Geographic variation in the foraging behaviour of South American fur seals

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ABSTRACT: The implicit assumption of many ecological studies is that animal behaviour and resource use are geographically uniform. However, central place foraging species often have geographically isolated breeding colonies that are associated with markedly different habitats. South American fur seals *Arctocephalus australis* (SAFS) are abundant and widely distributed colonial breeding central place foragers that provide potentially useful insights into geographic variation in animal behaviour and resource use. However, SAFS movement ecology is poorly understood. To address knowledge gaps and to explicitly test geographic variation in behaviour, we examined the foraging behaviour of 9 adult female SAFS from 2 Falkland Islands breeding colonies separated in distance by 200 km. A total of 150 foraging trips over 7 mo revealed striking colony differences. Specifically, SAFS that bred at Volunteer Rocks undertook long foraging trips (mean ± SD: 314 ± 70 km and 15.2 ± 2.7 d) to the Patagonian Shelf and shelf slope (bathymetric depth: 263 ± 28 m). In contrast, SAFS that bred at North Fur Island undertook short foraging trips (94 ± 40 km and 5.3 ± 2.1 d) and typically foraged near the Falkland Islands' coastline (bathymetric depth: 85 ± 24 m). Stable isotope analysis of vibrissae $\delta^{13}C$ and $\delta^{15}N$ values also revealed colony differences in the isotopic niche area occupied, which indicated that resource use also differed. Contrary to popular models (Ashmole's halo, hinterland model), colony size was unrelated to distance travelled, and SAFS did not necessarily use foraging grounds closest to their breeding colony. SAFS are likely subject to different selective pressures related to different environmental demands at the 2 breeding colonies. Accordingly, we reason that behavioural differences between breeding colonies reflect different phenotypes, and habitat use is more immediately influenced by phenotype, philopatry and the local environment, rather than density-dependent competition typically attributed to colony segregation in foraging areas.

KEY WORDS: Colony segregation · *Arctocephalus australis* · Patagonian Shelf · Stable isotopes · Resource partitioning · Satellite telemetry · Movement ecology

INTRODUCTION

Ecologists have long recognized the importance of individual and population differences in animal behaviour and resource use and the far-reaching implications for species ecology, evolution and wildlife management (Mayr 1956, Foster 1999). Although individual specialization has attracted considerable scientific interest (e.g. Bolnick et al. 2011), geographic variation in animal behaviour and resource use has received comparatively little attention. Indeed, animal behaviour and resource use are often only characterised for a single population, and the implicit assumption of many ecological studies is that

behaviour between populations is geographically uniform (Foster 1999). This assumption is problematic because habitat accessibility is often unequal between populations, and discrete populations are often associated with contrasting habitats, which profoundly influence animal behaviour and resource use (Tremblay & Cherel 2003, Staniland et al. 2010, Hückstädt et al. 2016, Handley et al. 2017). Hence, a single population may poorly represent species-typical behaviour. Quantifying geographic variation in animal behaviour and resource use is therefore crucial because it enables the development of coherent explanatory frameworks that carry across discrete populations and provides insights into phenotypic plasticity and eco-evolutionary dynamics.

Colonial breeding, central place foraging marine predators are ideal candidates to assess geographic variation in animal behaviour and resource use because they typically have extended breeding ranges. Given that foraging trip distance and duration are limited by the need to return to a central place, foraging areas between breeding colonies are often discrete and associated with contrasting habitats. At large spatial scales that span ocean basins, geographic variation in behaviour and resource use is predictable (Tremblay & Cherel 2003, Staniland et al. 2010, Wakefield 2011, Frederiksen et al. 2012, Nordstrom et al. 2013, Mendez et al. 2017). At smaller spatial scales (10s to 100s of km), the foraging area of individuals from neighbouring colonies could be within range of one another and overlap. In such scenarios, the emerging picture is that competition is mediated by colony-specific foraging areas, although the degree of partitioning varies from complete to partial segregation and seems to be influenced by population density (Grémillet et al. 2004, Robson et al. 2004, Baylis et al. 2008, Lea et al. 2008, Masello et al. 2010, Staniland et al. 2011, Wakefield et al. 2013, Angel et al. 2016). The partitioning of foraging areas between neighbouring colonies implies that geographic variation in behaviour and resource use may also occur across small spatial scales. However, quantifying geographic variation in behaviour ideally involves following individuals over an extended period to determine the temporal consistency of behaviours. Surprisingly, studies that address temporal consistency are rare for central place foraging marine predators, with most studies representing only a snapshot of the annual cycle. Here, we focussed on South American fur seals *Arctocephalus australis* (SAFS) at 2 breeding colonies separated in distance by 200 km to quantify geographic variation in behaviour and resource use by following individuals over 7 mo.

SAFS are colonial breeding central place foragers that breed along the Atlantic and Pacific coasts of South America from Uruguay to Peru. Two subspecies are currently recognized, with SAFS in Peru and northern Chile (*A. australis* unnamed) genetically distinct from SAFS breeding in southern Chile and the South Atlantic (Uruguay, Argentina, Falkland Islands; *A. australis australis*) (Oliveira & Brownell 2014). Despite the geographic range and abundance of SAFS (total population size is estimated to be larger than 200 000 individuals), knowledge of SAFS foraging behaviour is based on only 2 studies at 2 breeding colonies — a staggering statistic in this, the 'golden age' of biologging (Thompson et al. 2003, Crespo et al. 2015, Franco-Trecu 2015). Indeed, by necessity, SAFS movement ecology is still inferred from anecdotal observations dating back to the 1960s, re-sights of a handful of marked individuals or seasonal counts of abundance (Crespo et al. 2015, Bombau & Szteren 2017). Little progress has been made toward understanding SAFS at-sea behaviour, despite movement being a fundamental component in many eco-evolutionary processes.

The most comprehensive SAFS study to date has been at the Falkland Islands. Here, SAFS foraging trip distance and duration increases over the course of lactation, as is reported for many other fur seal species (from a mean ± SD of 8 ± 13 km and 12 ± 13 h in January to 127 ± 27 km and 126 ± 23 h in October–December; Thompson et al. 2003). However, the only dietary study at the Falkland Islands demonstrates that geographic variation in foraging ecology exists (Baylis et al. 2014). At other locations, SAFS behaviour and trophic ecology is typically inferred from stable isotope values of bone or vibrissae opportunistically collected from dead animals (e.g. Vales et al. 2015). The exception is a preliminary biologging study in Uruguay which revealed that adult female SAFS forage in association with the outer Patagonian Shelf during the austral summer (max. distance 531 ± 91 km; Franco-Trecu 2015). Although stable isotope studies are driven by the need for information on SAFS ecology, stable isotope analysis is a broad-scale, indirect method (Newsome et al. 2010). One potential criticism is that unambiguous interpretation of SAFS stable isotope values first requires knowledge of the species' ecology and sources of isotopic variance, which includes geographic variation in behaviour and resource use (e.g. Baylis et al. 2016).

To address knowledge gaps and assess geographic variation in behaviour and resource use, we compiled the most comprehensive SAFS data-set to date

and (1) characterised SAFS foraging behaviour using satellite telemetry, (2) characterised trophic ecology using stable isotope analysis of vibrissae and (3) tested whether behaviour and habitat use differed between breeding colonies. In doing so, we provide unprecedented insights into the movement ecology of this species.

MATERIALS AND METHODS

Study site and animal handling

SAFS breed at 10 locations around the Falkland Islands (Fig. 1). Our study was conducted at North Fur Island (51.129° S, 60.757° W) and Volunteer Rocks (51.513° S, 57.734° W). Although we were unable to undertake a formal census, the number of pups at North Fur Island was about 1500, whereas at Volunteer Rocks, we estimated a few hundred pups. The last SAFS census at the Falkland Islands was undertaken in 1965–1966, when 14 000 SAFS of all age classes were reported. A partial census in the 1980s estimated 20 000 SAFS (Strange 1992).

Like other temperate otariid species, adult female SAFS give birth during the austral summer and pro-

vision their offspring over an 8 to 10 mo period. In late May and early June 2015 (when pups were approximately 5 mo old), we equipped adult female SAFS with Argos linked Fastloc-GPS tags (Wildlife Computers TDR10-F). Adult female SAFS observed suckling a pup were selected at random. To limit disturbance in densely packed colonies, we initially chemically restrained adult female SAFS using tiletamine-zolazepam (Zoletil, Virbac; 1.5 mg kg^{-1}), remotely administered using 0.5 cc darts (Pneu dart) and a CO_2-powered tranquiliser gun (Dan Inject JM Standard) (Baylis et al. 2015b). Lightly immobilized adult female SAFS were then slowly approached and captured using a hoop net. Once in the net, adult female SAFS were masked, and anaesthesia was induced and maintained using isoflurane delivered via a portable gas anaesthetic machine (VOC Rota Flush, Medical Developments International). There were no complications during anaesthesia. Tags were attached using a 2-part epoxy glue (Devcon 5-minute epoxy) and body length was measured. Due to logistical constraints, we did not weigh animals. In total, 5 tags were deployed at North Fur Island and 4 tags at Volunteer Rocks (Fig. 1). We use NF SAFS and VR SAFS to refer to adult female SAFS that bred at North Fur Island and Volunteer Rocks, respectively.

Location data

Tags were programmed to acquire Fastloc-GPS location data at 10 min intervals and transmit Argos location data at 45 s intervals when at the surface. Briefly, partially processed GPS data (satellite pseudo-ranges) were stored on-board the tag and transmitted at user-defined periods based on Argos satellite pass predictions (GPS locations were determined via post-processing). In contrast, Argos location data reflected locations at the time of transmission. Accordingly, Fastloc-GPS data and Argos location data are complementary. To increase the temporal coverage of location data, our analysis combined GPS and Argos location data. We first identified foraging trips (periods when individuals were at-sea). We used haul-out and diving data, when available, to refine foraging trip start and end times and to confirm animals were at sea (diving and haul-out data
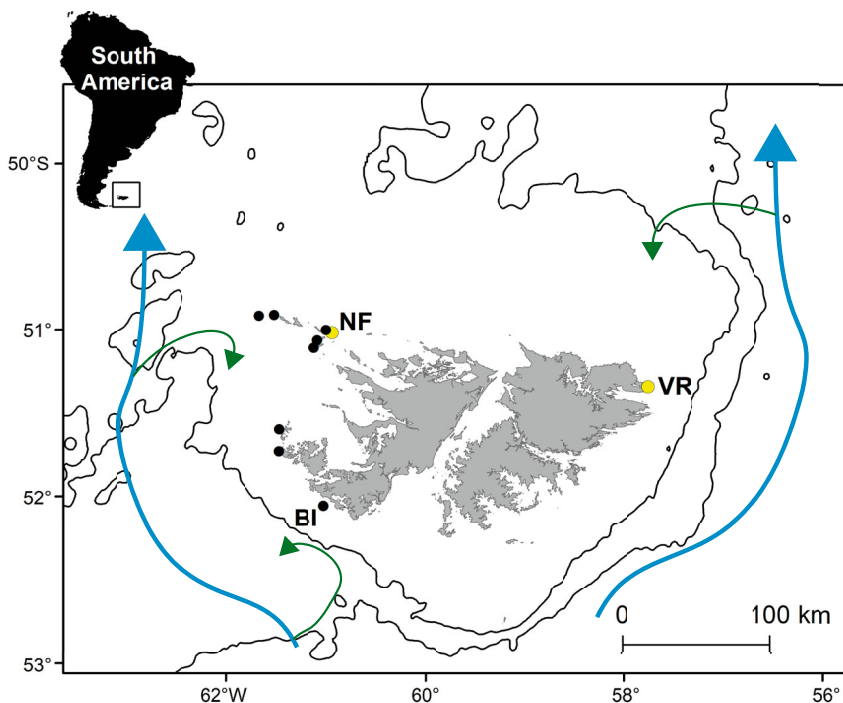

Fig. 1. Breeding locations of South American fur seals at the Falkland Islands (black dots) and a schematic of oceanographic features adapted from Arkhipkin et al. (2013). Blue lines represent the Falkland Current, and green lines represent the approximate position of frontal zones. Yellow dots are the study colonies: Volunteer Rocks (VR) and North Fur Island (NF). Thin black lines are the 200 and 400 m bathymetric contours. BI: Bird Island

were provided as a summary, rather than complete records). GPS locations calculated from only 4 satellites were removed, because initial data exploration revealed that these locations were unreliable. We then ran the location data through a speed filter (3 m s^{-1}) implemented within the R package Argosfilter. To address temporal gaps in location data and to avoid the unrealistic assumption of linear movement between locations, we analysed the data using a continuous time correlated random walk model implemented through the R package CRAWL (v2.1.1) (Johnson et al. 2008). The model accounted for error associated with the 6 Argos location classes (3, 2, 1, 0, A, B). We presumed that GPS locations were true locations, given that error is typically <100 m (Costa et al. 2010). The model produced a 'best-fit' track, with locations predicted hourly along the track. The 'best-fit' track was used for all subsequent analyses.

It was difficult to identify individual foraging trips for 3 adult female SAFS during late lactation when they dispersed away from the breeding colony because of gaps in daily location data combined with foraging trips of short distance and duration. For these individuals, we compared raw location data for the period when foraging trips could not be identified, with utilization distributions (UDs) calculated using foraging trips (UD method described below). UDs were broadly representative of habitat use (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m596p233_supp.pdf). Therefore, our analysis was based only on foraging trips.

For each foraging trip, we calculated maximum distance (km) and duration (d). We compared foraging trip metrics between colonies using linear mixed effects (LME) models, with individual included as a random effect. To assess whether foraging trip distance and duration increased over time, we used generalized additive mixed models (GAMMs) because our initial analysis revealed non-linear patterns in residuals. We accounted for autocorrelation using auto-regressive correlation structure of the order 1 within individual animals. The most parsimonious model was one that included a smoother for each breeding colony. Model validation included plotting residuals versus fitted values to test for homogeneity and quantile-quantile plots to test for normality.

To quantify habitat use, we calculated 50% (core area used) and 90% UDs for each breeding colony using the kernel method implemented within the R Package adehabitatHR (Calenge et al. 2009). The kernel smoothing parameter was the mean area-restricted search scale of 12.6 km, which was calculated using first passage time analysis (assessed from 1 to 150 km), averaged across all foraging trips and implemented using the fpt function in the R package adehabitatLT (Lascelles et al. 2016). Land was excluded from UDs by using bathymetry as a habitat grid. UDs were computed for each individual SAFS and then combined to create an overall colony UD. Each SAFS contributed equally to colony UD. We assessed whether our UDs were representative of each colony by calculating saturation curves based on 50% and 90% UDs. Specifically, we treated each foraging trip as an independent sample and randomly selected an increasing number of foraging trips, with the mean and confidence interval for each step calculated from 1000 iterations. The mean was modelled as a nonlinear asymptotic regression (Lascelles et al. 2016). We then calculated a 'representative value' by taking the area of the kernel UD at the colony level and dividing it by the area of the kernel UD at the asymptote (Lascelles et al. 2016). High values (>85%) were considered representative of the colonies tracked.

Seasonal shifts in habitat use are common among fur seals, including SAFS (Thompson et al. 2003). To assess whether habitat use varied seasonally, we compared 90% and 50% UDs for the austral winter months (May–August), with spring (September–November) and summer (December, which was the final month before tag batteries were exhausted). If a foraging trip spanned 2 seasons, it was assigned to the season where most time was spent.

Finally, for each location we extracted bathymetric depth (m), slope (°) and sea surface temperature (SST) using the GEBCO 30 arc-second grid and GRHSST 1 km dataset (G1SST). To visualize differences in environmental variables between breeding colonies, we calculated the proportion of foraging trip time associated with bathymetric depth, slope and SST. However, to test for differences in bathymetric depth, slope and SST between breeding colonies, we used LME modelling, with individual as a random factor, breeding colony as a fixed effect and month of the year as a covariate. We log transformed bathymetry to achieve homogeneity. As stated, model validation included plotting residuals versus fitted values.

Diving data

Eight of the 9 tags were programmed to store and transmit a summary of diving data (1 m depth resolution) collected over the previous 14 d. We defined a

dive as >10 m in depth and >30 s in duration. Therefore, our diving data could have been biased toward deeper, longer dives. Each dive location was calculated by matching the time at the start of the dive with a location along the 'best-fit' track. We extracted bathymetric depth for each predicted dive location and classified dives as either benthic or pelagic based on the ratio of dive depth divided by bathymetric depth. Dives were classified as benthic when this ratio was ≥0.80 (Baylis et al. 2015a). For each foraging trip, we calculated a mean benthic/pelagic dive index, diving depth (m), diving duration (s) and proportion of day dives (%). We used LME models to test whether diving metrics differed between breeding colonies, with individual included as a random effect.

Stable isotope analysis

Vibrissae are metabolically inert tissues that remain unchanged once grown. Therefore, longitudinal sampling of vibrissae provides information on an individual's trophic and spatial history (Newsome et al. 2010). Vibrissae were collected during tag deployment by cutting the largest vibrissae as close to the skin as possible. Hence, stable isotope data do not cover the deployment period and cannot be directly compared to movement data. Vibrissae length ranged from 95 to 139 mm (mean ± SD: 115 ± 15 mm). Although otariid vibrissae grow linearly over time, growth rates vary between and within species (McHuron et al. 2016). No vibrissae growth estimates are available for SAFS. However, given that the mean vibrissae growth rate is 0.87 ± 0.01 mm d^{-1} for adult female otariids, we presumed that the vibrissae we analysed integrated diet over a period of years (range: 3.0–4.4 yr) (McHuron et al. 2016).

Vibrissae were cleaned prior to analysis using a sponge and 95 % ethanol followed by an ultrasonic bath of distilled water for 5 min (Kernaléguen et al. 2015). Vibrissae were then dried and cut into 5 mm long consecutive segments starting from the proximal (facial) end (Baylis et al. 2017). It was necessary to subsample each 5 mm section to achieve our target mass of 0.5 mg. Samples were packed into tin containers, and carbon and nitrogen isotope ratios were determined by a Carlo-Erba elemental analyser interfaced with a Finnigan Delta Plus XP mass spectrometer (Stable Isotope Laboratory, University of California Santa Cruz, USA). Stable isotope ratios were measured in parts per mil (‰) deviation from international standards (Vienna-Pee Dee belemnite

for carbon and atmospheric air N_2 for nitrogen), according to the following equation: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$ where X is ^{15}N or ^{13}C and R is the corresponding ratio of (^{15}N:^{14}N) or (^{13}C:^{12}C). Stable isotope ratios are reported as $\delta^{13}C$ values for carbon and $\delta^{15}N$ values for nitrogen. Data were corrected for sample mass and instrument drift. Measurement precision (SD) was 0.03 ‰ for $\delta^{13}C$ and 0.06 ‰ for $\delta^{15}N$, based on within-run replicate measures of the laboratory standard (pugel).

We compared adult female SAFS $\delta^{13}C$ and $\delta^{15}N$ isotope values using LME models, with individual included as a random effect and a low order correlation structure to account for temporal autocorrelation (corARMA, p = 2) (Baylis et al. 2017). To test for overlap between isotopic niche areas, we used the mean stable isotope value for each individual to calculate standard ellipse area (SEA), which is a proxy for core isotopic area (analogous to SD for univariate data and contains approximately 40 % of the data). SEAs were calculated using Bayesian inference techniques, with uncertainty in SEA (credible intervals) calculated using 100 000 posterior draws, and overlap calculated from 1000 posterior draws (Jackson et al. 2011). All values are reported as mean ± SD.

RESULTS

Between May and December 2015, we recorded 150 foraging trips made by 9 adult female SAFS (Table 1). Adult female SAFS consistently returned to their respective breeding colonies until late lactation (September), when some adult female SAFS spent extended periods of time away from their breeding colonies — presumably after pups had weaned (Table S1 in the Supplement). Despite the low number of individuals sampled, 50 % UDs (core areas used) reached saturation (representative value of 87 % for VR SAFS and 97 % for NF SAFS; Fig. 2). However, the area associated with the 90 % UD may have been underestimated (representative value of 83 for VR SAFS and 77 % for NF SAFS; Fig. 2). On average, VR SAFS were significantly longer than NF SAFS (Welch's t-test: $t = -4.2$, df = 6.9, p = 0.004; Table 1).

VR SAFS undertook significantly longer foraging trips when compared with NF SAFS (LME$_{distance}$ $F_{1,7} = 34.9$, p < 0.001; LME$_{duration}$ $F_{1,7} = 39.3$, p < 0.001; Table 1). Foraging trip distance and duration increased significantly between May and December at both breeding colonies. However, our GAMMs and the resulting smoothers indicated that for the aver-

Table 1. Foraging trip and diving metrics for adult female South American fur seals that bred at Volunteer Rocks (n = 4) and North Fur Island (n = 5). Also presented are the mean vibrissae $\delta^{13}C$ and $\delta^{15}N$ values. Benthic dive ratio: dive depth/bathymetric depth. Values are mean ± SD; na: data not available

Seal ID	North Fur Island					Volunteer Rocks				Mean North Fur Island	Mean Volunteer Rocks
	148742	148743	148745	148748	148752	148746	148749	148753	148757		
Length (cm)	131	123	127	126	132	133	137	139	140	128 ± 4	137 ± 3
Location data											
Deployment period (d)	195	188	81	196	177	194	202	212	144	167 ± 49	188 ± 30
Mean trip duration (d)	5.8 ± 4.4	8.2 ± 4.8	4.9 ± 2.6	5.4 ± 2.9	2.3 ± 1.3	17.6 ± 5.8	12.8 ± 9.6	12.8 ± 3.7	17.4 ± 6.6	5.3 ± 2.1	15.2 ± 2.7
Max trip duration (d)	19.9	18.1	10.1	15.4	6.2	28.2	31.0	18.6	25.5	13.9 ± 5.7	25.8 ± 5.7
Total number of trips	17	19	12	26	34	9	13	14	6	108	42
Mean max distance (km)	97 ± 135	125 ± 98	63 ± 15	140 ± 176	45 ± 35	369 ± 275	268 ± 226	241 ± 123	378 ± 150	94 ± 40	314 ± 70
Max distance (km)	521	444	89	726	150	940	674	499	481	386 ± 265	648 ± 213
Mean distance winter (km)	50 ± 12	84 ± 41	63 ± 15	106 ± 114	43 ± 37	223 ± 14	218 ± 207	216 ± 120	360 ± 160	70 ± 26	254 ± 71
Mean distance spring (km)	449 ± 101	194 ± 129	na	194 ± 242	55 ± 8	692 ± 255	546 ± 115	338 ± 97	469	317 ± 253	451 ± 105
Mean distance summer (km)	na	na	na	na	na	128	107	132	na	na	122 ± 14
Dive data											
Total dive number	4107	4221	1980	4390	6285	1889	2613	3916	na	20983	8418
Mean bathymetric depth (m)	80 ± 26	115 ± 35	86 ± 17	94 ± 19	49 ± 28	267 ± 180	233 ± 153	288 ± 106	na	85 ± 24	263 ± 28
Benthic dive ratio	0.76	0.82	0.67	0.61	0.79	0.55	0.36	0.31	na	0.73 ± 0.09	0.41 ± 0.12
Mean diving depth (m)	53 ± 18	79 ± 22	54 ± 17	51 ± 25	28 ± 12	90 ± 39	51 ± 21	66 ± 23	na	53 ± 18	69 ± 19
Max diving depth (m)	142	238	142	166	178	202	276	356	na	173 ± 39	278 ± 77
Mean duration (s)	114 ± 22	138 ± 28	109 ± 21	102 ± 22	93 ± 15	142 ± 36	130 ± 32	136 ± 29	na	111 ± 17	136 ± 6
Proportion night dives (%)	44	35	36	48	64	41	53	40	na	45 ± 12	44 ± 7
Stable isotope values											
$\delta^{13}C$ (‰)	−15.2	−15.4	−15.3	−15.3	−15.3	−15.6	−15.3	−15.7	−15.7	−15.3 ± 0.1	−15.6 ± 0.2
$\delta^{15}N$ (‰)	14.9	14.7	14.6	15.2	14.3	14.4	14.4	14.1	13.9	14.7 ± 0.3	14.2 ± 0.3

age VR SAFS, foraging trip distance and duration had a curvilinear pattern over time, whereby distance and duration increased initially and then declined toward the end of the sampling period (GAMM$_{s(distance)}$ $F_{3.9}$ = 13.4, p < 0.001, GAMM$_{s(duration)}$ $F_{2.4}$ = 4.8, p = 0.005; Fig. 3 and Fig. S2). In contrast, for the average NF SAFS, foraging trip distance increased toward the end of the sampling period, and duration increased linearly (GAMM$_{s(distance)}$ $F_{3.9}$ = 10.2, p < 0.001; GAMM$_{s(duration)}$ $F_{1.0}$ = 16.9, p < 0.001; Fig. S2).

During winter, the 90% UD of VR SAFS was almost 3 times larger than NF SAFS (35500 versus 12000 km^2), and the core foraging area (50% UD) was over 4 times as large (6800 versus 1600 km^2; Fig. 3). VR SAFS typically foraged along the Patagonian Shelf slope to the north of the Falkland Islands, whereas NF SAFS foraged on the Patagonian Shelf, to the west of the Falkland Islands (foraging trip distance: 254 ± 71 km versus 70 ± 26 km, respectively; Table 1, Fig. 3).

During spring, the 90% UD of VR SAFS was almost 3 times larger when compared with winter (Fig. 3). Similarly, the 90% UD of NF SAFS was 6 times larger, when compared with winter (Fig. 3). VR SAFS foraged beyond the Patagonian Shelf during spring (Fig. 3). In contrast, NF SAFS typically remained on the Patagonian Shelf and frequented other SAFS breeding colonies in Argentina, notably Staten Island and Isla Rasa (Fig. 3). There was no overlap between colony 50% UDs (core areas used) in either winter or spring (Fig. 3). During December, VR SAFS foraged to the east of the Falkland Islands (Fig. 3).

In general, adult female SAFS spent the majority of foraging trip time (93%) in SST between 4 and 7°C in shallow water <400 m deep (also 93% of foraging trip time) that was associated with relatively flat-bot-
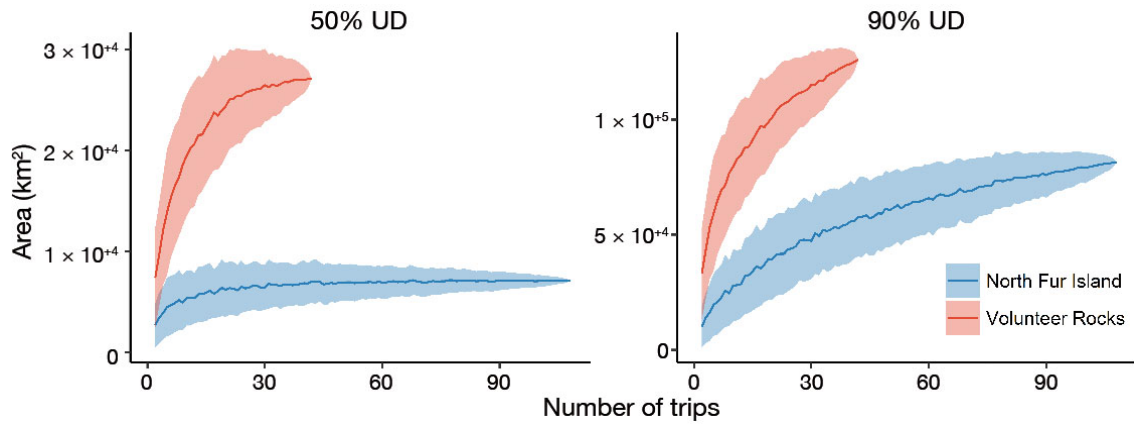
Fig. 2. The area of the 50 and 90 % utilization distributions relative to an increasing number of foraging trips were used to assess whether data were representative. Foraging trips were selected at random and the process iterated 1000 times to generate a mean (solid line) and 95 % confidence interval (shaded area)
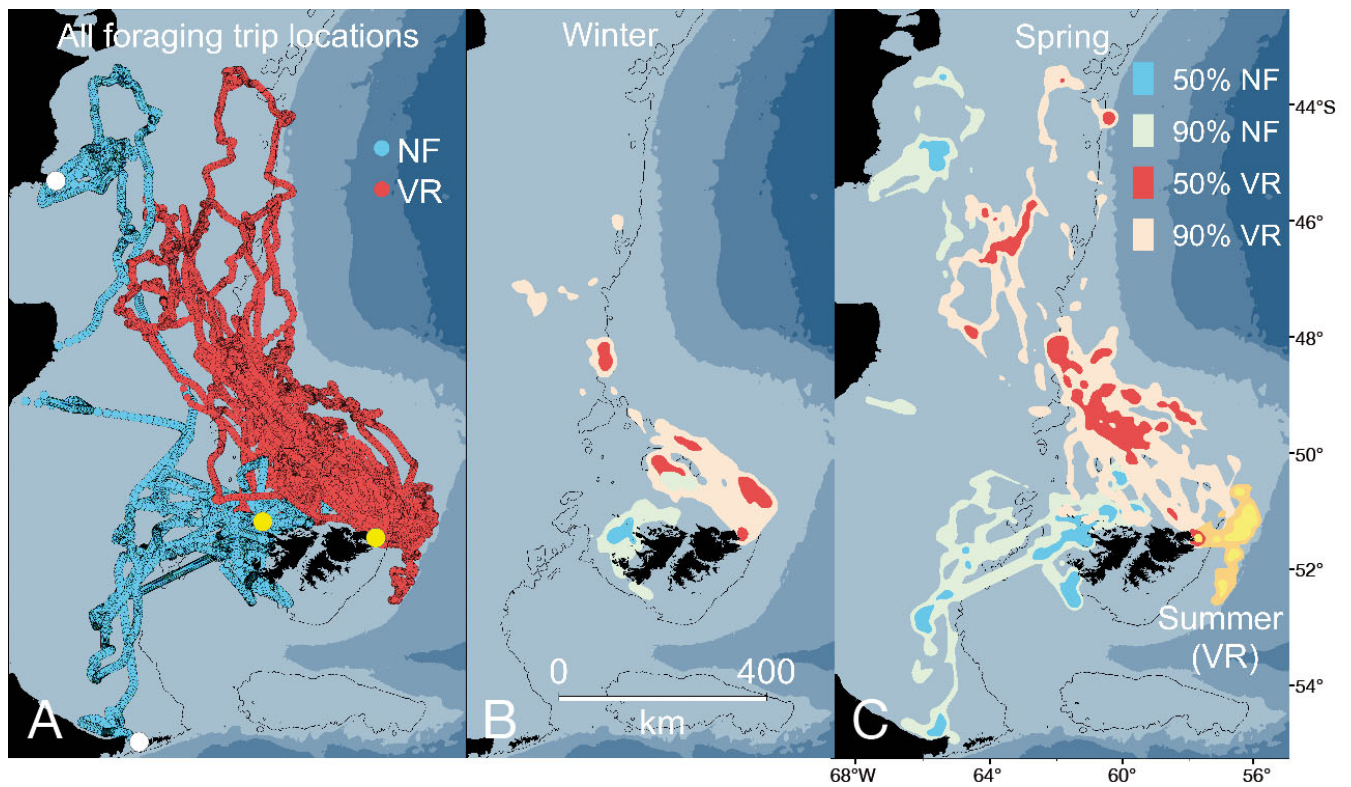

Fig. 3. Habitat use of 9 adult female South American fur seals breeding at North Fur Island (NF, n = 5) and Volunteer Rocks (VR, n = 4) between May and December 2015. (A) Foraging trip locations predicted hourly. Yellow dots represent the deployment locations, white dots represent Staten Island to the south and Isla Rasa to the north. (B,C) 50 and 90 % utilization distributions (UDs) in (B) winter and (C) spring and summer. Location data in summer were only available for Volunteer Rocks (yellow kernel = 50 % UD, orange kernel = 90 % UD). Thin black line shows the 200 m bathymetric contour

tomed topography (97 % of foraging trip time was associated with a sea floor slope of less than 2°; Fig. 4). SST was not significantly different between breeding colonies (5.9 ± 0.2°C versus 5.8 ± 0.6°C for VR SAFS and NF SAFS, respectively; LME_{SST} $F_{1,7}$ = 0.01, p = 0.96). However, foraging trips of VR SAFS, when compared with NF SAFS, were associated with deeper bathymetric depths (mean bathymetry 227 ± 56 m versus 89 ± 23 m, respectively; $LME_{bathymetry}$ $F_{1,7}$ = 24.6, p = 0.001), and steeper sea floor slopes (0.8 ± 0.1° versus 0.5 ± 0.1°, respectively; LME_{slope} $F_{1,7}$ = 21.1, p = 0.002).

Diving data

In total, 29 401 dives >10 m and >30 s were recorded from 8 adult female SAFS (3 VR SAFS and 5 NF SAFS). The total number of dives varied between individuals (range: 1889–4390) (Table 1). Diving occurred both day and night, and the mean diving depth was similar between breeding colonies (NF SAFS: 53 ± 18 m; VR SAFS: 69 ± 19 m; $LME_{mean\ depth}$ $F_{1,6}$ = 1.3, p = 0.29; Table 1). However, diving duration was significantly longer for VR SAFS when compared with NF SAFS (136 ± 6 s versus 111 ± 17 s, respectively; $LME_{duration}$ $F_{1,6}$ = 7.8, p = 0.031) and maximum dive depth was significantly deeper (278 ± 77 m versus 173 ± 39 m, respectively; $LME_{max\ depth}$ $F_{1,6}$ = 13.4, p = 0.010) (Table 1). NF SAFS had a greater proportion of dives closer to the sea floor when compared with VR SAFS (ratio of dive depth to the sea floor was 0.73 ± 0.09 versus 0.41 ± 0.12, respectively; Table 1).

Stable isotope analysis

In total, 172 vibrissae segments were analysed from 9 adult female SAFS (Fig. S3). Stable isotope values were not significantly different between colonies (LME $\delta^{13}C$: $F_{1,7}$ = −2.1, p = 0.074; LME $\delta^{15}N$: $F_{1,7}$ = 4.7, p = 0.067), and 1 VR SAFS (ID 148749) had $\delta^{13}C$ and $\delta^{15}N$ values that closely resembled NF SAFS (Table 1). However, the isotopic niche area differed between breeding colonies. Specifically, there was limited overlap between colony SEA, calculated from the mean isotope value of each individual (<1% overlap based on maximum likelihood estimates of standard ellipses corrected for small sample size, or an 84% chance of overlap being less than 5% based on 1000 posterior estimates of ellipse overlap). This measure is of course sensitive to ellipse size. When ellipse size was increased from 40 to 95% of the data, the proportion of overlap increased to 38% based on maximum likelihood fitted ellipses, or 50% chance of
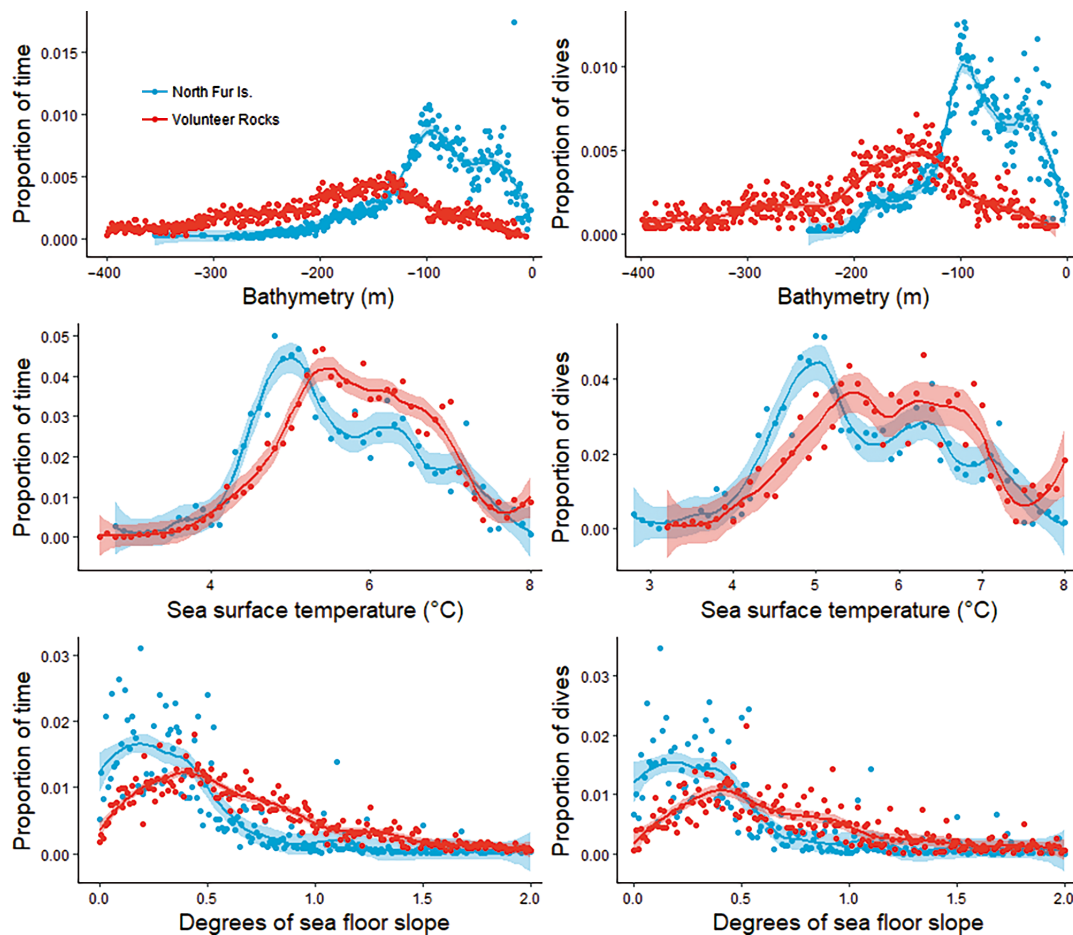

Fig. 4. Left: summary of environmental variables extracted for each hourly location (expressed as proportion of time). Right: for comparison, we also present environmental variables extracted for each dive location (expressed as proportion of dives). A loess smoother was added to aid visualization
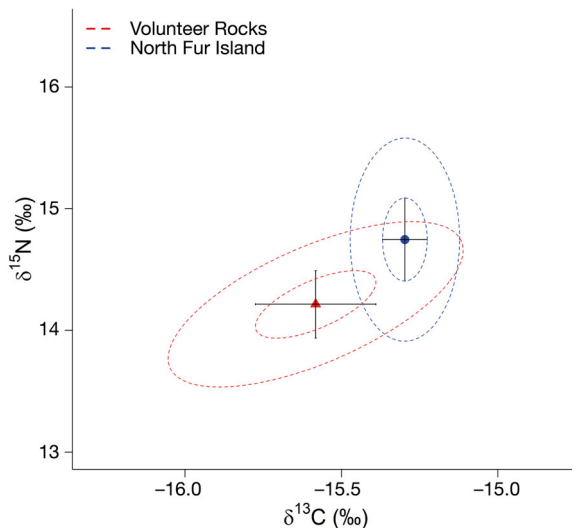
Fig. 5. Mean isotope values from 9 adult female South American fur seals (n = 4 at Volunteer Rocks and n = 5 at North Fur Island). Symbols are the mean values for Volunteer Rocks (red triangle) and North Fur Island (blue dot), while bidirectional error bars represent SD. Inner and outer dashed lines represent 40 and 95 % ellipse areas, respectively

overlap being less than 10 % based on 1000 posterior estimates of ellipse overlap (Fig. 5). The isotopic niche area of VR SAFS was almost twice as large as NF SAFS (0.19‰ versus 0.10‰, respectively; 95 % credible interval = 0.04−0.44‰ and 0.02−0.19‰, respectively). While these results must be interpreted with caution due to our small sample size, colony differences in isotopic niche area suggests that VR SAFS fed at a lower trophic level and in more pelagic habitat, when compared with NF SAFS.

DISCUSSION

SAFS at-sea behaviour is largely unknown. We combined SAFS movement ecology with trophic ecology and revealed strikingly different behaviour and to a lesser degree resource use, between breeding colonies separated in distance by only 200 km. Most obvious, VR SAFS typically undertook extended foraging trips to the Patagonian Shelf slope in the north of the Falkland Islands (mean bathymetric depth 263 ± 28 m). In contrast, NF SAFS typically foraged near the Falkland Islands' coastline, and foraging trips were constrained to the Patagonian Shelf (mean bathymetric depth 85 ± 24 m). Colony differences persisted throughout our 7 mo study and are therefore described with a high degree of confidence. Although 90 % UDs may have underestimated

area used, this is unlikely to influence the interpretation of overall trends because we expect distance-dependent travel costs to be minimised in obligate central place foragers, and spatial usage to eventually decline with distance from the colony (Orians & Pearson 1979). A fundamental aim in ecology is to understand the processes that shape animal behaviour and resource use, given that these attributes influence a host of eco-evolutionary factors such as community structure, metapopulation dynamics and disease ecology, and enable coherent conservation-oriented management policies to be developed (Morales & Ellner 2002). Accordingly, our study is important because it is the first to provide insights into the processes that shape spatial and temporal variation in SAFS behaviour.

Habitat selection is an important component of animal behaviour and a key determinant of individual survival, reproductive success and ultimately population dynamics. The maximum foraging trip distance in our study was 940 km, far greater than the 200 km separating the 2 colonies. Hence, the foraging areas used by adult female SAFS were accessible from either colony, despite the distance between breeding colonies and the central place foraging constraint placed upon females by the need to provision nutritionally dependent offspring. Yet, the foraging areas of VR SAFS and NF SAFS were mutually exclusive. Although some degree of overlap is likely to have occurred between breeding colonies that were not tracked (Fig. 1), our findings contribute to the growing body of literature that describes colony-specific foraging areas in colonial-breeding, central place foraging marine predators, and the profound influence colony location has on habitat selection and habitat preference (Robson et al. 2004, Baylis et al. 2008, Wakefield et al. 2013, 2017).

Ashmole's halo and the hinterland model are 2 models that are often used to provide a conceptual framework to understand the mechanisms that drive colony foraging (Ashmole 1963, Cairns 1989, Gaston et al. 2008, Masello et al. 2010, Wakefield et al. 2013). These models were developed for seabirds but are readily transferable to other colonial-breeding marine taxa, including pinnipeds in temperate ecosystems. Ashmole's halo predicts that density-dependent competition results in local prey depletion, requiring individuals to travel further to provision their young (Ashmole 1963). However, density-dependent competition and localised prey depletion are unlikely to explain patterns in SAFS habitat use at the Falkland Islands. Volunteer Rocks is smaller than North Fur Island, both in terms of annual pup production (fewer

than 500 pups versus approximately 1500 pups) and available breeding space (0.01 versus 0.04 km^2). Hence, according to Ashmole's halo model, we would expect the foraging trips of VR SAFS to be shorter in distance and duration, when compared with NF SAFS. Although many studies on central place foraging marine predators report a positive correlation between foraging trip distance, duration and colony size (e.g. Lewis et al. 2001, Ainley et al. 2004), we found no such a relationship. Indeed, foraging trip distance was over 3 times longer, and duration almost twice as long, for VR SAFS when compared with the larger North Fur Island breeding colony. The hinterland model predicts that individuals from different colonies segregate because travel costs differ between colonies and individuals should forage in areas closer to their own colony (Cairns 1989). However, the core foraging area of VR SAFS was often closer to North Fur Island than Volunteer Rocks. Hence, our results are inconsistent with popular models, and the segregation of SAFS foraging areas at the Falkland Islands is more complicated than a trade-off between density dependence and colony location.

For example, colony differences in habitat use were coupled with profound and consistent differences in behaviour, the most obvious being foraging trip distance and duration. Considering the distance between colonies, VR SAFS and NF SAFS are likely subjected to different selective pressures related to different local environmental demands. Hence, different behaviours between SAFS breeding colonies represent phenotypic plasticity, and phenotypes could differ between populations without underlying genetic differences (Foster 2013). In this context, we reason that SAFS behaviour and resource use may more immediately be influenced by phenotype, philopatry (common among otariids; Hoffman & Forcada 2012) and the local environment, rather than intraspecific competition and colony segregation per se.

Size differences further support the notion that phenotype differs between breeding colonies. Specifically, VR SAFS were longer when compared with NF SAFS. This crude proxy of size could be an artefact of our small sample size. However, geographic variation in body size among populations is commonplace (Mayr 1956). For instance, colony variation in body size is often reported for seals and seabirds (Goldsworthy et al. 2009, Staniland et al. 2010, 2011, Cook et al. 2013, Jeglinski et al. 2015, Orben et al. 2015). One hypothesis for colony differences in body size is colony demographics. For example, the available breeding area at Volunteer Rocks is smaller than North Fur Island. If we assume length

correlates with age, then larger, older adult females at Volunteer Rocks may outcompete younger, smaller adult females for limited breeding space, as proposed for Antarctic fur seals *Arctocephalus gazella* (Staniland et al. 2010). In addition, geographic variation in body size could reflect an adaptation to local environmental conditions, given that size differences between colonies are often correlated with contrasting foraging behaviours (Staniland et al. 2011, Cook et al. 2013, Orben et al. 2015). For example, diving depth and duration are positively correlated with body size in diving animals, because larger animals have lower mass-specific metabolic rates and greater oxygen stores (Costa et al. 2004). Hence, a larger size may confer a competitive advantage to VR SAFS, because increased diving capacity would enable more efficient longer and deeper dives (VR SAFS had longer diving durations and deeper maximum diving depths). Alternatively, higher absolute energy reserves and lower absolute metabolic rates may enable larger females to be more efficient at converting food into fat reserves, which is likely advantageous in the context of extended foraging trips (Festa-Bianchet et al. 1998, Beauplet & Guinet 2007).

Foraging theory predicts that animals adopt optimal strategies that maximise fitness by maximising foraging efficiency and offspring provisioning, and minimising the risk of starvation (Ydenberg et al. 1994). Long foraging trips may reduce provisioning opportunities, be energetically costly and increase predation risk (although adult female SAFS likely have few predators), when compared with short foraging trips. Hence, the extended distances travelled by VR SAFS must be offset by the quality or accessibility of prey. For example, adult female Antarctic fur seals that undertake long foraging trips have a higher-energy content diet relative to conspecifics that undertake short foraging trips, which is proposed to facilitate a relatively constant rate of energy delivery to offspring irrespective of foraging trip length (Staniland et al. 2007). Our stable isotope analysis indicated that despite considerable overlap and a small sample size, trophic ecology also varied between VR SAFS and NF SAFS. Benthic prey on the Patagonian Shelf have higher δ^{13}C and δ^{15}N values relative to pelagic prey (Vales et al. 2015). Hence, isotopic differences in niche areas between colonies presumably signify different trophic levels at which SAFS fed and different diets. SAFS diet includes crustaceans (lobster krill *Munida gregaria*), cephalopods (*Illex argentinus* and *Doryteuthis gahi*) and fish (predominantly notothenid species and *Sprattus fu-*

gensis) (Baylis et al. 2014). Different isotope values likely represent different combinations of these prey groups. This is supported by a preliminary analysis of a small number of scats collected from Volunteer Rocks and North Fur Island at the time of tag deployment (n = 21 and n = 60 scats, respectively). Volunteer Rocks scats contained a greater frequency of occurrence of fish when compared with North Fur Island (78 versus 30%, respectively), whereas North Fur Island scats contained more crustaceans (54 versus 21%, respectively; A. M. M. Baylis unpubl. data). Although we do not have sufficient data to resolve whether the energetic values of SAFS prey vary between breeding colonies, presumably both foraging strategies could be optimal if foraging areas were associated with predictable oceanographic features.

Volunteer Rocks and North Fur Island are located near the Falkland Current. The Falkland Current originates from the Antarctic Circumpolar Current, and when it reaches the continental shelf to the south of the Falkland Islands, it branches into 2 main northward flowing currents (Arkhipkin et al. 2012, 2013). Oceanography around the Falkland Islands is complex. Primary productivity is influenced by tidal movements, meso-scale fronts, quasi-stationary eddies and regions of upwelling in both summer and winter, with incursions of the Falkland Current slope waters reaching up to 150 km from the shelf-break, onto the Patagonian Shelf (Arkhipkin et al. 2012, 2013). The complexity of local oceanography notwithstanding, the foraging areas of adult female SAFS in winter were in the vicinity of quasi-stationary frontal zones that are located in the east (north eastern front) and west (west offshore front) of the Falkland Islands, which are most readily identified on the basis of strong salinity gradients (Fig. 1) (Arkhipkin et al. 2012, 2013). Although overly simplified, this implies that SAFS habitat use is explained by predictable ocean features, rather than differences in bathymetry and slope per se. The use of predictable oceanographic features is consistent with other temperate and polar fur seal species, which typically forage in association with seasonally predictable large-scale oceanographic features (frontal zones, coastal upwellings, shelf-break regions) (Beauplet et al. 2004, Page et al. 2006, Staniland et al. 2007, Baylis et al. 2012, Nordstrom et al. 2013, Wege et al. 2016).

During spring, SAFS foraging trip distance and duration increased. Seasonal changes in foraging trip distance and duration are broadly consistent with an earlier study that tracked SAFS from Bird Island (Fig. 1) (Thompson et al. 2003). Although we did not follow the fate of pups, foraging trip duration could

have been related to offspring age (as pups age they can withstand longer periods of fasting) or changes in the metabolic requirements of adult female SAFS or their offspring (Beauplet et al. 2004). Interpreting seasonal shifts is complicated during the latter part of spring because some foraging trips were likely associated with the post-weaning period, when adult female SAFS are free from central place foraging constraints. Nevertheless, in December, when pups should have already weaned, but prior to the 2016 breeding season, VR SAFS abruptly shifted their foraging behaviour and undertook short foraging trips beyond the Patagonian Shelf slope to the east of Volunteer Rocks. Although this could be related to the developing foetus and changes in female metabolic requirements just prior to parturition, intuitively, the seasonal changes in foraging areas that we report are ultimately linked to changes in the availability of preferred prey. For example, the abundance and distribution of finfish and squid around the Falkland Islands vary seasonally because of migrations associated with spawning and feeding (e.g. *D. gahi* has a summer and winter peak in biomass related to spring and autumn spawning cohorts) (Arkhipkin et al. 2012, 2013).

Finally, the geographic differences in behaviour and resource use that we describe raise intriguing questions regarding population connectivity and how maternal foraging strategies influence offspring survival. For example, movement ecology implies that female-mediated genetic exchange is more likely to occur between North Fur Island and breeding colonies in Argentina (e.g. Staten Island), when compared with Volunteer Rocks. Our results also highlight that SAFS will be differentially affected by anthropogenic hazards, such as hydrocarbon activities and fisheries, depending on colony location. Geographic variation in behaviour is likely to occur throughout the extended breeding range of SAFS. However, plasticity itself is also likely to be geographically variable and dependent on colony location and local environment factors, such as the distribution of preferred prey.

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