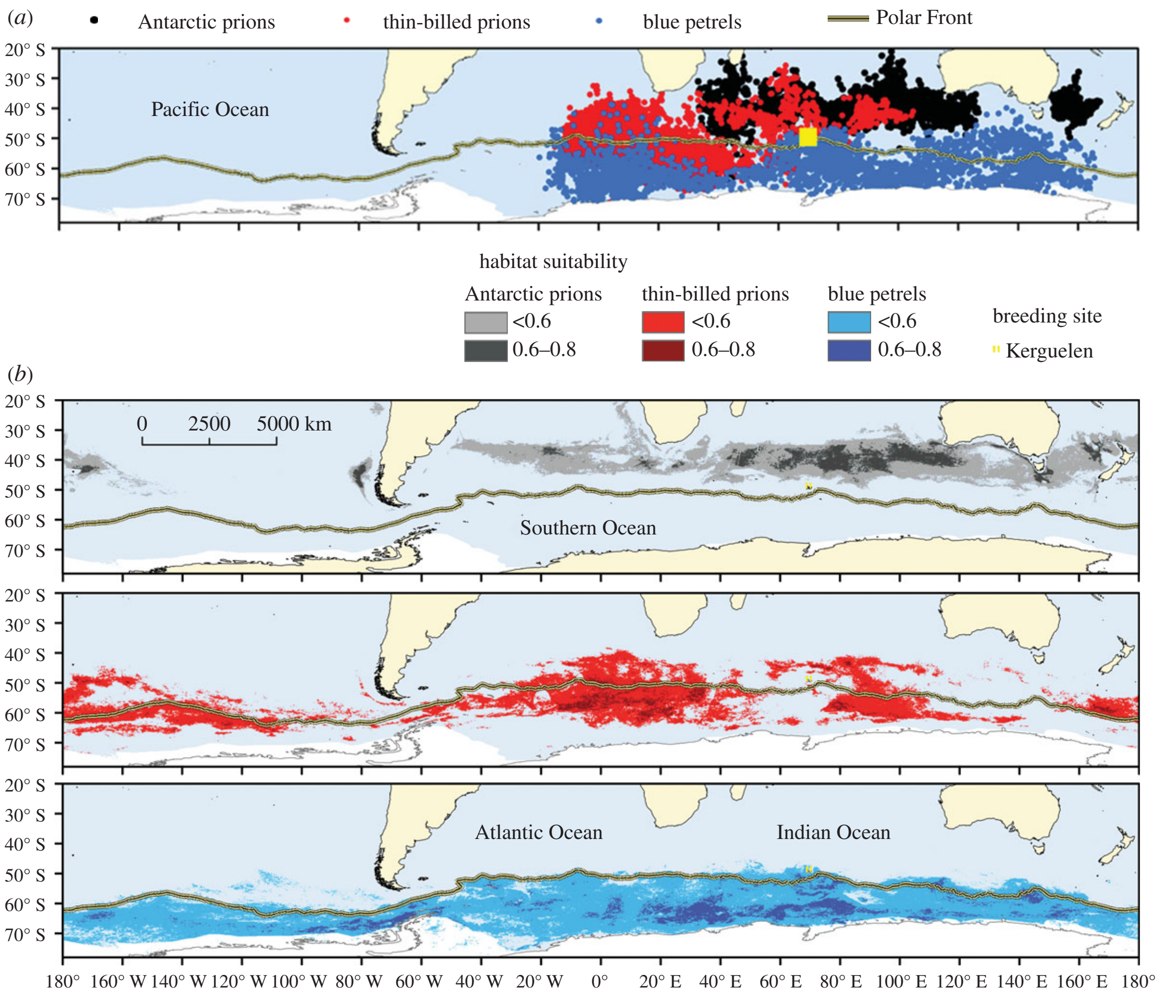

Figure 1. Interbreeding distribution of two prion species and blue petrels from Kerguelen. (*a*) Geolocation positions of Antarctic prions (n = 10 birds; 2916 positions, black dots), thin-billed prions (n = 15 birds; 3143 positions, pink dots) and blue petrels (n = 12 birds; 2237 positions, blue dots). (*b*) Habitat values from MaxEnt models. Values below the 10th percentile training presence logistic threshold (table 1) were omitted.

masses during the non-breeding period has, furthermore, been inferred from feather stable isotope ratios [11–13].

Here, we deployed geolocators during the non-breeding period and measured feather stable isotopes on three closely related species of petrels that breed in sympatry at the Kerguelen archipelago (southern Indian Ocean). The study highlights the spatial segregation and species-specific wintering strategies along a latitudinal gradient from Antarctica to the subtropics, where they all feed primarily on crustaceans.

2. Methods

Prions and blue petrels breed on Southern Hemisphere islands, mainly in sub-Antarctic waters. At Kerguelen, there are large colonies of Antarctic prions, thin-billed prions and blue petrels [14]. During the incubation period 2011/2012, we worked on two closely located islands of the Golfe du Morbihan to attach 1 g leg-mounted geolocators (GLS, see [10]) to 20 Antarctic prions at Ile Verte (49°51′ S, 70°06′ E), 29 thin-billed prions and 20 blue petrels at Ile Mayes (49°47′ S, 69°95′ E). Devices were retrieved in the following season from 10 Antarctic prions, 19 thin-billed prions and 16 blue petrels (see the electronic supplementary material, S1). Processing of geolocator data was carried out as described previously [10]. The realized niches of the two species were modelled and extrapolated using MaxEnt v. 3.3.3k [15], as described previously ([10], for details, see the electronic supplementary material, S2).

Feather stable isotope values were determined after recapture of the birds carrying GLS, and were thus grown simultaneously to the GLS tracking, in the austral winter 2012. For details on stable isotope measurements, see the electronic supplementary material, S2. Isotopic niches were compared using ANOVA in R v. 3.0.2., Layman metrics [16] and the Bayesian approach based on (small sample size corrected) standard ellipse metrics (SEAc) [17]. Data access: the datasets supporting this article will be uploaded to Movebank (www.movebank.org).

3. Results

The species showed strong spatial segregation in interbreeding distributions (figure 1*a*). Antarctic prions spent the winter north of the Polar Front, whereas blue petrels were found south of the Polar Front in Antarctic waters and thin-billed prions preferred intermediate latitudes, on both sides of the Polar Front (figure 1*a*). MaxEnt ecological niche models were fitted and achieved good area under curve (AUC) values (table 1). The projected suitable habitat likewise showed different areas for the three species, with a clear latitudinal segregation (figure 1*b*). The suitable habitat during the non-breeding season was most northerly for Antarctic prions, intermediate for thin-billed prions and most southerly for blue petrels (figure 1*b*).

Sea surface temperature was the only relevant parameter for blue petrels, the most important parameter for Antarctic prions, and it also achieved a high importance in the

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Table 1. (*a*) Stable isotope values (mean ± s.d.) and (*b*) estimates of model fit and relative contributions of the environmental variables to the MaxEnt model, normalized to percentages (values over 10% are marked in bold), for the non-breeding period of two prion species and blue petrels from Kerguelen. (To determine the permutation importance, for each environmental variable in turn, the values of that variable on training presence and background data are randomly permuted. The model is re-evaluated on the permuted data, and the resulting drop in training AUC is shown in the table, normalized to percentages. Values shown are averages over 50 replicate runs. No. cells, the number of cells with training samples.) SST, sea surface temperature.

	Antarctic prion	thin-billed prion	blue petrel
(*a*) stable isotope values			
$\delta^{13}C$	−18.2 ± 0.6	−23.1 ± 1.3	−24.7 ± 0.7
$\delta^{15}N$	9.6 ± 1.4	8.6 ± 0.4	8.4 ± 0.5
(*b*) MaxEnt model			
model parameter			
no. cells	2916	3143	2237
test AUC	0.833	0.840	0.824
10th percentile training presence logistic threshold	0.32	0.37	0.36
parameter contribution			
bathymetry	5.3	3.1	0.9
mean chlorophyll	**19.3**	9.8	1.6
min chlorophyll	4.5	2.9	1.2
min cloud cover	4.5	**55.5**	0.9
salinity	6.3	6.0	1.8
SST fronts	1.4	0.6	2.8
mean SST	**58.6**	**21.7**	**88.5**
min sea ice	0.0	0.3	2.3
permutation importance			
bathymetry	5.7	3.4	1.4
mean chlorophyll	**15.7**	**18.7**	5.1
min chlorophyll	4.6	2.5	2.0
min cloud cover	5.9	**42.1**	1.8
salinity	**13.5**	**13.5**	3.6
SST fronts	1.0	1.3	2.7
mean SST	**53.5**	**16.6**	**81.7**
min sea ice	0.1	2.0	1.6

permutation test for thin-billed prions (table 1). The preferred temperatures (probability of presence greater than 0.5) were 10.1–17.5°C for Antarctic prions, −0.8 to 5.4°C for thin-billed prions and −1.2 to 3.0°C for blue petrels (figure 2). Other key parameters were mean chlorophyll concentration and salinity for Antarctic prions and thin-billed prions and minimum cloud cover (only in thin-billed prions, table 1).

The species differed in $\delta^{13}C$ (table 1 and figure 2, ANOVA: $F_2 = 119.7$, $p < 0.001$, pairwise Tukey tests $p < 0.001$). Antarctic prions differed from blue petrels and thin-billed prions by higher $\delta^{15}N$ ($F_2 = 9.4$, $p < 0.001$, pairwise Tukey tests: blue petrel–Antarctic prion $p < 0.001$, thin-billed prion–Antarctic prion $p = 0.004$, thin-billed prion–blue petrel $p = 0.745$). Thin-billed prions used the widest range of oceanographic conditions (largest range in $\delta^{13}C$) and Antarctic prions the widest breadth of trophic levels (largest range in $\delta^{15}N$). The SEAc value was largest in Antarctic prions (2.48), intermediate in thin-billed prions (1.73) and smallest in blue petrels (0.89, see the electronic supplementary material, S3). There was no overlap between the ellipse areas of Antarctic prions and the two other species, whereas the overlap between thin-billed prions and blue petrels was small (20.4%, see electronic supplementary material, S2).

4. Discussion

To the best of our knowledge, this study is the first to look at spatial segregation in winter of three closely related seabirds breeding in sympatry, with the study being conducted in the same year.

Although the three species are very similar in size and feeding methods [8,9], and breed at the same site in very large numbers, our results indicate that the high mobility of these small petrels facilitates their spatial segregation at large scales far from their breeding grounds at Kerguelen. Thus, in winter, spatial segregation allows the coexistence of these three abundant species. The distribution of three species from Kerguelen did not result from random dispersal, but rather suggests a strong degree of specialization in wintering regions specific to the species. When comparing the wintering sites in

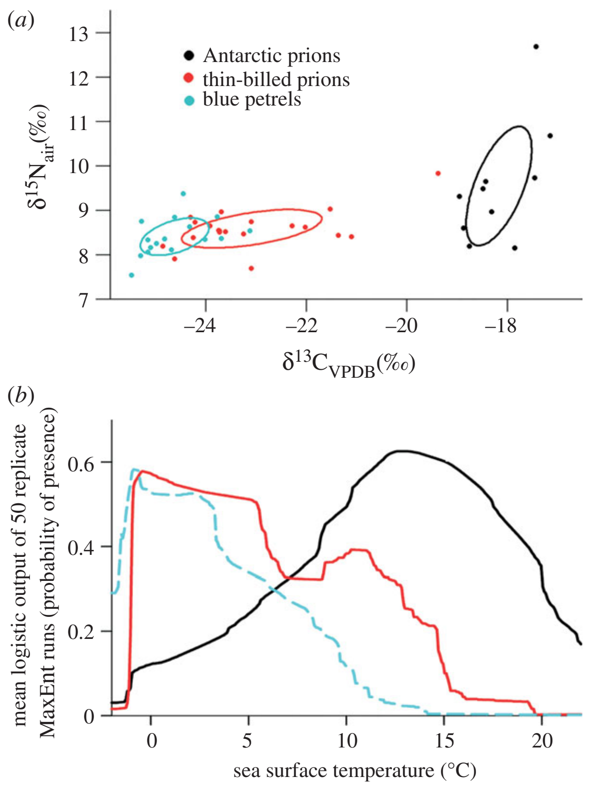

Figure 2. Isotopic niche space and temperature preferences for two prion species and blue petrels from Kerguelen, (*a*) body feather δ^{13}C- and δ^{15}N-values and standard ellipse areas corrected for small sample sizes (SEAc) using stable isotope Bayesian ellipses in R (SIBER). Feather isotopic values were determined after recapture of the birds carrying GLS (10 Antarctic prions, 19 thin-billed prions and 16 blue petrels), and were thus grown simultaneously to the GLS tracking. (*b*) Temperature preferences extracted from MaxEnt models. Temperatures correspond to mean annual sea surface temperatures.

the South Atlantic Ocean [10] versus Indian Ocean (this study) similar patterns were found: observed and predicted wintering sites for Antarctic prions are at lower latitudes than for thin-billed prions, and the most important oceanographic parameters identified by the models were sea surface temperature and mean chlorophyll *a* concentration. Stable isotope values of feathers grown during the non-breeding period [11–13] support these niche differences for multiple years. Antarctic and sub-Antarctic latitudes are characterized by a small number of dominant swarming crustacean species—krill and hyperiid amphipods—which is consistent with the small range in δ^{15}N-values in blue petrel and thin-billed prion compared with Antarctic prion with considerably more variation in its diet (figure 2).

The present data fit well within current ideas on the evolution of diversity along environmental gradients [18] and isolation by environment [19]. In the Southern Ocean, geographical barriers are lacking and given the high mobility of the petrels, allopatric speciation and isolation by distance are difficult to imagine. Doebeli & Dieckmann [18] modelled evolutionary branching along an environmental gradient, and found that mechanisms of frequency-dependent selection can readily result in patterns of spatial segregation and the emergence of sister species, even in the absence of geographical barriers. Thus, environmental gradients may lead to disruptive selection for specialization and the evolution of sister species with differential adaptations. As the Southern Ocean provides one of the most extended environmental gradients on Earth, the small, highly mobile petrels inhabiting it may offer fine models of isolation by environment and more specifically, the evolution of diversity along environmental gradients.

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References

1. Ainley DG, Dugger KD, Ford RG, Pierce SD, Reese DC, Brodeur RD, Tynan CT, Barth JA. 2009 Association of predators and prey at frontal features in the California Current: competition, facilitation, and co-occurrence. *Mar. Ecol. Prog. Ser.* **389**, 271–294. (doi:10.3354/meps08153)
2. Henkel LA. 2009 Co-occurrence and aggregation of marine birds and mammals in Monterey Bay, California, USA. *Mar. Ecol. Prog. Ser.* **387**, 295–303. (doi:10.3354/meps08082)
3. Navarro J, Forero MG, González-Solís J, Igual JM, Bécares J, Hobson KA. 2009 Foraging segregation between two closely related shearwaters breeding in sympatry. *Biol. Lett.* **5**, 545–548. (doi:10.1098/rsbl.2009.0150)
4. Wilson RP. 2010 Resource partitioning and niche hyper-volume overlap in free-living Pygoscelid penguins. *Funct. Ecol.* **24**, 646–657. (doi:10.1111/j.1365-2435.2009.01654.x)
5. Masello JF, Mundry R, Poisbleau M, Demongin L, Voigt CC, Wikelski M, Quillfeldt P. 2010 Diving seabirds share foraging space and time within and among species. *Ecosphere* **1**, 19. (doi:10.1890/ES10-00103.1)
6. Ridoux V. 1994 The diets and dietary segregation of seabirds at the subAntarctic Crozet Islands. *Mar. Ornithol.* **22**, 1–192.
7. Weiss F, Furness RW, McGill RAR, Strange IJ, Masello JF, Quillfeldt P. 2009 Trophic segregation of Falkland Islands seabirds: insights from stable isotope analysis. *Polar Biol.* **32**, 1753–1763. (doi:10.1007/s00300-009-0674-6)
8. Cherel Y, Bocher P, De Broyer C, 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. (doi:10.3354/meps228263)
9. Cherel Y, Bocher P, Trouvé C, Weimerskirch H. 2002 Diet and feeding ecology of blue petrels *Halobaena caerulea* at Iles Kerguelen, Southern Indian Ocean. *Mar. Ecol. Prog. Ser.* **228**, 283–299. (doi:10.3354/meps228283)
10. 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. (doi:10.1111/jbi.12008)
11. 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. (doi:10.1098/rsbl.2006.0445)
12. 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. (doi:10.3354/meps10795)

13. 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. (doi:10.3354/meps07751)
14. Weimerskirch H, Zotier R, Jouventin P. 1989 The avifauna of the Kerguelen Islands. *Emu* **89**, 15 – 29. (doi:10.1071/MU9890015)
15. Phillips SJ, Anderson RP, Schapire RE. 2006 Maximum entropy modeling of species geographic distributions. *Ecol. Model.* **190**, 231 – 259. (doi:10.1016/j.ecolmodel.2005.03.026)
16. Layman CA, Arrington DA, Montaña CG, Post DM. 2007 Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* **88**, 42 – 48. (doi:10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2)
17. Jackson AL, Inger R, Parnell AC, Bearhop S. 2011 Comparing isotopic niche widths among and within communities: SIBER – stable isotope Bayesian ellipses in R. *J. Anim. Ecol.* **80**, 595 – 602. (doi:10.1111/j.1365-2656.2011.01806.x)
18. Doebeli M, Dieckmann U. 2003 Speciation along environmental gradients. *Nature* **421**, 259 – 264. (doi:10.1038/nature01274)
19. Sexton JP, Hangartner SB, Hoffmann AA. 2014 Genetic isolation by environment or distance: which pattern of gene flow is most common? *Evolution* **68**, 1 – 15. (doi:10.1111/evo.12258)