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SPATIAL AND TEMPORAL VARIABILITY IN THE FORAGING AREAS OF BREEDING KING PENGUINS

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Abstract. King Penguins (*Aptenodytes patagonicus*) from breeding islands in the Indian Ocean (Crozet and Kerguelen Islands) and the Atlantic Ocean (South Georgia and Falkland Islands) were equipped with global location sensors to compare their foraging patterns during different times of the year. In summer, all birds investigated traveled toward the Antarctic Polar Front (APF), irrespective of whether they bred to the north (Crozet Islands, Falkland Islands), within (Kerguelen Islands) or to the south (South Georgia) of this hydrographic feature. Whereas most birds remained north of the APF and foraged in waters of the Antarctic Polar Frontal Zone, some penguins also traveled, or remained (South Georgia), south of the APF and foraged in Antarctic waters. It appeared that food resources in the vicinity of the APF were sufficiently predictable to warrant travel of several hundred km by King Penguins for foraging. Data collected on the winter distribution of King Penguins indicated at least two different foraging strategies. Birds from the oceanic Crozet Islands foraged beyond the APF in the Antarctic waters, whereas birds from the Falkland Islands relied also on the resources provided by the highly diverse and productive slope of the Patagonian Shelf. However, despite these differences, in both cases minimum distances of sometimes more than 10 000 km were covered. Further research on the foraging habitats of King Penguins over the entire breeding season and the temporal and spatial changes of oceanographic features is necessary to obtain a comprehensive picture on the variability in the foraging ranges of King Penguins.

Key words: Aptenodytes patagonicus, *Crozet, dispersal, Falkland Islands, global location sensors, Kerguelen, South Georgia.*

Variabilidad Espacial y Temporal en las Áreas de Forrajeo de Individuos Reproductivos de *Aptenodytes patagonicus*.

Resumen. Comparamos los patrones de forrajeo de individuos reproductivos de *Aptenodytes patagonicus* provenientes de las islas del Océano Índico (Islas Crozet y Kerguelen) y Océano Atlántico (Islas Georgia del Sur y Malvinas) durante diferentes períodos del año, equipando pingüinos con sensores de localización global. En el verano, todas las aves investigadas viajaron hacia el Frente Polar Antártico (FPA), independientemente de si se reprodujeron al norte (Islas Crozet, Islas Malvinas), en (Islas Kerguelen) o al sur (Islas Georgias del Sur) de aquella entidad hidrográfica. Aunque la mayoría de las aves permanecieron al norte del FPA y forrajearon en aguas de la Zona Polar Frontal Antártica, algunos pingüinos también viajaron hacia el sur del FPA y forrajearon en aguas antárticas. Al parecer los recursos alimenticios en el FPA fueron lo suficientemente predecibles como para justificar que los pingüinos viajen varios cientos de kilómetros para forrajear. Los datos colectados durante la distribución de invierno de *A. patagonicus* indicaron por lo menos dos estrategias de forrajeo diferentes. Las aves provenientes de las islas oceánicas Crozet forrajearon más allá del FPA en aguas antárticas, mientras que las aves provenientes de las Islas Malvinas dependieron además de los recursos que provee la diversa y productiva plataforma marítima patagónica. Sin embargo, a pesar de estas diferencias, en ambos casos a veces las aves cubrieron distancias mínimas de más de 10 000 km. Para obtener un panorama completo sobre la variabilidad en los rangos de forrajeo de *A. patagonicus* es necesario efectuar más investigaciones sobre los hábitats de forrajeo de estos pingüinos durante la totalidad de la época reproductiva y durante todos los cambios temporales y espaciales de las entidades hidrográficas.

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INTRODUCTION

Knowledge of the way in which pelagic seabirds make use of the marine habitat is crucial in understanding their foraging strategies and energy demands, and only this knowledge enables us to identify potential threats to them while at sea (Weimerskirch et al. 1997). Among seabirds, much research has been conducted on King Penguins (*Aptenodytes patagonicus*), because they travel considerable distances at sea (Pütz et al. 1999) and are also among the best avian divers (Kooyman et al. 1992). Furthermore, the accessibility of their breeding colonies and their comparatively large bodies (Williams 1995) have facilitated the use of sophisticated remote sensing devices to monitor their foraging ecology.

King Penguins are unique among penguins in that it takes more than one year from egg laying to fledging (Williams 1995). They breed on sub-Antarctic islands between 45°S and 55°S latitude in the Atlantic and Indian Oceans, generally within a distance of 400 km from the Antarctic Polar Front (APF). The APF represents the biological frontier of Antarctica and is defined by the 2°C isotherm at 200 m water depth (Deacon 1982), which usually coincides with the 4–5°C surface isotherm (Park et al. 1993). Waters bordered by the APF in the south and the Subantarctic Front (SAF) in the north are defined as the Antarctic Polar Frontal Zone (APFZ). The APFZ is the main summer foraging habitat for King Penguins breeding on Crozet Islands to the north of the APF (Bost et al. 1997, Pütz et al. 1999, Charrassin and Bost 2001). Interestingly, King Penguins breeding south of the APF forage to the north of their colony (Rodhouse et al. 1998, Moore et al. 1999). King Penguins feed predominantly on myctophid fishes (Cherel and Ridoux 1992), which dominate the total stock in terms of biomass and abundance at the APF (Pakhomov et al. 1994). However, our knowledge of the winter dispersal of these birds is scarce, although there is evidence that in winter King Penguins from Crozet forage farther south beyond the APF in Antarctic waters (Jouventin et al. 1994, Pütz et al. 1999, Charrassin and Bost 2001).

The aim of this study was to investigate simultaneously the foraging areas of King Penguins at various breeding islands situated to the north and to the south of the APF throughout the breeding season using global location sensors (GLS). Due to pronounced oceanographic differences compared with other, mainly oceanic, breeding sites, special attention was paid to birds from a recently established breeding colony on the Falkland Islands. This site differs in many aspects from all other King Penguin breeding sites, as the Falkland Islands are the most temperate, they are the farthest away from the APF, and they are located on the southern edge of the highly productive Patagonian Shelf.

METHODS

Fieldwork was conducted on Crozet Islands (Possession Island, 46°25′S, 51°40′E) between 1994 and 1996, on Kerguelen Islands (Cape Rathmanoff, 49°15′S, 70°30′E) in 1995, and on South Georgia (Husvik, 54°11′S, 36°40′W) and the Falkland Islands (Volunteer Beach, 51°29′S, 57°50′W) in 1996 (Table 1).

King Penguins were captured after feeding their chick. In order to ensure comparable breeding stages, only early breeders (i.e., birds with large chicks which were assumed to have hatched in January) were equipped with devices. The GLS were then attached along the midline of the birds on the lower back, about 5 cm above the preen gland, using a combination of tape (Tesa 4561, Beiersdorf AG, Hamburg, Germany), neoprene glue (Deutsche Schlauchbootfabrik, Eschershausen, Germany), and two-component epoxy glue (Loctite® 401, Loctite GmbH, München, Germany) according to the method described by Wilson et al. (1997). At Crozet Islands, a nearby station that was occupied year round allowed for continuous monitoring of the birds. None of the devices loosened to the point that they had to be removed. However, in cases where the fate of the chick was uncertain (i.e., the study bird did not associate with its chick while ashore), devices were removed and attached to other birds rearing chicks. On Kerguelen Islands, fieldwork was conducted in summer months only, from a nearby field station. On South Georgia, the lack of a nearby station restricted the recovery of the devices to a single-day visit. On the Falkland Islands, the breeding colony and nearby areas were checked daily during a six-week stay in early spring.

The GLS consisted essentially of a data-logger with 128 kB memory (Driesen + Kern GmbH, Bad Bramstedt, Germany) with 8-bit resolution, connected to a sensor recording light intensity (BPY 54, Siemens, Berlin, Germany).

TABLE 1. Details of the foraging trips by King Penguins tracked with global location sensors during 1994–1996. Bird codes consist of location (C = Crozet, K = Kerguelen, S = South Georgia, F = Falklands), actual bird number, year, and letters for foraging trip number. The minimum distance covered was derived by adding the distances between all fixes in a trip, and does not take into account deviations from a straight-line course. The maximum distance from the colony was calculated as the distance between the colony and the farthest location recorded during a foraging trip.

Study site Season	Bird code	Start of foraging trip	Duration (days)	Min. distance traveled (km)	Max. distance from the colony (km)
Crozet Islands					
Summer 1994	C-1/94	2 Feb	6	558	260
	C-2/94	20 Feb	9	839	335
	C-3/94	1 Feb	8	1021	497
	C-4/94	17 Feb	9	823	332
	C-5/94	27 Feb	6	636	298
	C-6/94	1 Feb	5	689	337
	C-7/94	22 Feb	4	629	298
	C-8/94	1 Mar	7	1069	518
	Median		6.5	756	333.5
Summer 1995	C-1/95	26 Jan	9	844	388
	C-2/95	7 Feb	9	1016	449
	C-3/95	30 Jan	5	806	385
	C-4/95	5 Feb	15	1690	694
	C-5/95a	21 Feb	10	869	384
	C-6/95a	28 Jan	7	659	312
	C-6/95b	10 Feb	5	523	247
	C-6/95c	21 Feb	10	1326	378
	C-6/95d	6 Mar	15	2598	796
	Median		9	869	385
Winter 1995	C-5/95c	20 Apr	53	4921	1816
	C-6/95e	21 Apr	59	5075	1603
	Median		56	4998	1709.5
Winter 1996	C-1/96	27 Apr	126	9474	1974
	C-2/96a	27 Apr	19	1907	725
	C-2/96b	17 May	89	6780	1883
	C-3/96	27 Apr	118	10 653	2239
	Median		103.5	8127	1928.5
Kerguelen Islands					
Summer 1995	K-1/95	28 Feb	4	277	104
	K-2/95	10 Mar	9	859	243
	K-3/95	11 Mar	7	498	169
	K-4/95	1 Mar	9	1239	292
	Median		8	678.5	206
South Georgia					
Summer 1996	S-1/96a	27 Feb	7	981	301
	S-1/96b	10 Mar	11	1617	626
	Median		9	1299	463.5
Winter 1996	S-1/96c	6 Apr	25	3773	661
Falkland Islands					
Early winter 1996	F-1/96a[a]	24 Mar	24	3062	1398
	F-1/96b	27 Apr	27	2637	1122
	F-2/96a[a]	24 Mar	55	4182	1186
	F-3/96a	20 Apr	4	620	260
	F-3/96b	25 Apr	7	1317	374
	F-3/96c	2 May	4	516	224
	F-3/96d	10 May	11	918	281
	F-3/96e	21 May	10	1370	386
	F-3/96f	5 Jun	9	800	247
	F-4/96a	8 Apr	48	4082	1187
	F-5/96a	7 Apr	26	3591	981
	F-5/96b	10 May	15	1305	509
	F-5/96c	28 May	17	1789	485
	Median		15	1370	485

TABLE 1. Continued.

Study site Season	Bird code	Start of foraging trip	Duration (days)	Min. distance traveled (km)	Max. distance from the colony (km)
Late winter 1996	F-1/96c	5 Jun	86	8190	1265
	F-2/96b	14 Jun	33	1556	233
	F-2/96c	24 Jul	30	3394	772
	F-3/96g	2 Jul	54	4818	784
	F-4/96b	5 Jun	97	10 696	1547
	F-5/96d	19 Jun	34	3444	903
	F-5/96e	2 Aug	20	2805	669
	F-5/96f	29 Aug	11	1337	459
	Median		33.5	3419	778
Early summer 1996	F-6/96	5 Oct	10	1292	352
	F-7/96	18 Oct	8	607	207
	F-8/96	8 Oct	15	2005	592
	F-9/96	7 Oct	18	2147	580
	F-10/96	6 Oct	17	1685	329
	Median		15	1685	352

[a] Proximity of equinox prevented calculation of positions for the initial 10 days of the trip.

The light sensor was covered by a blue filter (BG 28, Schott Glaswerke, Mainz, Germany) and light intensities were measured between 1 and 10 lux at intervals of 128 sec. All light intensities exceeding 10 lux were stored as 10 lux. The streamlined devices weighed between 90 and 150 g, depending on number and size of batteries, with maximum dimensions of 125 × 38–65 × 25 mm.

Externally attached units are likely to increase the hydrodynamic resistance of the penguins (Bannasch et al. 1994), which may result in greater energy expenditure or reduced swim speed (Culik and Wilson 1991). For example, in several studies birds with externally attached devices spent longer foraging, with less success, compared with unequipped conspecifics (Ropert-Coudert et al. 2000). In order to minimize this potential impact, the devices were hydrodynamically shaped according to the recommendations of Bannasch et al. (1994) to reduce resistance while penguins swam underwater, and were attached to the birds using a method that did not interfere with their insulation (Wilson et al. 1997). Consequently, I assumed that the GLS did not interfere substantially with the birds' activity and foraging patterns. This assumption was supported by the fact that nearly all birds were still feeding healthy chicks upon the retrieval of the devices.

Data on ambient light intensity derived from GLS can be used to determine the geographic position of the device because day length and the time of midday, compared to GMT, are a function of geographic locality and date (Wilson et al. 1992, Hill 1993). This method has been successfully used to determine the foraging habitats of various far-ranging marine top predators such as penguins (Wilson et al. 1995, Pütz et al. 1998), albatrosses (Gremillet et al. 2000, Weimerskirch and Wilson 2000), and seals (DeLong et al. 1992, Le Boeuf et al. 1993). All GLS were calibrated at the study site before, and in some instances after, their deployment to determine the exact light intensity corresponding to sun elevation angles of 4.9° (Wilson et al., in press). Data were analyzed with regard to position using specifically designed software (GLOBUS and LOCATE, Jensen Software Systems, Kiel, Germany). For the purpose of this article, foraging trips starting between 23 September and 21 March (equinoxes) were defined as summer trips, whereas those starting between 21 March and 23 September were defined as winter trips.

The positional data obtained refer nominally to the position of birds at midday and midnight. However, in order to reduce the error associated with individual positional fixes, an iterative smoothing procedure was performed (see Wilson et al., in press). Furthermore, an odd number of smoothing operations, each one given by $Lat_{new} = ((Lat_n + Lat_{n+1})/2)$ and $Long_{new} = ((Long_n + Long_{n+1})/2)$, will indicate the position of the birds at 06:00 and 18:00. In general, data were smoothed three times. However, for birds from Kerguelen Islands, due to the proximity of

the equinox, data had to be smoothed 7 times to gain a realistic picture of the foraging patterns (see Wilson et al., in press). The horizontal distance between two positional fixes was calculated using the program HOWFAR (Jensen Software Systems).

The quality of positional fixes is dependent on a number of biotic and abiotic factors such as variations in cloud cover, proximity to the equinox (affecting latitudinal fixes only), animal orientation, debris covering the sensor, diving activity, distance traveled between dawn and dusk or dusk and dawn, as well as inaccuracies in the quartz timer or insensitivity of the photo cell (see Wilson et al. 1992, in press; Hill 1993). However, most factors cancel each other out to a large extent and consequently the potential inaccuracy of each fix is not represented by a sum of all errors (Wilson et al., in press). Furthermore, hardware measures and software corrections can reduce these inaccuracies. The errors associated with each positional fix were assumed to be ±40 km, determined using data collected from stationary and moving devices at known locations all over the world, as well as from a free-ranging King Penguin equipped simultaneously with a GLS and a satellite transmitter (Wilson et al., in press). However, to avoid overinterpretation of the accuracy of each positional fix, multiple positional fixes for particular sites and season were combined to create an area utilization plot (for Crozet Archipelago, Kerguelen and Falkland Islands) using the raster grid procedure integrated in MapInfo Professional 5.0 (MapInfo Corporation, Troy, New York). All raster grids were based on a resolution of 0.5° latitude × 0.5° longitude, except for the summer data from Crozet, which were based on a resolution of 0.25° latitude × 0.25° longitude. The levels of shading are proportionate to the number of positions obtained in each grid square: the higher the number of positions, the darker the shading. As only one bird was successfully tracked at South Georgia, data are shown as individual foraging tracks for this site only.

Due to the low sample sizes, the occurrence of multiple trips by individual birds, and interannual as well as spatial biases, a detailed statistical comparison of different foraging parameters could not be performed.

RESULTS

Overall, 56 foraging trips (summer, $n = 28$; winter, $n = 28$) of 32 King Penguins from four breeding islands were obtained during the study period. A more detailed description of the number of devices deployed, the attachment periods, and the foraging trips within the study period is given in Table 1.

CROZET ISLANDS

At Crozet, 17 King Penguins were successfully equipped with GLS for up to six months. All King Penguins equipped for only one foraging trip continued to breed after removal of the GLS. However, it remains unclear whether all birds equipped for longer periods successfully raised chicks, although all were last seen with their chick before their final foraging trip. Further evaluation of chick survival was impossible due to extensive movements of the chicks in large crèches, exacerbated in some cases by loss of flipper bands.

In summer 1994 and 1995 at Crozet all King Penguins investigated foraged to the south of the breeding site (Fig. 1a). The area most frequented ranged directly south of the islands, between longitudes 51°E and 52°E. Only 4 of the 14 birds moved beyond 50°S, the approximate position of the APF (Fig. 1). In summer 1994, the median foraging trip duration was shorter than in summer 1995 (Table 1). The interannual difference in foraging trip duration was also reflected in both the calculated median maximum distance to the colony (i.e., the farthest position reached by any bird) and the total distance covered (i.e., the sum of the distances between all consecutive pairs of positional fixes; Table 1). Because of low sample size I pooled data for both summers (Table 1) to create a density plot of the summer foraging areas (Fig. 1a).

Five birds were successfully tracked between April and June 1995 and between April and August 1996 (Table 1), and these trips were pooled to create a density plot of winter foraging areas (Fig. 1b). All birds foraged to the south of Crozet Islands, with highest densities occurring as far south as 60°S (Fig. 1b). However, some penguins reached as far south as 63°S, and one bird moved westward and back at about 60°S (Fig. 1b). Median foraging trip duration was higher in 1996 than in 1995 (Table 1), and this was reflected in both the total distance covered and the maximum distance to the colony. One bird performed a comparatively short foraging trip (C-2/96a) with a duration of only 19 days.

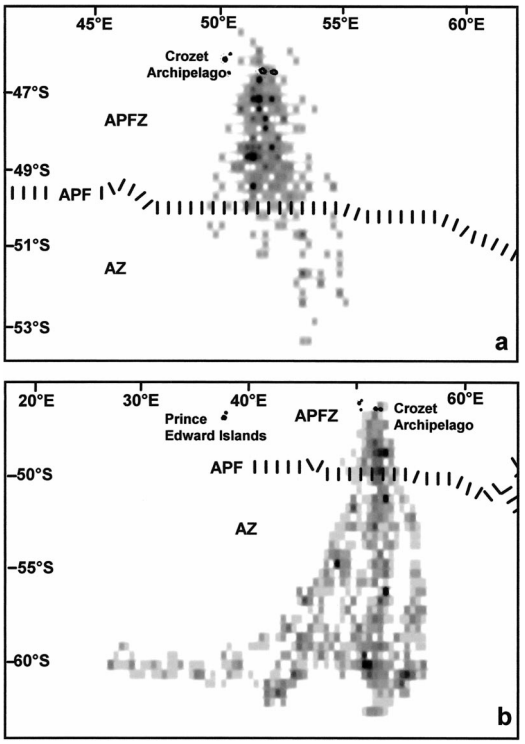

FIGURE 1. Density plot of the foraging areas of King Penguins breeding on Crozet Islands in (a) summer 1994 (n = 8 birds, 8 trips) and 1995 (n = 6 birds, 9 trips), and (b) winter 1995 (n = 2 birds, 2 trips) and 1996 (n = 3 birds, 4 trips). Darker shading denotes areas with more penguin locations. APFZ = Antarctic Polar Frontal Zone, APF = Antarctic Polar Front, AZ = Antarctic Zone, as determined from Park et al. (1993). Note that (a) and (b) are drawn at different scales.

KERGUELEN ISLANDS

At Kerguelen Archipelago, data from four foraging trips of four different King Penguins were obtained in late summer 1995 (Table 1). All study birds continued to breed after GLS removal. Highest bird densities occurred to the east of the breeding colony at approximately the location of the 1000-m depth contour (Fig. 2).

SOUTH GEORGIA

One bird was tracked over three consecutive foraging trips at South Georgia in 1996 (Table 1). When the GLS was removed, the bird was still rearing a chick. Foraging trip duration, maximum distance to the colony, and total distance covered increased as the season progressed. The first two trips were to the northeast, and the third

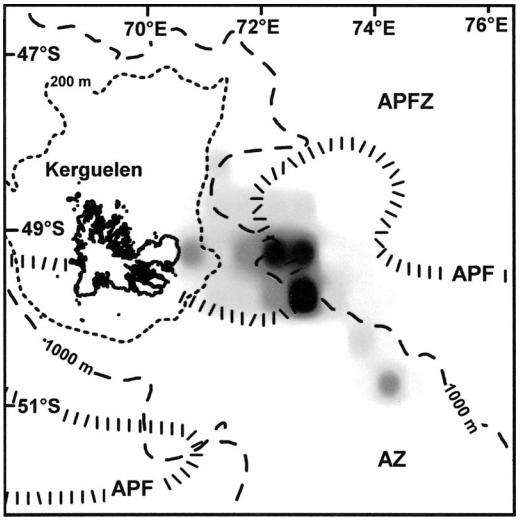

FIGURE 2. Density plot of the foraging areas of 4 King Penguins breeding at Kerguelen Islands in summer 1996. Darker shading denotes areas with more penguin locations. APFZ = Antarctic Polar Frontal Zone, APF = Antarctic Polar Front, AZ = Antarctic Zone, as determined from Park et al. (1993).

foraging trip was westward (Fig. 3). Although there was a shift in the direction of the foraging trips, the maximum distance to the colony of the third trip was only marginally greater than that achieved during the second trip.

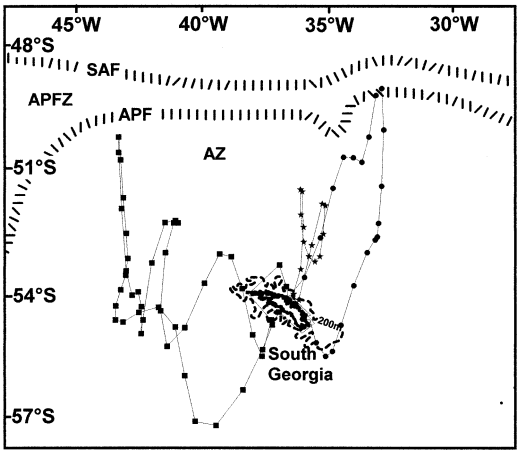

FIGURE 3. Consecutive foraging trips of a King Penguin breeding at Husvik, South Georgia, in summer 1996 (stars = first trip, filled circles = second trip, filled squares = third trip). SAF = Subantarctic Front, APFZ = Antarctic Polar Frontal Zone, APF = Antarctic Polar Front, AZ = Antarctic Zone, as determined from Peterson and Whitworth (1989).

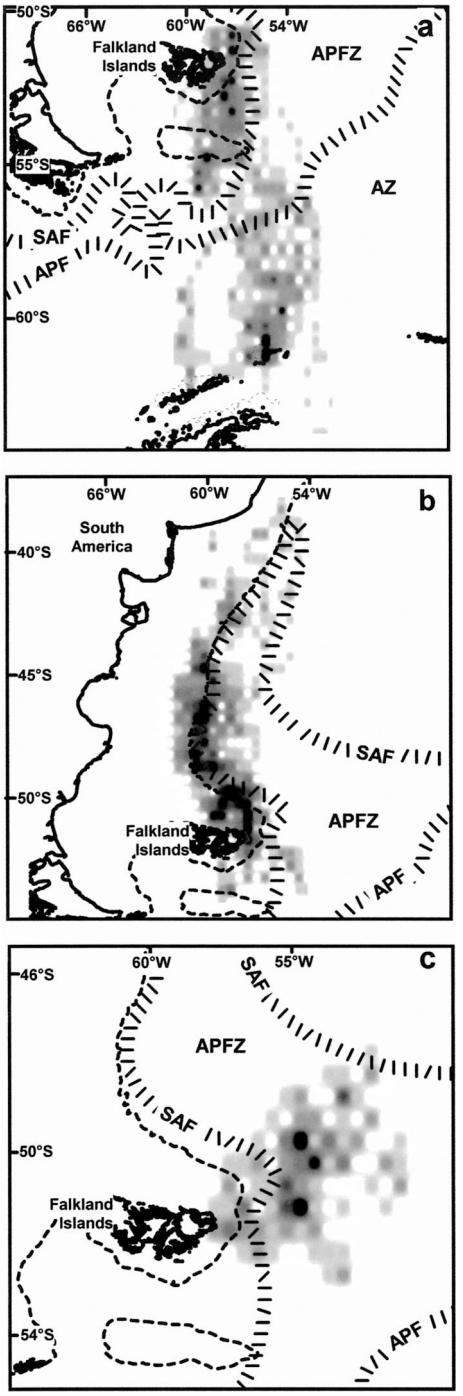

FIGURE 4. Density plot of the foraging areas of King Penguins breeding at Volunteer Beach, Falkland Islands, during (a) early winter (n = 5 birds, 13 trips), (b) late winter (n = 5 birds, 8 trips) and (c) early summer (n = 5 birds, 5 trips) 1996. Darker shading denotes areas with more penguin locations. The dotted line indicates the 200-m depth contour. SAF = Subantarctic Front, APFZ = Antarctic Polar Frontal Zone, APF = Antarctic Polar Front, AZ = Antarctic Zone, as determined from Peterson and Whitworth (1989). Panels are drawn at different scales.

FALKLAND ISLANDS

Overall, 10 King Penguins were tracked with GLS at the breeding colony at Volunteer Beach, Falkland Islands, from March 1996 onwards (Table 1). Nine of the birds recovered were still rearing chicks, whereas one bird had started to molt. Due to the proximity of the equinox, the initial 10 days of two foraging trips (F-1/96a and F-2/96a) could not be calculated and these periods were not taken into consideration while creating the density plots (Fig. 4). Foraging areas of King Penguins differed according to the onset of the foraging trip. All birds leaving the colony before 5 June headed south (Fig. 4a). Highest densities occurred in the vicinity of the 200-m depth contours to the south and in an area around Elephant Island, the northernmost of the South Shetland Islands, about 1000 km from the breeding ground. Two birds even traveled beyond, one into the Weddell Sea and another one toward Livingston Island, South Shetland Islands, at about 62°S. King Penguins departing the colony to forage after 5 June moved generally northward (Fig. 4b). However, of three birds that left the colony on exactly 5 June, one left for a short trip of 9 days to the south, and the other two for extended foraging trips of 86 days and 97 days, respectively, to the north (Table 1). Highest densities occurred along the Patagonian Shelf break up to 45°S, although birds traveled as far north as 43°S. The median foraging trip duration during this period was more than twice as long as at the onset of winter. The longer trip duration was also reflected in the total distance covered, and, to a lesser extent, maximum distance to the colony (Table 1). In early summer 1996, foraging trips from five different birds rearing large chicks were all directed to the east (Fig. 4c), with highest densities occurring at about 55°W.

DISCUSSION

To my knowledge, this is the first study to investigate the foraging range of a pelagic seabird simultaneously at various breeding sites using

the same technology. The results indicate that King Penguins consistently utilize specific oceanic areas, at least during summer, irrespective of the particular location of their breeding site.

SUMMER FORAGING RANGE

With respect to the summer foraging range of King Penguins, the results obtained in this study confirm the findings of previous investigations at various breeding islands (Bost et al. 1997, 2002, Rodhouse et al. 1998, Moore et al. 1999, Pütz et al. 1999, Charrassin and Bost 2001). In summer, all King Penguins investigated foraged in the direction of, or even beyond, the APF, irrespective of the location of their breeding island in relation to this frontal zone. Accordingly, birds from Crozet Islands, located to the north of the APF, foraged mainly in the APFZ, whereas the bird from South Georgia, situated to the south of the APF, exploited Antarctic waters. King Penguins breeding on the Kerguelen Islands foraged to the east; this archipelago lies directly within the APF. Birds from the Falkland Islands also traveled eastward, although the APF is situated to the south and east of this breeding island (Fig. 4c). However, more information is needed on the foraging range of King Penguins from the Falkland Islands in late summer, when they are rearing small chicks, to confirm these findings. Thus, it appears that in general the APF and adjacent areas, as first suggested by Jouventin et al. 1994, represent the main summer foraging habitat of King Penguins. The APF is also frequently exploited by other seabirds such as Royal Penguins (*Eudyptes schlegeli*; Hull et al. 1997) or Grey-headed Albatrosses (*Diomedea melanophrys*; Rodhouse et al. 1996), indicating the importance of this oceanographic feature for the foraging success of marine top predators.

Surprisingly, none of the birds from Crozet Island headed east to forage. Jouventin et al. (1994) and Bost et al. (1997) reported that a few King Penguins equipped with satellite transmitters also traveled eastward toward the Subantarctic Front. The exact reasons for the lack of foraging trips to the east in this study are as yet unknown, but the breeding status of the birds investigated or interannual changes in prey density and distribution at the two frontal zones may play a part (Jouventin et al. 1994, but see Guinet et al. 1997).

Dietary studies have shown that, in summer, King Penguins feed predominantly on myctophid fishes (Cherel et al. 1993, 1996, Olsson and North 1997, Moore et al. 1998). The APF is considered to offer optimum conditions for the formation of myctophid concentrations (Maslennikov and Solyankin 1993), and they dominate the total fish stock in terms of biomass and abundance (Pakhomov et al. 1994). Therefore, it can be assumed that, at all breeding sites, areas adjacent to the APF are of major importance to the foraging success of King Penguins during summer. Minor interannual modifications in the distances traveled are a direct consequence of the variability in the position and structure of the APF in the Indian Ocean (Nagata et al. 1988) as well as the Atlantic Ocean (Hunt et al. 1992).

WINTER FORAGING RANGE

In winter, King Penguins stop feeding their chicks for up to five months, which has been assumed to be linked to food shortage, and spend extended periods at sea (Weimerskirch et al. 1992). Furthermore, they switch to a diet dominated by squid (Cherel et al. 1993, 1996, Moore et al. 1998). How are these changes reflected in the foraging habitats of King Penguins? There is evidence that in winter King Penguins from Crozet Islands forage further south in Antarctic waters close to the northern limit of the pack ice (Jouventin et al. 1994, Pütz et al. 1999, Charrassin and Bost 2001, this study). Furthermore, Moore et al. (1999) reported that the feeding areas of King Penguins from Heard Island were also located in Antarctic waters, as far south as 65°S. Thus, it appears that in winter food availability at the APF is reduced, forcing birds to exploit Antarctic waters. At the northern ice edge primary production is enhanced (Knox 1994), resulting in high densities of marine top predators (Ribic et al. 1991).

In contrast to King Penguins from oceanic breeding islands, for which Antarctic waters seem to be the most favorable alternative, a different foraging pattern is exhibited by the King Penguins breeding on the Falkland Islands. At the onset of winter, birds also traveled south beyond the APF. However, by midwinter birds changed the direction of their foraging trips and foraged to the north of their breeding site along the continental slope in the APFZ. Presumably, food availability in this particular area is enhanced by regional upwelling, and thus may offer a suitable alternative as winter foraging ground not only for King Penguins, but also for

Rockhopper Penguins (*Eudyptes chrysocome*) from the Falkland Islands (Pütz et al., in press), Wandering Albatrosses (*Diomedea exulans*) breeding on South Georgia (Prince et al. 1998) or Southern Giant Petrels (*Macronectes giganteus*) breeding in Argentina (Quintana and Dell-'Arciprete 2002). The switch from foraging grounds in Antarctic waters to areas along the Patagonian Shelf was also reflected in the diversity of accumulated squid beaks in the stomachs of King Penguins from the Falkland Islands. Overall, 10 squid species were identified, indicating that birds foraged in an area ranging from Antarctic to subtropical waters, at slope regions and in oceanic waters (Piatkowski et al. 2001).

The limited data on the winter foraging trips of King Penguins suggest that birds from the Falkland Islands experienced a higher foraging success compared to their conspecifics at Crozet Islands. On average, the foraging trips of the penguins from the Falkland Islands were shorter, and the total distance traveled and the maximum distance from the colony were smaller. This should, together with the more temperate climate in the Falkland Islands, result in a higher chick survival during the winter and subsequently an overall higher breeding success compared with birds from the Crozet Islands. This suggestion is further supported by the fact that winter mortality of chicks in the Falkland Islands is extremely low (KP, pers. obs.) compared with other breeding sites (Williams 1995). However, more research is needed on the breeding biology of the King Penguins from the Falkland Islands to confirm this hypothesis.

DISTANCE TRAVELED

Aerial locomotion is substantially different from locomotion in water, and penguins are believed to be 10 times slower than flying birds (Wilson et al. 1989). With this in mind, the distances traveled by King Penguins throughout their breeding season are remarkable. The distances traveled of between 47 and 188 km per day (calculated from Table 1) correspond well with those obtained from birds equipped with satellite transmitters. For example, in 1993 one King Penguin was tracked for 35 days during his winter foraging trip while traveling at least 3893 km (Jouventin et al. 1994), corresponding to an average traveling speed of 111 km per day. Furthermore, in two instances minimum distances covered during individual winter foraging trips exceeded 10 000 km (Table 1). The long periods during which King Penguins stay away from their chicks, and the distances traveled during that time, may indicate lower food availability in winter than in summer. Whereas in summer King Penguins travel several hundred km to feed at the APF, potential food resources are located even farther away in winter. More research on the foraging ecology of King Penguins during winter is needed to put their unusual breeding cycle into perspective.

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