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Winter foraging site fidelity of king penguins breeding at the Falkland Islands

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Abstract Foraging site fidelity has profound consequences for individual fitness, population processes and the effectiveness of species conservation measures. Accordingly, quantifying site fidelity has become increasingly important in animal movement and habitat selection studies. To assess foraging site fidelity in king penguins (*Aptenodytes patagonicus*) breeding at the Falkland Islands (51.48°S, 57.83°W), we measured overlap in time spent in foraging areas (at a $0.1° × 0.1°$ grid resolution) between successive foraging trips and foraging route consistency during the crèche period. In total, 30 complete foraging trips from seven king penguins were recorded between April and October 2010. King penguins predominantly foraged on the highly productive Patagonian slope, to the north of the Falkland Islands [median foraging trip distance 213 km (SD = 215 km) and duration 12.8 days (SD = 14.7 days)]. Overlap in time spent in an area on consecutive foraging trips ranged between 2 and 73 % (mean 27 %, SD = 22 %). Bearing during the outbound portion of foraging trips was typically highly repeatable for individual birds, but foraging trip duration and distance were not. Travel during the outbound phase of foraging trips was consistent with the direction of the northward-flowing Falkland Current that may act as a directional cue or facilitate rapid transit to foraging areas. Flexibility in foraging trip distances and durations may be a response to changes in resource availability and changes in the energetic requirements of adults and chicks over an extended breeding cycle.

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Introduction

Foraging site fidelity (the return to a previously occupied foraging area) has profound consequences for individual fitness, population dynamics, ecological processes and the efficiency of species' conservation measures (Bradshaw et al. 2004; Hillen et al. 2009; Piper 2011; Monsarrat et al. 2013; Wakefield et al. 2013; Augé et al. 2013; Van Beest et al. 2013). Accordingly, quantifying site fidelity has become increasingly important in animal movement and habitat selection studies (reviewed in Piper 2011). Foraging site fidelity is reported in a diverse range of taxa including colonial breeding marine central place foragers, such as seals and seabirds (Irons 1998; Hedd et al. 2001; Call et al. 2008; Chilvers 2008; Baylis et al. 2011; Robinson et al.

2012; Harris et al. 2014). For these animals, foraging site fidelity during the breeding season is an optimal foraging strategy when prey resources are associated with spatially predictable ocean features such as ocean fronts (Weimer-skirch 2007). This is because the distance and duration of foraging trips are restricted by the need to return to a central place and provision dependent offspring. However, marine central place foragers with extended provisioning periods (>6 mo) must also contend with seasonal changes in resource availability and distribution (Beauplet et al. 2004; Womble and Sigler 2006; Baylis et al. 2008; Ville-gas-Amtmann et al. 2012). Consequently, extreme faithfulness to a foraging area can lead to a mismatch between foraging effort and prey availability, implying that the degree of foraging site fidelity may not be consistent over time, but constitute a trade-off between diminishing returns and searching for new, potentially more profitable foraging regions.

During the breeding season, penguins are central place foragers with parents alternating shifts between foraging at sea and returning to incubate eggs or provision chicks. Penguins typically have short breeding cycles (coinciding with the austral summer) and when freed from the constraints of provisioning offspring, most species undertake winter migrations, presumably an adaptation to reduce density-dependent competition during seasonal changes in resource availability (Dingle and Drake 2007; Ratcliffe et al. 2014). However, king penguins (*Aptenodytes patagonicus*) are unique in that their breeding cycle takes over a year to complete (Le Bohec et al. 2007 and references therein). Therefore, king penguins are an ideal sub-antarctic seabird species to assess foraging site fidelity during winter, when resource abundance, availability and distribution may be less predictable than in summer.

King penguins have a circumpolar breeding distribution, with two sub-species currently recognised (king penguins breeding in the South Atlantic Ocean (*A. p. patagonicu*s) are separated from those breeding in the southern Indian and Pacific Oceans (*A. p. hali*)) (reviewed in Bost et al. 2013). However, irrespective of breeding location, during the austral summer, king penguins predominantly feed on myctophids and typically in association with the Antarctic Polar Front (APF), although the sub-antarctic front is also frequented (Cherel et al. 2002; Bost et al. 2013). In comparison, during the austral winter, adults tend to undertake extended foraging trips to the marginal ice zone in response to reduced resource availability in the Antarctic Polar Frontal Zone (the water masses between the sub-antarctic front to the north and the APF to the south) (Jouventin et al. 1993; Charrassin and Bost 2001; Bost et al. 2004). For example, at the Crozet Islands, maximum foraging trip distance and duration range from 406 ± 149 km, lasting 8 ± 3 days in summer,

to 1,613 ± 388 km, lasting 77 ± 41 days in winter (see 'Appendix'; Charrassin and Bost 2001; Pütz 2002). The exception to long winter foraging trips is king penguins breeding at the Falkland Islands (south-west Atlantic Ocean), where winter foraging trip distance and duration are 727 ± 428 km and 30 ± 26 days, respectively (Pütz 2002; 'Appendix').

The Falkland Islands are at the temperate boundary of the species range being the furthest king penguin breeding colony from the APF and the only colony within close proximity to the Patagonian Shelf, the largest continental shelf in the Southern Ocean (Arkhipkin et al. 2012). The highly productive Patagonian Shelf is dominated by the cold-water Falkland Current between 55°S and 37°S, a northward-flowing current originating from the Antarctic Circumpolar Current (Peterson and Whitworth 1989; Acha et al. 2004). A previous study on king penguins at the Falkland Islands reported a shift in foraging regions, from the south of the Falkland Islands in autumn/early winter (including extended foraging trips beyond the APF to the marginal ice zone) to the north of the Falkland Islands by late winter/spring (on the Patagonian Shelf slope) (Pütz 2002). The comparatively short foraging trips of king penguins breeding at the Falkland Islands during the austral winter, combined with a shift in foraging regions (north vs. south), provide a unique opportunity to assess how foraging site fidelity and foraging flexibility are mediated in a central place forager, over a period when resources may be less predictable than summer (Pütz 2002; Rivas et al. 2006). Here, (1) we test for individual foraging site fidelity of king penguins during the chick-rearing phase, (2) we explore whether a subset of environmental variables can explain the amount of time penguins spend in a given area and (3) given that the regions oceanography is dominated by the Falkland Current, we test for associations between current direction and penguin travel.

Methods

Study site and device deployment

The Falkland Islands are located approximately 600 km east of mainland South America (Fig. 1). Approximately 720 pairs of king penguins breed at Volunteer Point (51.48°S, 57.83°W), the largest king penguin breeding colony at the Falkland Islands (Pistorius et al. 2012). The incubation period of king penguins breeding at Volunteer Point is 55 ± 2 days (based on only six pairs) (Otley et al. 2007). Chicks typically hatch between January and early February and fledge 10–13 mo later (Otley et al. 2007). In April 2011, during crèche, eight king penguins were
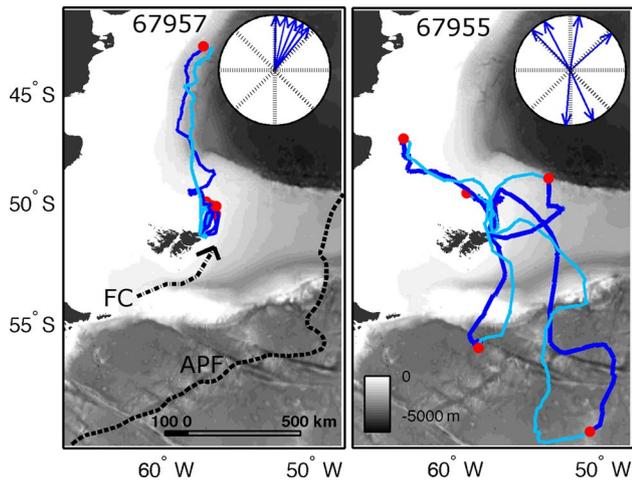
Fig. 1 Repeat foraging trips for two king penguins that undertook extended foraging trips from the Falkland Islands during crèche in 2011. The *arrow bars* indicate the bearing to maximum distance, while the *red dots* are the maximum distance to which bearing is measured. The *dark blue* portion of the king penguin foraging trip represents movement to the maximum distance, while *light blue* is the return portion of the foraging trip. The grey scale of 0 to −5000 represents shaded-relief bathymetry (m), with the Patagonian Shelf being white (i.e. <200 m depth). APF: Antarctic Polar Front (source Orsi and Ryan 2001); FC: the eastern branch of the Falkland Current (source Arkhipkin et al. 2004)

captured after feeding their chick (to ensure that they were breeding penguins of comparable breeding stages) and fitted with satellite tags (Sirtrack® Kiwisat 101's) (Table 1). Satellite transmitters were hydro-dynamically streamlined and attached to the back feathers using Tesa® tape (4651) and cyanoacrylate glue (Loctite®401). Satellite tags were programmed to transmit every 45 s with a 12-h on/off duty cycle interval. Although satellite tags may increase foraging trip duration and have deleterious effects on foraging efficiency (Wilson et al. 2004), we could not assess whether the attachment of the satellite tags influenced the foraging behaviour of king penguins, due to logistical constraints. However, a similar king penguin study reported that meal size and breeding failure were comparable between control and instrumented penguins (Cotté et al. 2007).

Processing location data

We pre-processed our Kalman-filtered ARGOS data by omitting Z class hits (for which the location process failed) and filtered our data for erroneous locations using a maximum speed of 14 km/h (Cotté et al. 2007) and the 'speed filter' function in the R package 'trip' (R core team 2013; Sumner 2010). The filtered data were then processed using a continuous-time correlated random walk model, which predicted penguin locations at equally

spaced points in time (hourly and including periods when the satellite tag was off) (R package 'CRAWL', Johnson et al. 2008). This permitted the calculation of time spent in a cell of a regular grid (0.1° × 0.1°) created in Arc-Map (ESRI®ArcGIS v10.0™, ESRI, California, USA). Although a degree-based grid implies that cell area will vary depending on location, most foraging trips had a narrow range of latitude. A 0.1° × 0.1° grid was chosen because it has previously been used to calculate king penguin time spent in area (Péron et al. 2012) and it approximates the resolution at which most habitat variables could be extracted (see below).

Time spent in an area

Longer residence time in foraging king penguins is associated with periods of intensive prey searching and a greater number of foraging dives (Péron et al. 2012). Hence, we used the time spent in an area as a proxy of foraging effort. To assess how environmental variables influenced the time spent in an area, we extracted sea surface temperature (SST; NASA JPL-L4UHfnd-GLOB-MUR, 0.011° × 0.011°), sea surface height (SSH; AVISO Global DT-Ref Merged MSLA; 1° × 1°), eddy kinetic energy (EKE; NOAA OSCAR, 0.1/3° × 0.1/3°), significant wave height (Wave; AVISO, 0.1° × 0.1°), mixed layer depth (MLD; HYCOM GLBa.08, 0.08° × 0.08°) and mixed layer pressure (MLP; mixed layer thickness defined as the depth at which the temperature change from the surface temperature is 0.2 °C, HYCOM GLBa.08, 0.08° × 0.08°) using the R version of NOAA's Xtractomatic data client (http://coastwatch.pfel.noaa.gov/xtracto/) and MGET 0.8a49 (using ArcMap 10.0) (Roberts et al. 2010). We also extracted bathymetry (ETOPO 1 arc-min data set) and calculated bathymetric slope (Slope) using ArcMap. These broad-scale environmental variables are proxies for ocean processes and features that influence the aggregation of prey (*e.g.* fronts and meso-scale ocean features) and typically influence penguin foraging behaviour (Péron et al. 2012). Environmental variables were extracted at each location along a foraging route, and an average calculated for each 0.1° × 0.1° grid cell.

Given that our data comprised multiple foraging trips from the same individuals and exploratory analysis revealed nonlinear trends in residuals, we included a random effect of individual and trip within a generalised additive mixed model (GAMM) implemented using the R package mgcv (Wood 2006). Smooth terms were fitted to all predictor variables using penalised thin plate regression splines (Wood 2006). We log-transformed time spent in an area due to heterogeneity in model residuals. A Gaussian distribution with an identity link function was used for

Table 1 Foraging trip characteristics of seven king penguins breeding at the Falkland Islands. Foraging trips are separated into months based on the start date

ID	Trip	Duration (d)	Max. distance (km)	SI max. distance	SI outbound phase	Start date 2011	End date 2011
67954	1	8.3	183	0.75	0.97	17-Apr	25-Apr
67954	2	47.3	492	0.53	0.96	06-May	22-Jun
67955	1	5.5	164	0.90	0.94	05-May	10-May
67955	2	48.7	950	0.54	0.58	12-May	29-Jun
67955	3	27.6	227	0.32	0.92	06-Jul	02-Aug
67955	4	26.6	631	0.70	0.84	15-Aug	10-Sep
67955	5	16.6	402	0.63	0.95	14-Sep	30-Sep
67955	6	16.6	505	0.76	0.87	03-Oct	19-Oct
67957	1	4.6	128	0.82	0.85	01-May	05-May
67957	2	9.2	165	0.55	0.68	06-May	15-May
67957	3	6.8	152	0.67	0.94	17-May	24-May
67957	4	13.2	163	0.40	0.92	27-May	09-Jun
67957	5	68.2	971	0.59	0.90	18-Jun	25-Aug
68032	1	11.7	198	0.84	0.87	12-Apr	23-Apr
68032	2	20.7	175	0.85	0.96	03-May	23-May
68034	1	8.1	169	0.81	0.96	07-Apr	15-Apr
68034	2	7.1	181	0.90	0.98	19-Apr	26-Apr
68034	3	7.4	197	0.81	0.92	30-Apr	07-May
68034	4	15.2	270	0.78	0.95	12-May	27-May
68034	5	10.0	173	0.85	0.95	04-Jun	14-Jun
68034	6	18.3	264	0.60	0.90	22-Jun	10-Jul
68048	1	12.9	250	0.56	0.90	02-May	15-May
68048	2	12.7	256	0.95	0.97	18-May	30-May
68048	3	22.3	221	0.35	0.95	08-Jun	30-Jun
680251	1	6.3	210	0.92	0.96	05-Apr	11-Apr
680251	2	6.3	210	0.88	0.93	13-Apr	19-Apr
680251	3	5.4	178	0.88	0.99	22-Apr	27-Apr
680251	4	9.1	225	0.58	0.92	02-May	11-May
680251	5	13.3	216	0.70	0.94	15-May	28-May
680251	6	26.3	334	0.42	0.76	10-Jun	06-Jul
Median		12.8 ± 14.7	213 ± 215	0.72 ± 0.18	0.93 ± 0.09		
Mean		17.1 ± 14.7	295 ± 215	0.69 ± 0.18	0.90 ± 0.09		
Min.		4.6	127.0	0.32	0.58		
Max.		68.2	971.0	0.95	0.99		
April		7.6 ± 2.1	191 ± 16	0.85 ± 0.06	0.95 ± 0.04		
May		16.4 ± 14.7	277 ± 222	0.68 ± 0.17	0.89 ± 0.12		
June		29.0 ± 22.7	393 ± 329	0.56 ± 0.20	0.89 ± 0.08		

SI straightness index

the response variable. The degree of colinearity between the covariates was tested using Pearson's correlations and variance inflation factors (Zuur et al. 2010). Due to colinearity, we removed SST prior to analysis. Model selection was performed by removing the least significant term in the model. The most parsimonious model was associated with the lowest Akaike information criterion (AIC) value. Model validation followed Wood (2006) and included plotting the residuals against the fitted values and each covariate in the model, as well as residuals against covariates excluded from the final model.

Consistency in foraging trip characteristics

We also used the time spent in an area (0.1° × 0.1° grid) to calculate whether individuals returned to (and spent
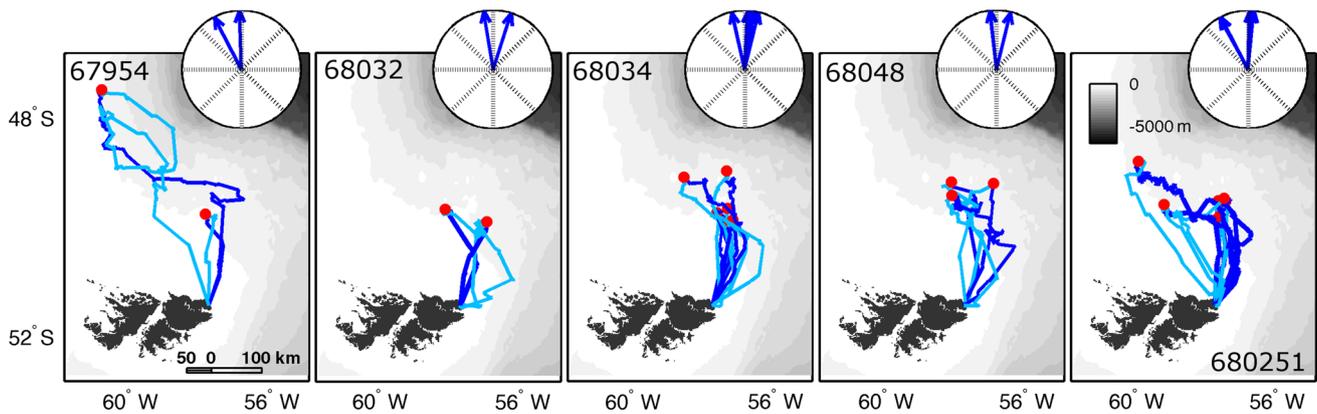
Fig. 2 Same as Fig. 1, but repeat foraging trips for the remaining five king penguins tracked at the Falkland Islands during crèche in 2011

time in) previously visited areas on the preceding foraging trip. In addition to time spent in an area, consistency in foraging behaviour was measured using four variables describing movement: (1) foraging trip duration (h), (2) maximum distance from the colony (km), (3) bearing to furthest location from the colony and (4) departure bearing (mean bearing during outbound portion of the foraging trip). The outbound portion of each foraging trip was defined as the period of travel (limited to the maximum distance from the colony) where the running averages of five consecutive swimming speeds were higher than the mean swimming speed of the whole foraging trip (Cotté et al. 2007). To explore within versus between individual variance for trip distance and duration, we used linear mixed effects models with a restricted maximum likelihood (REML), implemented using the R package 'rptR' (Nakagawa and Schielzeth 2010). Response variables were log-transformed to approximate a Gaussian error. In the case of bearing to furthest location, repeatability (R) was calculated using the equation (Lessells and Boag 1987), $R = \frac{S_A^2}{(S^2 + S_A^2)}$ where

$$S^2 = \text{Mean Square}_{\text{Between groups}}$$

$$S_A^2 = (\text{Mean Square}_{\text{Between groups}} - \text{Mean Square}_{\text{within groups}})/n_0$$

n_0 = coefficient related to the sample size per group

We used a circular ANOVA in the R package 'circular' to estimate mean square variance components for the bearing to the furthest location (Patrick et al. 2014).

In addition, to assess whether king penguins travelled directly to foraging areas, we also calculated a straightness index to (i) maximum distance (maximum distance/total distance travelled) and (ii) a straightness index during the outbound phase of the foraging trip (maximum distance

during outbound phase/total distance travelled during the outbound phase). A value of one represents the most direct route of travel (Benhamou 2004).

Association with current direction

We were also interested in testing whether the outbound portion of an individual's foraging trip was associated with current direction, as previously reported at other breeding locations (Cotté et al. 2007). Deviations in the bearing between penguin directions and underlying current directions (AVISO geostrophic current products derived from sea level anomalies and NOAA OSCAR products) were calculated. A bearing deviation from 0 to 90 and from 270 to 360 indicated penguins travelled in a similar direction to the current, while a bearing deviation from 90 to 270 indicated opposing directions (Cotté et al. 2007). To test for similarity between penguin and current direction, we calculated a circular–circular correlation in the R Package 'CircStats'. All values are presented as mean ±SD, unless otherwise stated.

Results

One satellite tag stopped transmitting 23 days into deployment and was excluded from analysis. For the remaining seven penguins, a total of 7,080 at-sea locations were received during 30 complete foraging trips (two to six foraging trips for each bird) (Table 1). The maximum foraging trip distance and duration were on average 213 ± 215 km and 12.8 ± 14.7 days, respectively. Two penguins undertook extended foraging trips of greater than 900 km from the colony (Table 1; Fig. 1). Twenty-nine of the 30 foraging trips were associated with the Patagonian Shelf to the north-east of the Falkland Islands at some point during the foraging trip (Figs. 1, 2).
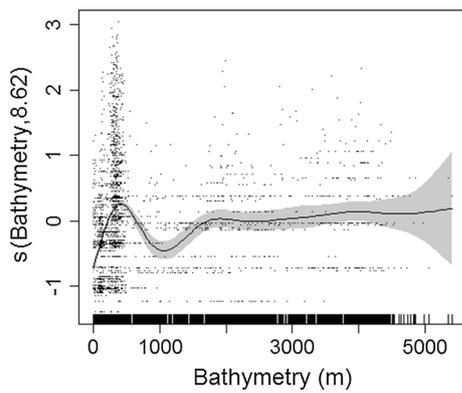
Fig. 3 Smoothed partial residual plots of bathymetry, the only significant smooth term derived from our generalised additive mixed model (GAMM)

Fig. 4 Frequencies of bearing deviations between current direction and king penguin locations during the outbound portion of foraging trips. Similar travel to the current direction is represented as 270° to 90°, while opposing travel to current direction is represented as 90° to 270°

Time spent in an area

Over 80 % of all penguin time was spent on the continental slope to the north-east of the Falkland Islands (mean bathymetry of 314 ± 115 m). The most parsimonious model of time spent in an area contained the variable bathymetry and factor month (described below) (Table 2). Bathymetry had a positive effect on time spent in an area up to 400 m. Between 400 and 1,000 m, bathymetry had a negative effect on the time spent in an area, and for depths >1,000 m, the relationship between time spent in an area and bathymetry was constant, with large confidence intervals at the end of the smoother corresponding to few data points (Fig. 3). Although the relationship between bathymetry and king penguin time spent in an area was significant, it only explained a small proportion of the variance (7 %).

Consistency in foraging trip characteristics

Overlap in time spent in an area between consecutive foraging trips was variable within and between individuals (mean 25 ± 21 %, range 2–73 %) (Table 3). The mean distance and duration travelled increased between April and July (Table 1). The maximum distance individuals travelled from the colony and the duration of foraging trips were not repeatable
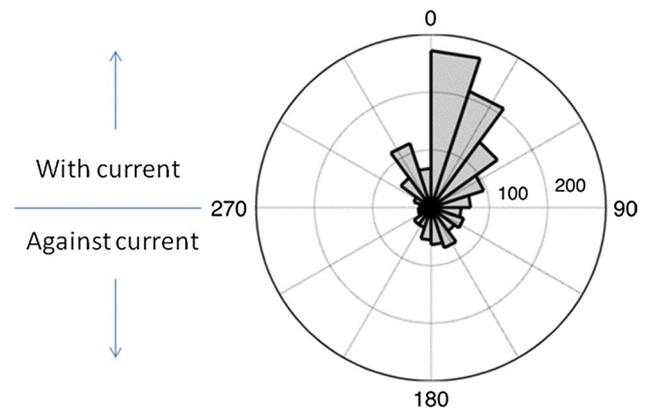
($R = 0.10 \pm 0.14$ and $R = 0.01 \pm 0.10$, $P > 0.05$, respectively). Bearing on the outbound portion of the trip was, however, highly repeatable ($R = 0.96$) and, to a lesser extent, bearing to maximum distance travelled ($R = 0.31$). The mean straightness index during the outbound phase of foraging trips was high (0.90 ± 0.06), but the straightness index to maximum distance was variable, being higher in April (0.85 ± 0.06) when compared with other months (Table 1).

Association with current direction

Bearing deviations suggested that king penguins tended to swim in a similar direction as the current during the outbound phase of foraging trips (Fig. 4; circular correlation coefficient, $r = 0.03$, $F = 1.32$, $P = 0.19$). The mean current speed during the outbound phase of penguin travel was 0.14 ± 0.10 ms^{-1}.

Discussion

Our study revealed that king penguins typically foraged within a narrow range of bearings on successive foraging

Table 2 Proportion of overlap ($0.1° \times 0.1°$ grid cell) in time spent in an area between consecutive king penguin foraging trips

PTT	FT1&2 overlap (%)	FT2&3 overlap (%)	FT3&4 overlap (%)	FT4&5 overlap (%)	FT5&6 overlap (%)
67954	10				
67955	24	4	21	2	2
67957	14	21	65	25	
68032	14				
68034	52	65	47	10	73
68048	25	25			
680251	12	15	8	19	13

Table 3 To assess how environmental variables influenced the amount of time penguins spent in an area, we implemented generalised additive mixed models (GAMMs), using id and trip as random effects

Competing models						Significance of smooth terms in model 10			
Model	Random effects	Factors	Df	AIC	Δ AIC	Variable	edf	F	p value
(1) Global	ID	–	16	7,010.174	90.255	Bathymetry	8.9	32.9	<0.001
(2) Global	ID|Trip	–	18	6,941.737	21.818				
(3) Global	ID|Trip	Month	22	6,936.623	16.704				
(4) -s(MLD)	ID|Trip	Month	20	6,932.357	12.438				
(5) -s(EKE)	ID|Trip	Month	18	6,929.126	9.207				
(6) -s(Wind)	ID|Trip	Month	16	6,925.503	5.584				
(7) -s(Slope)	ID|Trip	Month	14	6,922.666	2.747				
(8) -s(SSH)	ID|Trip	Month	13	6,921.621	1.702				
(9) -s(MLP)	ID|Trip	Month	12	6,921.201	1.282				
(10) -s(Wave)	ID|Trip	Month	10	6,919.919	0				

The global models contain all environmental variables. Other models denote the interaction term that is removed from the global model and the change in AIC this produced. Model selection is based on AIC. The final model (model 10) contained the smooth term bathymetry and the factor month

MLD mixed layer depth, *EKE* eddy kinetic energy, *Wind* wind speed, *Slope* bathymetric slope, *Wave* significant wave height, *MLP* mixed layer pressure, *SSH* sea surface height

trips and travelled directly to the Patagonian Shelf slope, a region associated with a shelf-break front and enhanced levels of primary productivity (Franco et al. 2008). Despite consistency in foraging trip bearings and direct travel to the spatially predictable Patagonian Shelf slope, the environmental variables in our models (that included bathymetry) were weak predictors of king penguin time spent in an area, and overlap in time spent in an area on consecutive foraging trips was variable. Overall, foraging trip distance and duration increased between April and July and foraging routes became more tortuous (although these indices were variable both between and within individuals). This may reflect flexible foraging strategies or search behaviours that improved the chance of prey encounters once king penguins had reached the Patagonian Shelf slope. Progressively longer foraging trips over the course of the chick-rearing period is widely reported among seabirds and is typically a consequence of declining resources or a response to intrinsic factors (*e.g.* changes in the dietary requirements of adults and chicks, or improved chick fasting capability) (Charrassin et al. 1998; Mori and Boyd 2004; Ronconi and Burger 2008; Montevecchi et al. 2009; Vaillant et al. 2013).

Penguin 67955 (Fig. 1) was unique because of the limited overlap between consecutive foraging trips compared with all other king penguins tracked. This may reflect sexual differences in foraging strategies (*e.g.* Vaillant et al. 2013) and highlights one caveat of our study—we did not determine the sex of the penguins tracked. The consistency in foraging trip bearings for the remaining six penguins studied is remarkable considering the displacement

king penguins are likely to encounter en route (*e.g.* due to wind and waves) and given navigation in the open ocean must rely on cues other than local topography. Although poorly understood, seabird navigation integrates olfactory cues, bearing and distance orientation and complex spatial memory-based strategies (Nevitt et al. 2004; Bingman and Cheng 2005; Trathan et al. 2008; Gagliardo et al. 2013). In our study, travel during the outbound phase of foraging trips was also consistent with the direction of the northward-flowing Falkland Current, as previously reported for sympatric breeding Rockhopper penguins (*Eudyptes c. chrysocome*) and Magellanic penguins (*Spheniscus magellanicus*) (Pütz et al. 2002, 2003). The Falkland Current may act as a directional cue or facilitate rapid transit to foraging areas. However, the average current speed encountered by king penguins was below the average speed reported for the Falkland Current (0.4–0.5 m/s^{-1}), indicating king penguins travelled peripherally to the main current flow (Peterson 1992). Hence, the degree to which the Falkland Current facilitates king penguin navigation and movement remains unclear. Given the directional fidelity observed, it is also plausible that king penguins remember the direction to foraging areas and use this knowledge on subsequent foraging trips, as proposed for fur seals and other seabird species (Bonadonna et al. 2001; Hamer et al. 2001; Baylis et al. 2011; Regular et al. 2013; Patrick et al. 2014). While we cannot link spatial memory to fitness, it is often presumed that long-lived animals benefit from familiarity with resources because familiarity facilitates direct travel to foraging areas that may reduce the energetic costs of travel (Bradshaw et al. 2004; Piper 2011; Fagan et al. 2013).

Table 4 Published data on king penguin foraging trip distances and durations over autumn and winter

Breeding location	Foraging trip duration (d)	Max. foraging trip distance from colony (km)	Source
C	53	1,816	Pütz (2002)
C	59	1,603	
C	126	1,974	
C	19	725	
C	89	1,883	
C	118	2,239	
C	–	1,608	Charrasin and Bost (2001)
C	–	1,856	
C	–	1,475	
C	–	1,495	
C	–	1,842	Bost et al. (2004)
C	–	1,856	
C	–	1,650	
C	–	1,984	
C	–	1,475	
C	–	1,419	
C	–	1,138	
C	–	1,487	
C	–	865	
C	–	1,495	
C	–	1,667	
H	–	2,330	Moore et al. (1999)
H	–	1,220	
MEAN	77 ± 39	1,632 ± 411	
FI	24	1,398	Pütz (2002)
FI	27	1,122	
FI	55	1,186	
FI	4	260	
FI	7	374	
FI	4	224	
FI	11	281	
FI	10	386	
FI	9	247	
FI	48	1,187	
FI	26	981	
FI	15	509	
FI	17	485	
FI	86	1,265	
FI	33	233	
FI	30	772	
FI	54	784	
FI	97	1,547	
FI	34	903	
FI	20	669	
FI	11	459	
MEAN (FI)	30 ± 26	727 ± 428	

C Crozet Islands, *H* Heard Island, *P* Possession Islands, *FI* Falkland Islands

How animals maximise their fitness by optimising time spent foraging in different areas is a fundamental question in optimal foraging theory (Charnov 1976). Patchily distributed prey is scale dependant (Weimerskirch 2007). At spatial scales of tens to hundreds of kilometres, features such as shelf breaks concentrate zooplankton, fish and squid (Weimerskirch et al. 2007; Nordstrom et al. 2013). Consumers should aggregate in the most predictable or profitable regions of prey availability (Stephens and Krebs 1986; Benoit-Bird et al. 2013). Accordingly, king penguins predominantly foraged in the region of the shelf slope because prey is presumably more predictable (temporally persistent) and foraging efficiency may be higher compared with other regions (*e.g.* Arkhipkin et al. 2012). This hypothesis is compelling because the energy budget rule predicts that when energy returns are above a threshold, animals should be risk averse and select the least variable option (in this case, the shelf slope) to minimise the risk of starvation (Stephens and Krebs 1986; Hurly 2003). In addition, site fidelity to the shelf slope could reflect the accessibility of foraging habitats (*e.g.* Watanuki et al. 2003; Wakefield et al. 2011). Specifically, the central place foraging constraint imposed during winter (despite being relaxed by increased fasting capacity of chicks) implies foraging habitats are not equally accessible to king penguins (i.e. APF, Patagonian Shelf, marginal ice zone). King penguins may optimise foraging at the Patagonian shelf slope because the costs of travel (time and energy) offset the gains of moving to other, more profitable regions (Matthiopoulos 2003; Trathan et al. 2008). This could explain why only two king penguins undertook extended foraging trips, when at other breeding locations, extended foraging trips over winter are common (Jouventin et al. 1993; Charrassin and Bost 2001; Bost et al. 2004).

The comparatively short winter foraging trips undertaken by king penguins breeding at the Falkland Islands presumably confers an advantage over conspecifics at other breeding locations (Jouventin et al. 1993; Charrassin and Bost 2001; Bost et al. 2004). Specifically, king penguins breeding at the Falkland Islands should expend less energy reaching foraging grounds and have the capacity to allocate more resources to chicks over winter by feeding chicks more often. Although we did not weigh chicks during the study, previous studies at the Falkland Islands report that chicks retain body mass for longer over winter when compared with other breeding locations (Otley et al. 2007). Therefore, the comparatively short foraging trip durations over winter should yield higher breeding success as previously proposed (Pütz 2002). However, over the past 40 years, the number of breeding pairs at the Falkland Islands has only increased to around 700 pairs (Pistorius et al. 2012). In contrast, the number of king penguins breeding at Macquarie Island increased (recovery from exploitation) from 3,400 to 218,000 breeding pairs between 1930 and 1980, while the number of breeding pairs at St Andrews Bay, South Georgia, increased from 700 in 1928 to now in excess of 150,000 breeding pairs (Rounsevell and Copson 1982; Trathan et al. 2008). It is unlikely that access to favourable habitat limits population growth at the Falkland Islands, given the expanse and productivity of the Patagonian Shelf slope and the proximity of the Falkland Islands to the shelf slope. The dive depth of king penguins breeding at the Falkland Islands is also comparable to that reported at other breeding colonies, suggesting the vertical accessibility of prey is similar to other sites (Charrassin et al. 1998; Pütz and Cherel 2005). Given that the Falkland Islands are at the edge of the king penguin breeding range, population growth may be impeded by marginal breeding habitat (e.g. temperate may be warmer but also wetter) that could result in high chick mortality, as previously reported during some winters (Pistorius et al. 2012).

Finally, we found no evidence to support a shift in foraging habitat between early and late winter, as previously described (Pütz 2002). In our study, king penguin foraging trips during winter were shorter in distance and duration when compared with Pütz (2002) (average 295 ± 215 vs. 727 ± 428 km, and 17 ± 15 vs. 30 ± 26 days, respectively). Discrepancies could reflect inter-annual variability in resource availability and distribution, implying the degree of foraging site fidelity may also vary inter-annually. However, differences in the maximum distances reported are accentuated by differences in the accuracy of biologging devices used (geolocators used by Pütz (2002) are typically associated with large location errors when compared to satellite tags) (Phillips et al. 2004; Costa et al. 2010). Inter-annual variability in foraging habitat and site fidelity could be resolved by combining trophic markers such as stable isotopes with inter-annual tracking studies.

Appendix

See Table 4.

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