

FORAGING AREAS OF KING PENGUINS *APTENODYTES PATAGONICUS* BREEDING AT POSSESSION ISLAND, SOUTHERN INDIAN OCEAN

K. PÜTZ^{1,2}, Y. ROPERT-COUDERT³, J.-B. CHARRASSIN³ & R.P. WILSON¹

¹Institut für Meereskunde, Abt. Meereszoologie, Düsternbrooker Weg 20, D-24105 Kiel, Germany

²Current address: Antarctic Research Trust, PO Box 685, Falkland Islands
(pentag@horizon.co.fk)

³Centre d'Ecologie et de Physiologie Énergétiques, C.N.R.S., 23 rue Becquerel, 67087 Strasbourg, France

SUMMARY

PÜTZ, K., ROPERT-COUDERT, Y., CHARRASSIN, J.-B. & WILSON, R.P. 1999. Foraging areas of King Penguins *Aptenodytes patagonicus* breeding at Possession Island, southern Indian Ocean. *Marine Ornithology* 27: 77–84.

Between January and March 1994 and between January and June 1995 we used Global Location Sensors (GLS) to determine the feeding areas of King Penguins *Aptenodytes patagonicus* breeding at Possession Island, Crozet Archipelago. In both years, the preferred feeding area during summer was located about 300 km south of the island, being slightly more distant in 1995. Mean foraging trip duration was 5.7 ± 1.1 days ($n = 6$) during summer 1994 and 8.9 ± 3.7 days ($n = 9$) during summer 1995, respectively. During summer the travelling speed of the King Penguins studied was highest at the first and last days of the foraging trip (c. 8 km/h). During the middle days of foraging trips travelling speeds were much lower (< 5 km/h). In early winter, between late April and mid-June 1995, two King Penguins equipped with GLSs executed foraging trips with durations of 53 and 59 days, respectively. Both birds travelled beyond 60°S with maximum distances to the colony of 1600 and 1800 km, respectively, and total distances covered of about 5000 km. The winter trips were characterized by alternating periods of higher and lower distances covered, indicating a highly variable feeding success at different localities. The relationships between foraging trip duration (days) and maximum distance to the colony (km) and total distance covered (km) were calculated to be maximum distance = $210 + 27$ d and total distance = $340 + 85$ d.

INTRODUCTION

The breeding cycle of the King Penguin *Aptenodytes patagonicus* is characterized by the comparatively long foraging intervals of the parents. For example, the duration of a foraging trip at Possession Island during summer is rarely shorter than four days (Pütz 1994, Bost *et al.* 1997, Pütz *et al.* 1998) and during winter chicks are fed infrequently or not at all (Weimerskirch *et al.* 1992). As a consequence, chick rearing can last up to 13 months (Jouventin & Lagarde 1995), which makes the breeding cycle of King Penguins the longest of all penguins.

Until recently, elucidation of the preferred feeding areas of seabirds was only possible by indirect methods (Williams & Siegfried 1980, Stahl *et al.* 1985, Wilson *et al.* 1989). For example, Stahl *et al.* (1985) conducted ship-based observations to determine the at-sea distribution of King Penguins in the southern Indian Ocean. However, such methods are subject to many biases (Tasker *et al.* 1984, van Franeker 1994), not least of which is the unknown status of sighted birds.

Radiotelemetry and dead reckoning have proved to be useful in determining area utilization of penguins foraging inshore and for short periods (e.g. Trivelpiece *et al.* 1986, Wilson *et al.* 1994). In addition, the development of satellite transmitters has recently enabled researchers to determine the movements of flying and non-flying seabirds such as Emperor Penguins *A. forsteri* (Ancel *et al.* 1992, Kooyman *et al.* 1996, Kirkwood & Robertson 1997), King Penguins (Jouventin *et al.*

1994, Guinet *et al.* 1997, Bost *et al.* 1997), Adélie Penguins *Pygoscelis adeliae* (Davis & Miller 1992, Kerry *et al.* 1995, Davis *et al.* 1996) and Wandering Albatrosses *Diomedea exulans* (Jouventin & Weimerskirch 1990, Prince *et al.* 1992, Weimerskirch *et al.* 1993) while foraging in remote areas. Data derived from satellite-tracking studies on far-ranging seabirds have been discussed with respect to the opportunity they offer of monitoring environmental parameters (Ancel *et al.* 1992, Weimerskirch *et al.* 1995, Rodhouse *et al.* 1996, Guinet *et al.* 1997).

The development of miniaturized Global Location Sensors (GLS) (Wilson *et al.* 1992, Hill 1993) has been proved to be a suitable and less expensive alternative for the determination of the foraging ranges of long-distance travelling seabirds (Pütz 1994, Wilson *et al.* 1995) and marine mammals (Le Boeuf *et al.* 1993, Stewart & DeLong 1993, Jonker & Bester 1994, Le Boeuf *et al.* 1996). GLS record ambient light intensity, which, together with knowledge of the exact time, can be used to calculate the position of the unit. The aim of this study was to determine the foraging areas of individual King Penguins for long periods with Global Location Sensors (GLS) and to compare the findings with regard to individual, seasonal and annual variability.

MATERIALS AND METHODS

This study was carried out at Possession Island (46°25'S, 51°40'E), Crozet Archipelago, between February and March

1994 and between January and June 1995 in three different breeding colonies with a maximum distance of 15 km to each other (Table 1). King Penguins were captured after a change-over had occurred and Global Location Sensors (GLS) were attached mid-line of the birds to the lower back with tape (Tesa 4561, Beiersdorf AG, Hamburg, Germany) modifying the method described by Wilson & Wilson (1989). In brief, overlapping layers of waterproof tape sandwiched between layers of feathers were wrapped round the device. Additionally, in 1995 the bases of the devices were covered with neoprene glue (Deutsche Schlauchbootfabrik, Eschershausen, Germany) to ensure a secure attachment for several months. Finally, the upper surface of the device was covered by two-component epoxy glue (Loctite).

The efficiency of the attachment system was examined each time birds equipped with GLS returned to their breeding site. None of the devices had to be removed due to a loose attachment of the device during the following foraging trip. However, in cases where the fate of the chick was uncertain, the devices were removed and attached to birds known to be rearing a chick. The foraging trips successfully recorded are summarized in Table 1.

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

interval was 128 s. Two different logger modifications were used. In 1994, all units were powered by 5×1.2 V rechargeable NiCd batteries placed in series and completely embedded in epoxy resin (Glosscoat, Vosschemie, Uetersen, Germany). Mass of the streamlined devices was 60 g and maximum dimensions were $115 \times 22 \times 20$ mm. Light intensity was measured between 1 and 25 lux (for details see Pütz *et al.* 1998). The devices used in 1995 were powered by parallel sets of 2×3 V DL1/3N lithium batteries placed in series to ensure data storage for longer periods. The units were encased in a glass housing and embedded in epoxy resin. The streamlined devices weighed 90 g and had maximum dimensions of $125 \times 38 \times 25$ mm. Light intensity was measured between 1 and 10 lux.

Data on ambient light intensity derived from GLS can be used to determine the geographic position of the device because daylength and the time of mid-day (based on Greenwich Mean Time) are a function of geographic locality and date (Wilson *et al.* 1992, Le Boeuf *et al.* 1993, Hill 1993, Stewart & DeLong 1993, Jonker & Bester 1994, Wilson *et al.* 1995, Le Boeuf *et al.* 1996). All GLS were calibrated at the study site before and after their deployment to determine the exact light intensity corresponding to sun elevation angles of -0.095 rads. Data were analyzed with regard to position using specifically-designed software (GLOBUS and LOCATE, Jensen Software Systems, Kehl, Germany). A detailed description of the analysis and of accuracy of the calculations is given by Wilson *et al.* (in press). In a King Penguin additionally equipped with a

TABLE 1

Summary of data derived from King Penguins equipped with GLS in 1994 and 1995.
Breeding colonies are Crique de la Chaloupe (LC), Jardin Japonais (JJ) and Grande Manchotiere (GM)

King Penguin No.	Breeding colony	Start of foraging trip	Foraging trip duration (days)	Total distance travelled (km)	Maximum distance to colony (km)	Tot. dist./ trip dur. (km/d)	Tot. dist./ max. dist.
1/94	LC	01.02.94	7.5	1021	497	135.1	2.1
2/94	LC	01.02.94	5.0	689	337	137.8	2.0
3/94	LC	02.02.94	5.5	558	260	101.5	2.1
4/94	JJ	22.02.94	4.0	629	298	157.3	2.1
5/94	GM	27.02.94	5.5	636	298	115.6	2.1
6/94	GM	01.03.94	6.5	1069	518	164.5	2.1
Summer 1994	Mean		5.7	767	368	135.3	2.1
	SD		1.1	201	101	21.9	0
1/95	GM	26.01.95	9.0	844	388	93.8	2.2
2/95-1	GM	28.01.95	6.5	659	312	101.4	2.1
2/95-2	GM	10.02.95	5.0	523	247	104.6	2.1
2/95-3	GM	21.02.95	10.0	1326	378	132.6	3.5
2/95-4	GM	06.03.95	15.0	2598	796	173.2	3.3
3/95	GM	30.01.95	4.5	806	385	179.1	2.1
4/95	GM	07.02.95	9.0	1016	449	112.9	2.3
5/95	GM	07.02.95	15.0	1690	694	112.7	2.4
6/95-1	GM	22.02.95	6.0	869	384	144.8	2.3
Summer 1995	Mean		8.9	1148	448	128.3	2.5
	SD		3.7	611	169	29.5	0.5
2/95-6	GM	21.04.95	59.0	5075	1603	86.0	3.2
6/95-3	GM	20.04.95	53.0	4921	1816	92.8	2.7
Winter 1995	Mean		56.0	4998	1710	89.4	3.0

satellite transmitter (Toyocom PTT 2038) positional fixes between the two devices differed by a mean of 70 km (SD = 17, $n = 16$) after correction for diving behaviour and movement and being smoothed three times (Wilson *et al.* in press). The positional data refer nominally to the position of birds at mid-day and mid-night. An odd number of smoothing operations, each one given by:

$$\text{Lat}_{\text{new}} = ((\text{Lat}_n + \text{Lat}_{n+1})/2) \text{ and}$$

$$\text{Long}_{\text{new}} = ((\text{Long}_n + \text{Long}_{n+1})/2),$$

therefore will indicate the position of the birds at 06h00 and 18h00. The program HOWFAR (Jensen Software Systems, Kehl) was used to determine the horizontal distance between two positional fixes, which was divided by time to derive travelling speed. Night time was considered to occur between 18h00 and 06h00 and day time to occur between 06h00 and 18h00.

RESULTS

Twelve King Penguins from three different breeding colonies were successfully equipped for up to five months with Global Location Sensors (GLS) (Table 1). Two devices, which remained for periods of up to 10 months on three different birds contained no data due to water leakage and/or flat batteries. All King Penguins equipped for only one foraging trip continued to breed afterwards. However, it is not clear whether the birds equipped for longer periods successfully raised a chick, although they were last seen with a chick in April. Further evaluation of chick survival was impossible due to extensive movements of the chicks in large crèches exacerbated by possible loss of flipper bands.

During summer 1994 (January–March) the mean foraging trip duration of the birds investigated was 5.7 d (SD = 1.1, range 4–7.5 d, $n = 6$), which did not differ ($t = 0$, $P > 0.05$) from that of non-equipped birds (5.7 ± 1.1 d, range 4–7 d, $n = 22$). All King Penguins investigated foraged south of the breeding site (Fig. 1a) and the area most frequented occurred between 48° and 49°S and 51° and 52°E at a distance of approximately 300 km to the colony. However, the two birds with the longest foraging trip durations ranged beyond 50°S. The calculated mean maximum distance to the colony, i.e. the distance between the furthest position reached by any bird and the colony, was 368 km (SD = 101, range 260–518 km), the total distance covered, i.e. the sum of the distances between consecutive positional fixes, was on average 767 km (SD = 201, range 558–1069 km) which corresponds to a distance of 135.3 km covered per day (SD = 21.9, range 101.5–164.5 km) (Table 1).

The mean foraging trip duration during summer 1995 (January–March) was 8.9 d (SD = 3.7, range 4.5–15 d, $n = 9$), which did not differ significantly ($t = 1.44$, $P > 0.05$) from that of non-equipped birds (6.8 ± 1.9 d, range 5–9 d, $n = 8$). As in 1994, all King Penguins travelled south, but the calculated positional fixes were less concentrated in an specific area (Fig. 1b). However, highest bird densities occurred in an area between 49° and 50°S and 51° and 54°E, about 350 km south of the breeding site. Two birds executed less directional trips and reached 52°S and 53°S, respectively, which resulted in the longest foraging trip durations (15 d) measured during this period (Table 1). The mean maximum distance to the colony was 448 km (SD = 169, range 247–694 km) and the total distance covered was on average 1148 km (SD = 611, range 523–

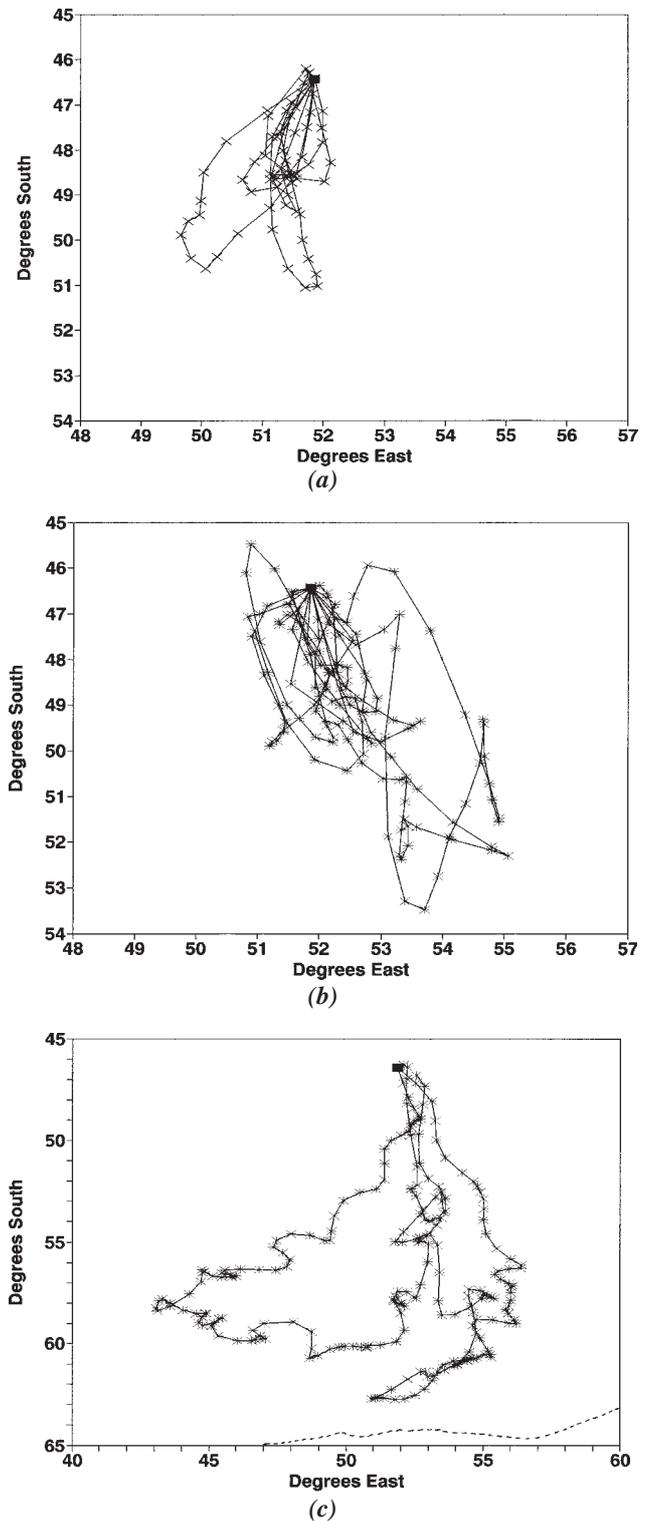


Fig. 1. Routes taken by King Penguins during their foraging trips in (a) summer 1994, (b) summer 1995 and (c) winter 1995. Each cross indicates a positional fix corresponding to 06h00 or 18h00. The dotted line in (c) indicates the northern pack-ice limit (density 3–5).

2598 km). The mean distance covered per day was 128.3 km (SD = 29.5, range 93.8–179.1 km) (Table 1). Four consecutive foraging trips of varying durations could be investigated in bird No. 2, which were all directed to different localities.

Interannual comparison of results obtained during the summer periods (Table 1) revealed no significant differences ($P > 0.05$)

with respect to foraging trip duration ($t = 2.04$), total distance travelled ($t = 1.46$), maximum distance to the colony ($t = 1.04$) and distance travelled per day ($t = 0.50$).

Two birds successfully tracked between April and June 1995 (2/95-6 and 6/95-3) executed foraging trips with durations of 53 and 59 days, respectively (Table 1). During this time both

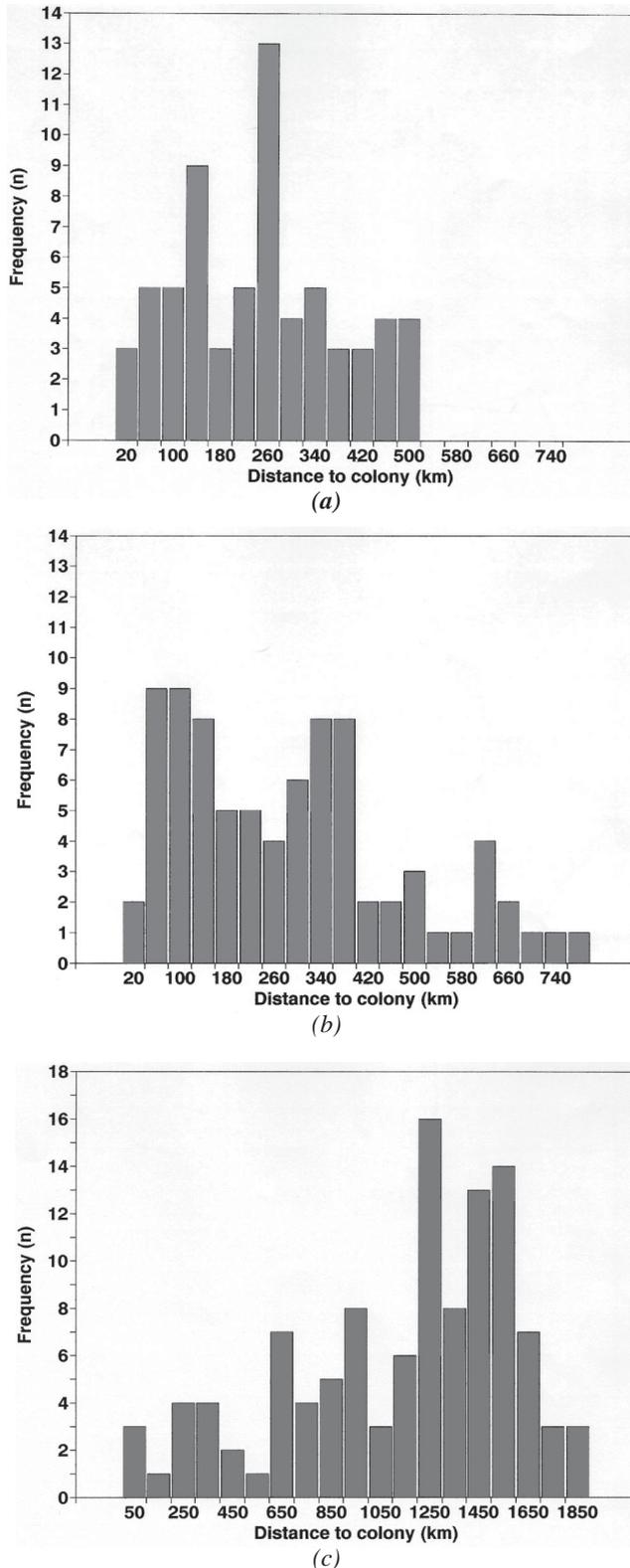


Fig. 2. Frequency distribution of the distance to the colony of King Penguins while at sea during (a) summer 1994, (b) summer 1995 and (c) winter 1995.

birds travelled beyond 60°S (Fig. 1c) with maximum distances to the colony of 1600 and 1800 km, respectively (Table 1). One King Penguin (6/93-3) headed more or less directly south reaching 63°S, which was about 200 km north of the pack-ice limit during this time (pack-ice density 3–5, data from Naval Ice Center, Washington DC, USA). The other bird (2/95-6) executed a less directional trip between 43° and 54°E. The total distance covered during the winter trips was about 5000 km for each bird, resulting in distances of 86.0 and 92.8 km covered per day, respectively.

Interseasonal comparison of the frequency distribution of the distance to the colony revealed a distribution skewed to the left for birds during the summer (Fig. 2a,b) whereas distribution for winter birds was skewed to the right (Fig. 2c). In summer 1994 and summer 1995 the average distances to the colony were 247 km (SD = 134, median 246 km) and 286 km (SD = 191, median 256 km), respectively, and 1134 km (SD = 450, median 1232 km) during winter 1995. Pooled data for both study periods revealed the following regressions between trip duration (days) and maximum distance to the colony (km) and total distance covered (km):

$$\text{Maximum distance} = 210 + 27 \times \text{duration} \quad (r^2 = 0.95)$$

$$\text{Distance covered} = 340 + 85 \times \text{duration} \quad (r^2 = 0.96)$$

The mean travelling speeds of King Penguins during summer 1994 and 1995 are shown in Fig. 3. The travelling speeds calculated for the first and last two days of the trip were *c.* 8 km/h in both years, whereas during the central days of the foraging trips values were less than 5 km/h. Travelling speeds at night were always higher than the corresponding distances travelled during hours of daylight. Overall, the mean travelling speed during the foraging trip was 5.6 ± 0.9 km/h during summer 1994 and 5.3 ± 1.2 km/h during summer 1995.

In winter, the distances travelled by King Penguin 6/95-3 were highly variable but periodic throughout the foraging trip, i.e. days with higher values were followed by days with lower values (Fig. 3c). The same pattern was obvious in the second winter-tracked bird. The highest travelling speeds were calculated to occur in the beginning and at the end of the foraging trip, being highest in both birds on the third day of the foraging trip (13.2 km/h and 14.5 km/h, respectively). On average, higher travelling speeds occurred every 4.5 d (SD = 1.4, range 3–7 d, $n = 12$) in bird 6/95-3 and every 5 d (SD = 1.6, range 2–7 d, $n = 12$) in bird 2/95-6. This difference was not significant ($t = 0.81$, $P > 0.05$). The overall travelling speeds during foraging were 3.6 and 3.9 km/h, respectively.

In order to investigate the performance of the foraging trips the total distance travelled was divided by the maximum distance to the colony (Table 1). Direct trips typically should exhibit factors equal or close to 2, whereas ideal round trips have factors equal or close to 3.14 ($= \pi$). The mean factor in summer 1994 was 2.1 (SD = 0, range 2.0–2.1), whereas in summer 1995 it was 2.5 (SD = 0.5, range 2.1–3.5). The higher latter value is mainly a consequence of the extended foraging trips executed by two birds during trips of 15-d duration (Table 1). However, the difference was not significant ($t = 1.93$, $P > 0.05$). The two birds tracked in winter had factors of 2.7 and 3.2, respectively.

DISCUSSION

King Penguins equipped with satellite transmitters on Possession Island are reported to engage in direct trips south to the

Antarctic Polar Front or, to a lesser extent, in trips directed eastwards to the Sub-Antarctic Front (Jouventin *et al.* 1994, Bost *et al.* 1997). In our study, all summer birds executed more or less direct trips southwards and no positional fixes were recorded north of 45°S. Only one bird (2/95-4) travelled at least during a part of the foraging trip in an easterly direction. In contrast to this, 29% of King Penguins equipped with satellite transmitters were found to engage in circular trips directed eastwards (Jouventin *et al.* 1994, Bost *et al.* 1997). Jouventin *et al.* (1994) suggested that the circular trips mainly occur at the end of the incubation period when foraging time is limited by the nearness of hatching. However, our results as well as those obtained by Bost *et al.* (1997) do not confirm this suggestion. Therefore we assume that variations in the preferred feeding areas of King Penguins from the Crozet Islands are not due to the breeding status but influenced by other factors, which remain unknown.

Our results indicate that the foraging patterns of King Penguins are characterized by interannual and interseasonal differences. For example, compared to summer 1994 the King Penguins studied in 1995 tended to travel to areas located farther south. Apart from possible errors in the measurement, this could be explained by a change in the position of the Antarctic Polar Front (APF), which is reported to be the main feeding area of King Penguins (Jouventin *et al.* 1994, Bost *et al.* 1997, Guinet *et al.* 1997). The APF is defined to be located at the 2°C isotherm at 200 m depth, which normally coincides with sea surface temperatures of between 4°C and 5°C (Park *et al.* 1991, 1993). A 20-year study showed that in the vicinity of the Crozet Islands this frontal system is located between 49° and 53°S (Nagata *et al.* 1988). King Penguins feed predominantly on myctophids (e.g. Cherel & Ridoux 1992), which dominate the total stock in terms of biomass and abundance at frontal regions (Pakhomov *et al.* 1994). Generally, the APF is considered to be a region with optimum conditions for the formation of feeding myctophid fish concentrations (Maslennikov & Solyankin 1993). For example, the greatest concentrations of *Electrona carlsbergi* and *Krefflichthys anderssoni*, the main prey items, are found at the APF (Kozlov *et al.* 1990, Koubbi 1993). Although King Penguins feed already while travelling south (Bost *et al.* 1997), the position of the APF seems to have an important influence on the breeding biology of King Penguins as the proximity of the frontal system is likely to determine foraging trip duration and consequently the intervals at which chicks are provisioned with food. Guinet *et al.* (1997) report that the position of the APF was moving farther south during the years 1992–1994. These variations in the position of the APF might explain the different foraging trip durations obtained in our study in the summer periods. Thus, that the average foraging trip duration was higher in 1995 might indicate that the APF was located even farther south than in previous years. The overall breeding success during one year is therefore likely to be as dependent on the position of the APF as the mass of chicks prior to the winter influences survival rates.

The maximum foraging ranges obtained in this study during summer 1994 compare well with those found by Bost *et al.* (1997) at the same time using satellite transmitters. The maximum distance to the colony can again be used as an indicator of the position of main feeding areas. For example, with regard to the distance between the breeding colony and the position of the APF King Penguins from Marion Island are comparable to those breeding on the Crozet Islands. Indeed, the calculated relationships between total distance travelled and foraging trip duration are also comparable to the relationship found

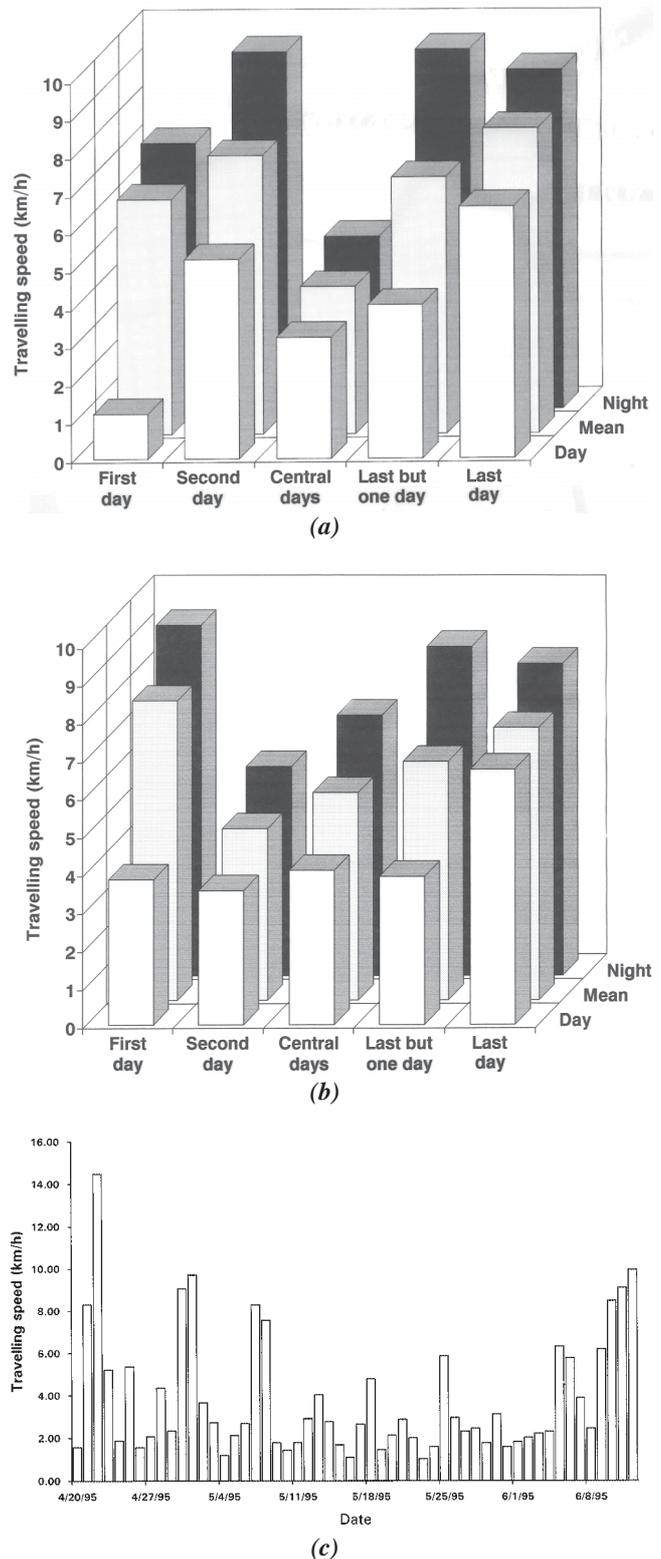


Fig. 3. Mean travelling speeds of King Penguins in relation to time into foraging trip during (a) summer 1994, (b) summer 1995 and (c) winter 1995.

by Adams (1987) for King Penguins from Marion Island feeding large chicks after winter starvation. Surprisingly, birds feeding small chicks, as was the case in our study, exhibited much shorter distances travelled (Adams 1987). This difference again may be an indication of the varying hydrographic features within the preferred feeding area of King Penguins, i.e. variations in the position of the APF.

The predictability of food resources and its influence on seabird foraging strategies has been discussed for many seabird species (e.g. Hunt 1990, Schneider 1991). In King Penguins, the predictable food resources at the APF would tend to make foraging trips composed of directional travelling periods to and from the feeding area on a more or less constant course, which would result in relationships between the total distance travelled and the maximum distance to the colony close or equal to 2. Foraging trips to less-predictable feeding areas should exhibit variations from this ideal pattern due to increased prey searching. For example, occasional prey searching after leaving the colony would result in so-called 'looping courses' (cf. Wilson 1995), where birds move away from the colony deviating from a straight line course due to foraging, before directly returning to the colony after having fed. Such looping courses occur, for example, in Magellanic Penguins *Spheniscus magellanicus* during the incubation period (Wilson *et al.* 1995) as well as in *Pygoscelis* penguins foraging for their offspring (Wilson 1995). The 'circular' trips obtained by Jouventin *et al.* (1994) for King Penguins engaging in eastward trips might be an indication of a reduced food availability in this area. The relationships between total distance travelled and maximum distance to the colony would then increase with decreasing foraging success. A non-predictable prey distribution consequently would result in an increasing component of prey searching and travelling, and accordingly, an increased relationship between distance travelled and maximum distance to the colony. All King Penguins studied during summer 1994 exhibited factors between 2.0 and 2.1, indicating a highly direct course to a predictable feeding area. During summer 1995 prey distribution seemed to be less predictable because only 33% of the foraging trips had factors of 2.1. Forty-four percent of the foraging trips included a higher prey searching component after birds had left the colony (factors 2.2–2.5), whereas two foraging trips had factors of 3.3 and 3.5, indicating much less directional movements due to a non-predictable prey distribution. Nevertheless, short-term variations in the oceanographic features may force the birds to change their effort to find appropriate prey concentrations. This may have been the case in bird No. 2: two relatively short foraging trips directed to the APF (factor 2.1) were followed by two foraging trips revealing factors >3.3, indicating changes in prey distribution.

A further indication of the different foraging patterns of King Penguins is evident from the travelling speed. Adams (1987) reports King Penguins foraging for large chicks travel at mean speeds of 8.7 ± 1.2 km/h, which compares well with our calculated travelling speeds at the beginning and at the end of the summer foraging trips. However, during the middle part of the foraging trips, these values are lower thus reducing the overall travelling speeds during a foraging trip. In King Penguins equipped with satellite transmitters foraging for small chicks, travelling speeds on average did not exceed 3 km/h (calculated from Jouventin *et al.* 1994). Furthermore, Bost *et al.* (1997) divided the foraging trips of King Penguins into two distinct phases according to the travelling speeds of the individuals. In the first phase, between the departure from the colony and the farthest point reached, the speed was lower than the average for the whole trip (on average 2.8 km/h, calculated from Bost *et al.* 1997). In the second phase, on the way back to the colony travelling speeds were on average higher (on average 3.6 km/h, calculated from Bost *et al.* 1997), indicating a rapid movement back to the colony to provision the chick with food. During the first phase so-called 'slowing down periods'

occurred which compare well with the lower speeds apparent during the central days in our study. Finally, Bost *et al.* (1997) found no distinction into the two phases in birds travelling eastwards, which supports the assumption of a less predictable food availability in this particular area. The reasons for this discrepancies in the travelling speeds remain unknown, although mean foraging trip durations were much higher in the birds equipped with satellite transmitters (15 d, calculated from Jouventin *et al.* 1994, and 12 d, calculated from Bost *et al.* 1997), indicating possible device effects resulting in longer stays at the feeding areas, which thus reduced the overall travelling speeds.

A completely different foraging pattern is exhibited during winter. In this period chicks are fed only infrequently or not at all for at least three months (Weimerskirch *et al.* 1992). The two King Penguins successfully tracked in winter were away for nearly two months during which time they travelled far south, presumably reaching the pack ice zone. The period between May and September is characterized by a low productivity in the Southern Ocean (Hart 1942, Foxtton 1956) and obviously food abundance during this time is not sufficient to meet the energy requirements of King Penguins. Consequently, stomach contents of adults returning to the colony are lighter and diet composition is different with squid being the major prey component (Cherel *et al.* 1993). The probable patchy distribution of prey is most evident from the distances travelled exhibited by the birds, where higher and lower horizontal displacements vary continuously throughout the foraging trip. Furthermore, there is evidence that duration of daylight may be a limiting factor of the foraging success, as this is known to be highly dependent on ambient light levels (Wilson *et al.* 1993, Pütz & Bost 1994). Daylight duration did not exceed eight hours when birds remained south of 60°S. If we assume dive durations of 380 s while diving to 250 m and surface times of 90 s (Pütz *et al.* 1998), King Penguins are able to perform eight deep dives per hour. With regard to the reduced food availability during winter, a total of 64 dives per day may be too low to provision the chick with a sufficient amount of food and to meet the energy demands of the bird itself.

Future research on the foraging areas utilized by King Penguins during the winter period should include the deployment of stomach temperature sensors to determine where and when the birds actually feed (cf. Bost *et al.* 1997). This would elucidate the inter-seasonal and inter-annual changes in food availability. Finally, the large-scale movements undertaken by King Penguins make them useful monitors of hydrographic features, as already been shown to be the case in Wandering Albatrosses *Diomedea exulans* (Weimerskirch *et al.* 1995).

ACKNOWLEDGEMENTS

Logistical and financial support was provided by the Deutsche Forschungsgemeinschaft, the Institut Français pour la Recherche et la Technologie Polaire and the Terres Australes and Antarctiques Françaises. We are grateful to Yvon Le Maho, Charly Bost and Mandy Kierspel as well as to all members of Mission 32 at Base Alfred Faure for their help. David McLennan-Smith gave advice during the final stage of revision. Olof Olsson and one anonymous referee provided many useful comments on the manuscript.

REFERENCES

- ADAMS, N.J. 1987. Foraging range of King Penguins *Aptenodytes patagonicus* during summer at Marion Island. *J. Zool., Lond.* 212: 475–482.
- ANCEL, A., KOOYMAN, G.L., PONGANIS, P.J., GENDNER, J.P., LIGNON, J., MESTRE, X., HUIN, N., THORNSON, P.H., ROBISSON, P. & LE MAHO, Y. 1992. Foraging behaviour of Emperor Penguins as a resource detector in winter and summer. *Nature* 360: 336–339.
- BOST, C.A., GEORGES, J.Y., GUINET, C., CHEREL, Y., PÜTZ, K., CHARRASSIN, J.-B., HANDRICH, Y., ZORN, T., LAGE, J. & LE MAHO, Y. 1997. Foraging habitat and food intake of satellite-tracked King Penguins during the austral summer at Crozet Archipelago. *Mar. Ecol. Prog. Ser.* 150: 21–33.
- CHEREL, Y. & RIDOUX, V. 1992. Prey species and nutritive value of food fed during summer to King Penguin (*Aptenodytes patagonicus*) chicks at Possession Island, Crozet Archipelago. *Ibis* 134: 118–127.
- CHEREL, Y., VERDON, C. & RIDOUX, V. 1993. Seasonal importance of oceanic myctophids in King Penguin diet at Crozet Islands. *Polar Biol.* 13: 355–357.
- DAVIS, L.S., BOERSMA, P.D. & COURT, G.S. 1996. Satellite telemetry of the winter migration of Adélie Penguins (*Pygoscelis adeliae*). *Polar Biol.* 16: 221–225.
- DAVIS, L.S. & MILLER, G.D. 1992. Satellite tracking of Adélie Penguins. *Polar Biol.* 12: 503–506.
- FOXTON, P. 1956. The distribution of the standing crop of zooplankton in the Southern Ocean. *Disc. Rep.* 28: 191–236.
- GUINET, C., Koudil, M., BOST, C.A., DURBEC, J.P., GEORGES, J.Y., MOUCHOT, M.C. & JOUVENTIN, P. 1997. Foraging behaviour of satellite-tracked King Penguins in relation to sea-surface temperatures obtained by satellite telemetry at Crozet Archipelago, a study during three austral summers. *Mar. Ecol. Prog. Ser.* 150: 11–20.
- HART, T.J. 1942. Phytoplankton periodicity in Antarctic surface waters. *Disc. Rep.* 21: 261–356.
- HILL, R.D. 1993. Theory of geolocation by light-levels. In: Le Boeuf, B.J. & Laws, R.M. (Eds). *Elephant seals: population ecology, behavior and physiology*. Berkeley: University of California Press. pp. 227–236.
- HUNT, G.L. 1990. The pelagic distribution of marine birds in a heterogeneous environment. *Polar Res.* 8: 43–54.
- JONKER, F.C. & BESTER, M.N. 1994. The diving behaviour of adult southern elephant seal, *Mirounga leonina*, coveys from Marion Island. *S. Afr. J. Antarct. Res.* 24: 75–93.
- JOUVENTIN, P., CAPDEVILLE, D., CUENOT-CHAILLET, F. & BOITEAU, C. 1994. Exploitation of pelagic resources by a non-flying seabird: satellite tracking of the King Penguin throughout the breeding cycle. *Mar. Ecol. Prog. Ser.* 106: 11–19.
- JOUVENTIN, P. & LAGARDE, F. 1995. Evolutionary ecology of the King Penguin *Aptenodytes patagonicus*: the self-regulation of the breeding cycle. In: Dann, P., Norman, I. & Reilly, P. (Eds). *The penguins: ecology and management*. Chipping Norton: Surrey Beatty & Sons. pp. 80–95.
- JOUVENTIN, P. & WEIMERSKIRCH, H. 1990. Satellite tracking of Wandering Albatrosses. *Nature* 343: 746–748.
- KERRY, K.R., CLARKE, J.R. & ELSE, G.D. 1995. The foraging range of Adélie Penguins at Bechervaise Island, MacRobertson Land, Antarctica as determined by satellite telemetry. In: Dann, P., Norman, I., & Reilly, P. (Eds). *The penguins: ecology and management*. Chipping Norton: Surrey Beatty & Sons. pp. 216–243.
- KIRKWOOD, R. & ROBERTSON, G. 1997. The foraging ecology of female Emperor Penguins in winter. *Ecol. Monogr.* 67: 155–176.
- KOOYMAN, G.L., KOOYMAN, T.G., HORNING, M. & KOOYMAN, C.A. 1996. Penguin dispersal after fledging. *Nature* 383: 397.
- KOZLOV, A.N., SHUST, K.V. & ZEMSKY, A.V. 1991. Seasonal and inter-annual variability in the distribution of *Electrona carlsbergi* in the southern Polar Front Area. Selected Scientific Papers, WG-FSA-90/35, CCAMLR, Hobart, Australia pp. 337–367.
- KOUBBI, P. 1993. Influence of the frontal zones on ichthyoplankton and mesopelagic fish assemblages in the Crozet Basin (Indian Sector of the Southern Ocean). *Polar Biol.* 13: 557–564.
- LE BOEUF, B.J., CROCKER, D.E., BLACKWELL, S.B., MORRIS, P.A. & THORSON, P.H. 1993. Sex differences in diving and foraging behaviour of Northern Elephant Seals. In: Boyd, I.L. (Ed.). *Marine mammals: advances in behavioural and population biology*. *Symp. Zool. Soc. Lond.* 66: 149–178.
- LE BOEUF, B.J., MORRIS, P.A., BLACKWELL, S.B., CROCKER, D.E. & COSTA, D.P. 1996. Diving behavior of juvenile Northern Elephant Seals. *Can. J. Zool.* 74: 1632–1644.
- MASLENNIKOV, V.V. & SOLYANKIN, E.V. 1993. Oceanic fronts in the Southern Ocean as the main locations of myctophid and krill aggregations. *Antarktika* 32: 86–93.
- NAGATA, Y., MICHIDA, Y. & UMIMURA, Y. 1988. Variation of positions and structures of the oceanic fronts in the Indian Ocean sector of the Southern Ocean in the period from 1965 to 1987. In: Sahrhage, D. (Ed.). *Antarctic ocean and resources variability*. Berlin: Springer Verlag. pp. 92–98.
- PAKHOMOV, E.A., PERISSINOTTO, R. & McQUAID, C.D. 1994. Comparative structure of the macrozooplankton/micronekton communities of the Subtropical and Antarctic Polar Fronts. *Mar. Ecol. Prog. Ser.* 111: 155–169.
- PARK, Y.H., GAMBERONI, L. & CHARRIAUD, E. 1991. Frontal structure and transport of the Antarctic Circumpolar Current in the south Indian Ocean sector. *Mar. Chem.* 35: 45–62.
- PARK, Y.H., GAMBERONI, L. & CHARRIAUD, E. 1993. Frontal structure, water masses and circulation in the Crozet Basin. *J. Geophys. Res.* 98: 12 361–12 385.
- PRINCE, P.A., WOOD, A.G., BARTON, T. & CROXALL, J.P. 1992. Satellite tracking of Wandering Albatrosses (*Diomedea exulans*) in the South Atlantic. *Antarct. Sci.* 4: 31–36.
- PÜTZ, K. 1994. Aspects of the feeding ecology of Emperor Penguins (*Aptenodytes forsteri*) and King Penguins (*Aptenodytes patagonicus*). *Rep. Polar Res.* 136: 1–139. [in German].
- PÜTZ, K. & BOST, C.A. 1994. Feeding behavior of free-ranging King Penguins (*Aptenodytes patagonicus*). *Ecology* 75: 489–497.
- PÜTZ, K., WILSON, R.P., CHARRASSIN, J.-B., RACLOT, T., LAGE, J., LE MAHO, Y., KIERSPEL, M.A.M., CULIK, B.M. & ADELUNG, D. 1998. Foraging strategy of King Penguins (*Aptenodytes patagonicus*) during summer at the Crozet Islands. *Ecology* 79: 1905–1921.
- RODHOUSE, P.G., PRINCE, P.A., TRATHAN, P.N., HATFIELD, E.M.C., WATKINS, J.L., BONE, D.G., MURPHY, E.J. & WHITE, M.G. 1996. Cephalopods and mesoscale oceanography at the Antarctic Polar Front: satellite tracked predators locate pelagic trophic interactions.

- Mar. Ecol. Prog. Ser.* 136: 37–50.
- SCHNEIDER, D.C. 1991. The role of fluid dynamics in the ecology of marine birds. *Oceanogr. Mar. Biol. Ann. Rev.* 29: 487–521.
- STAHL, J.-C., JOUVENTIN, P., MOUGIN, J.-L., ROUX, J.-P. & WEIMERSKIRCH, H. 1985. The foraging zones of seabirds in the Crozet Island sector of the Southern Ocean. In: Siegfried, W.R., Condy, P.R. & Laws, R.M. (Eds). *Antarctic nutrient cycles and food webs*. Berlin: Springer Verlag. pp. 478–486.
- STEWART, B.S. & DELONG, R.L. 1993. Seasonal dispersion and habitat use of foraging Northern Elephant Seals. In: Boyd, I.L. (Ed). *Marine mammals: advances in behavioural and population biology*. *Symp. Zool. Soc. Lond.* 66: 179–194.
- TASKER, M.L., JONES, P.H., DIXON, T. & BLAKE, B.F. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. *Auk* 101: 567–577.
- TRIVELPIECE, W.Z., BENGTON, J.L., TRIVELPIECE, S.G. & VOLKMAN, N.J. 1986. Foraging behavior of Gentoo and Chinstrap Penguins as determined by new radiotelemetry techniques. *Auk* 103: 777–781.
- VAN FRANEKER, J.A. 1994. A comparison of methods for counting seabirds at sea in the Southern Ocean. *J. Field Orn.* 65: 96–108.
- WEIMERSKIRCH, H., SALAMOLARD, M., SARRAZIN, F. & JOUVENTIN, P. 1993. Foraging strategy of Wandering Albatrosses through the breeding season: a study using satellite telemetry. *Auk* 110: 325–342.
- WEIMERSKIRCH, H., STAHL, J.-C. & JOUVENTIN, P. 1992. The breeding biology and population dynamics of King Penguins *Aptenodytes patagonica* at the Crozet Islands. *Ibis* 134: 101–117.
- WEIMERSKIRCH, H., WILSON, R.P., GUINET, C. & KOUDIL, M. 1995. Use of seabirds to monitor sea-surface temperatures and to validate satellite remote-sensing measurements in the Southern Ocean. *Mar. Ecol. Prog. Ser.* 126: 299–303.
- WILLIAMS, A.J. & SIEGFRIED, W.R. 1980. Foraging ranges of krill-eating penguins. *Polar Rec.* 20: 159–162.
- WILSON, R.P. 1995. Foraging ecology. In: Williams, T.D. (Ed.). *The penguins Spheniscidae*. Oxford: Oxford University Press. pp. 81–106.
- WILSON, R.P., CULIK, B.M., BANNASCH, R. & LAGE, J. 1994. Monitoring Antarctic environmental variables using penguins. *Mar. Ecol. Prog. Ser.* 106: 199–202.
- WILSON, R.P., DUCAMP, J.-J., REES, W.G., CULIK, B.M. & NIEKAMP, K. 1992. Estimation of location: global coverage using light intensity. In: Priede, I.G. & Swift, S.M. (Eds). *Wildlife telemetry*. Chichester, England: Ellis Horwood. pp. 131–134.
- WILSON, R.P., NAGY, K.A. & OBST, B. 1989. Foraging ranges of penguins. *Polar Rec.* 25: 303–307.
- WILSON, R.P., PÜTZ, K., BOST, C.A., CULIK, B.M., BANNASCH, R., REINS, T. & ADELUNG, D. 1993. Diel dive depth in penguins in relation to vertical migration of prey: Whose dinner by candlelight? *Mar. Ecol. Prog. Ser.* 94: 101–104.
- WILSON, R.P., REES, W.G., LAGE, J., PÜTZ, K., KIERSPEL, M.A., COOPER, J., BOST, C.A., SCOLARO, J.A. & CULIK, B.M. in press. Determination of seabird position at sea using changes in diel light intensity. In: Le Maho, Y. & Zorn, T. (Eds). *Wildlife telemetry. Proceedings of the Strasbourg Conference*. Strasbourg: Centre d'Ecologie et Physiologie Energetiques, CNRS.
- WILSON, R.P., SCOLARO, J.A., PETERS, G., LAURENTI, S., KIERSPEL, M., GALLELLI, H. & UPTON, J. 1995. Foraging areas of Magellanic Penguins *Spheniscus magellanicus* breeding at San Lorenzo, Argentina, during the incubation period. *Mar. Ecol. Prog. Ser.* 129: 1–6.
- WILSON, R.P. & WILSON, M.P. 1989. Tape: a package attachment technique for penguins. *Wildl. Soc. Bull.* 17: 77–79.
-