Vol. 283: 293–297, 2004 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published November 30

NOTE

Exploitation of distant marginal ice zones by king penguins during winter

C. A. Bost[1,*], J. B. Charrassin[2], Y. Clerquin[3], Y. Ropert-Coudert[4], Y. Le Maho[3]

[1]Centre d'Etudes Biologiques de Chizé, CNRS, Villiers en Bois, 79360 Beauvoir/Niort, France
[2]Laboratoire d'Océanographie Physique, Museum National d'Histoire Naturelle, 75005 Paris, France
[3]Centre d'Ecologie et de Physiologie Energétiques, CNRS, 23 rue Becquerel, 67087 Strasbourg Cedex 2, France
[4]National Institute of Polar Research, 1-9-10 kaga, Itabashi-ku, Tokyo, 173-8515 Japan

ABSTRACT: We investigated the use of Antarctic waters by king penguins in a 2 yr study based on the satellite tracking of 10 penguins from the Crozet Islands (SW Indian Ocean). All the penguins travelled towards the pack ice, with 3 of them ending their journey at the edge between the marginal ice and the dense pack ice. The mean maximum foraging range and minimal distance travelled were 1620 and 4095 km, respectively. The effect of the satellite transmitter (PTT) attachment on foraging trip duration and colony attendance was much more important in winter in comparison to the summer. The penguins spent around 24 % of their trip at sea in the marginal ice zone. They explored the ice-covered habitat non-randomly as revealed by compositional analysis. The marginal ice was more used than free ice and floes areas. The strategy of travelling towards the marginal ice zone during winter ensures that the penguins have access to predictable feeding areas at a time when food availability is very low in the polar frontal zone. The diet of king penguins when foraging in Antarctic waters is unknown but may be different to their summer food at the Polar Front.

KEY WORDS: Feeding ecology · Satellite tracking · King penguins · Marginal ice zone

INTRODUCTION

During the winter period, southern seabirds may have to endure large drops in marine resources if they do not migrate to richer waters (Croxall 1984). Little is known, however, about their foraging ecology at this time of the year, which is critical for their survival (Croxall & Davis 1998). Most penguin species generally desert their colonies as early as the end of summer and disperse at sea between breeding seasons. They probably travel to more favourable regions but quantitative data about their foraging zones are still lacking (Wilson et al. 1998, Kooyman et al. 1999, Davis et al. 2001).

The king penguin is an oceanic, deep diver and one of the major avian consumers of the southern ocean (Woehler 1995, Bost et al. 1997, Kooyman et al. 1999, Charrassin & Bost 2001). The breeding cycle is characterized by a winter period of chick fasting, the parents returning irregularly to feed chicks because of the drastic drop in food availability (Koslov et al. 1991). From autumn to the end of winter, breeders usually leave their foraging grounds to spend most of their time at sea. Previous studies have shown that, during winter, king penguins considerably increase their foraging range, travelling as far south as the pack ice region (Jouventin et al. 1994, Moore et al. 1999, Charrassin & Bost 2001). We show here the first detailed data on the winter migratory movements of breeding king penguins obtained from a 2 yr study based on satellite tracking. Our objective was to investigate the use of Antarctic waters by these subantarctic predators and especially of the marginal ice edge zone, i.e. the transitional region between completely ice-free water and the dense pack ice (Knox 1994). We compare the at-sea distribution of the penguins with contemporaneous sea ice maps and discuss the use of the physical areas with respect to the potential availability of prey.

*Email: bost@cebc.cnrs.fr

MATERIALS AND METHODS

The study was carried out at La Grande Manchotière colony, at Possession Island (46° 25′ S, 51° 45′ E), Crozet Archipelago, SW Indian Ocean. About 30 000 pairs of king penguins breed in this colony, while the whole Crozet population (1×10^6 pairs) constitutes more than 50% of the world population (Guinet et al. 1996). In 1996 and 1997, 10 penguins were fitted with satellite transmitters (PTTs) from June to October 1996 (n = 5 birds) and from June to November 1997 (n = 5 birds) (Table 1). We used Telonics ST10 transmitters. The transmission interval was 60 s with an on-off emission interval of 6 h. The basic cylindrical shape of the PTT had a cross sectional area of 4.9 cm and weighed 270 g. The top of the transmitters was hydrodynamically shaped to reduce the drag effect (Bannasch et al. 1994). The transmitters were attached with cable-ties to a small grid glued to the feathers of the back with fast epoxy. The penguins were flipper marked with coloured tape. Fitting took a total of ca. 40 min. All birds with PTTs attached were rearing a chick. Premature failure of certain transmitters precluded following 6 of the 10 birds over their entire trip. Eight birds were successfully tracked until they crossed the limit of the pack ice area (Fig. 1). During the deployment period, the colony was checked several times a day to recover the birds as they came back from the sea. Positional data were analysed using customized software following Charrassin & Bost (2001). The at-sea distribution was compared with contemporaneous weekly sea ice maps from ERS data (CERSAT, IFREMER, France). Four categories of habitats were considered: free water (no ice), floes (large and flat sheets of sea-ice floating in open sea), marginal ice (a mixture of small broken floes) and pack ice (frozen sea water a year or more old). Habitat use in terms of ice cover was tested for with a compositional analysis method using custom software (Resource Selection for Windows©, Leban 1999. Available at http://members.xroom.com/fred_leban). This method takes into account the fact that an animal's use of one habitat is dependent on its use of other habitat types (Aebischer et al. 1993).

RESULTS AND DISCUSSION

During the winters of 1996 and 1997, all the tracked penguins performed long-range foraging trips towards the Antarctic. The birds dispersed over an area of 4×10^6 km^2 of ocean (Fig. 1). The mean trip duration of the 4 birds tracked over their whole trip was 91.5 ± 8.5 d. This corresponds to a mean maximum foraging range and a minimal total distance travelled of 1620 ± 176 and 4095 ± 635 km, respectively (Table 1). These birds spent a substantial proportion of their time at sea below the northern sea ice limit (i.e. south of 55.8 to 57° S), in the marginal ice zone (MIZ, 23.7 ± 13%, Table 1). In the MIZ, the penguins generally travelled at a slower speed in contrast to open water conditions (except bird 600, Table 1).

Among the 7 penguins having crossed the sea ice limit, 3 reached the edge between the marginal ice and the dense pack ice. These penguins explored the ice-covered habitat non-randomly as revealed by compositional analysis. The ranking from most to least explored habitat was marginal ice > free ice > floes, with significant differences. They used the areas classified as marginal ice more than free ice (p = 0.02) and floes areas (p = 0.04). In 1996, the maximal foraging range of the penguins tracked appeared to be greater than in 1997 ($U = 2$, $p < 0.05$), possibly because the limit of the pack ice area was extended about 180 km further south.

Table 1. Details of long distance foraging trips performed by king penguins during winter (Crozet Islands, SW Indian Ocean, 1996–1997). The minimal distance covered and the time spent in the pack-ice zone have been calculated only from complete trips. Speed values for the same bird not sharing a common superscript letter are significantly different ($p < 0.05$, U-test). Marg.: Marginal ice

Bird	Departure (d/mo/yr)	Return (d/mo/yr)	Track duration (d)	Locations received (n)	Maximum foraging range Distance (km)	Maximum foraging range Coordinates	Minimal distance covered (km)	Mean distance travelled d^{-1} (km)	Outward speed (km h^{-1}) Free water	Outward speed (km h^{-1}) Marg.	Time spent in marg. zone (d) (% of trip)
597	30/05/96	–	20[c]	48	1842[c]	56.55° E–62.77° S	–	86	5.1 ± 3.8^a	4.2 ± 2.5^b	–
598	02/06/96	20/08/96	79	34	1856	42.01° E–62.13° S	4557	58	5.9 ± 4.7^a	1.8 ± 1.1^b	14 (18)
570	09/06/96	12/09/96	95	4	1650	40.50° E–59.64° S	3393	–	–	–	23 (24)
600	15/06/96	–	51[c]	14	1984[c]	66.45° E–60.5° S	–	41	1.9 ± 0.3^a	2.4 ± 2.3^b	–
315-1	01/07/96	02/10/96	94	154	1475	45.93° E–59.2° S	3729	38	2.2 ± 1.9^a	1.7 ± 1.1^b	15 (16)
994	24/06/97	–	25[c]	80	1419[c]	65.80° E–55.73° S	–	69	–	–	–
995	02/07/97	–	21[c]	39	1138[c]	60.01° E–55.29° S	–	137	–	–	–
315-2	06/07/97	–	43[c]	61	1487[c]	63.50° E–57.75° S	–	43	2.1 ± 1.6^a	1.9 ± 0.9^a	–
993	18/07/97	–	20[c]	32	865[c]	63.79° E–52.79° S	–	138	–	–	–
571	02/08/97	08/11/97	98	53	1495	55.17° E–59.76° S	4704	48	4.1 ± 4.4^a	3.2 ± 4.2^b	43 (44)

[c]Premature battery failure excluded following the whole trip

These data confirm the extraordinarily wide range covered by breeding king penguins during winter when attending chicks at their colony. In addition, the importance of the MIZ as a foraging area for such subantarctic predators is shown. The mean trip duration of the penguins successfully tracked was 30% longer than found from contemporaneous data based on the automatic monitoring of penguins fitted with transponders from the same colony (65 d, Descamps et al. 2002). Additionally, 6 of the 10 birds fitted with PTTs deserted their breeding colony. As the birds were unbanded, to limit adverse effects (Culik et al. 1993), it was impossible to determine whether they returned to the colony the following breeding season. External devices can strongly alter the foraging efficiency of penguins by inducing additional drag (e.g. Bannasch et al. 1994), which affect the bird's swimming speed and energy expenditure (Wilson et al. 1986, Wilson & Culik 1992). The effect is likely to be even more pronounced with PTTs, as the antenna may add substantially to the drag caused by the backpack. During summer, i.e. when food availability is high, the trip duration of king penguins fitted with similar PTTs was increased by up to 30%. However, their breeding success and colony attendance do not differ significantly compared to birds without PTTs attached (Charrassin & Bost 2001, C. A. Bost unpubl. data). During winter, i.e. when food availability is much reduced, the effect of the instruments on penguins foraging appears more important, as indicated by data from other species of penguins (Pütz et al. 2000, Davis et al. 2001). The adverse responses observed in terms of trip duration and colony desertion can result from the cumulative effects of a higher foraging cost and endocrine response to stressful conditions, inducing a decrease in parenting behaviour (Wingfield 1993). Although the PTTs certainly had a negative effect on the foraging behaviour of equipped king penguins, it seems unlikely that their general migratory path would have been radically affected. Previous studies using miniaturized Global Location Sensors have also suggested that king penguins from Heard (53° 05′ S, 73° 30′ E) and Crozet Islands swim south to 63–65° S (Moore et al. 1999, Pütz et al. 1999).

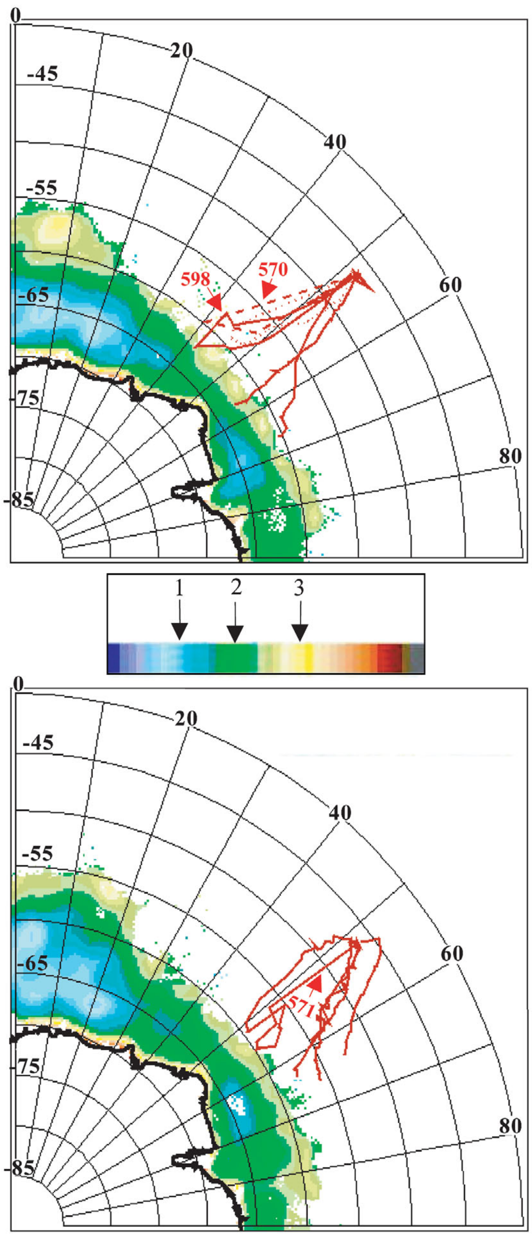

Fig. 1. Migratory routes of king penguins from Crozet Islands (SW Indian Ocean) towards Antarctic waters during the winters of 1996 (n = 5 birds) and 1997 (n = 5 birds). Also shown is the ice coverage map from 22/08/96 and 08/09/97 (satellite imagery derived from ERS, CERSAT, IFREMER. Smooth first-year ice: 1, Pack ice: 2, Marginal ice: 3). The arrows indicate the outbound leg of the complete tracks

The extensive use of the MIZ indicates that the penguins had access to a higher prey availability than in the polar frontal zone where the penguins forage in summer (Bost et al. 1997). Myctophid fish constitute the main prey of king penguins (e.g. Cherel et al. 1993). During winter, these fish are found at a much greater depth in the polar frontal zone (i.e. 49 to 53° S) than in summer (Koslov et al. 1991). In contrast, several myctophid species have been recorded in substantial numbers during winter and spring in the MIZ (Scotia Sea), with a trend of increasing biomass moving south to north in the region, followed by a drop north of 58° S (Torres et al. 1984). The northern part of the MIZ coincides precisely with the main foraging habitat of king penguins during winter. The fish biomass peak observed there corresponds to a pronounced marine productivity in the northern part of the MIZ. The primary and secondary productions are generally greater at the pack ice than in open waters because of physical features such as a more stable water column and a decrease in turbulence (Knox 1994).

In the MIZ, *Electrona antarctica* and *Gymnoscopelus braueri* constitute the dominant myctophid fish in the upper 500 m of the water column during winter (Lancraft et al. 1991). There, they exhibit vertical diel migrations as in the other localities of their range (Duhamel et al. 2000). However, the daytime depth of distribution of *E. antarctica* and *G. braueri* is between 500 and 1000 m (Lancraft et al. 1991), i.e. beyond the king penguin's diving range (maximal diving depth 440 m, J. B. Charrassin & C. A. Bost unpubl. data). During the night, these fish are distributed between depths of 0 and 300 m (Lancraft et al. 1991). King penguins are primarily visual foragers (Wilson et al. 1993, Bost et al. 2002) and they forage mainly from dawn to dusk especially during winter (Charrassin et al. 2002). One can, therefore, hypothesize that king penguins foraging in the MIZ can catch these prey mostly at dawn, when the descent migration occurs. Such limited access to myctophids raises the question of a possible dependence on other prey species, such as krill *Euphausia superba*. Indeed, *E. superba* is the only potential prey species to inhabit the mixed layer at all times of the day (Lancraft et al. 1991). The depth range actively exploited by king penguins during winter lies between 200 and 250 m (Charrassin & Bost 2001), precisely overlapping the depth range of *E. superba*. Also, *E. superba* massively migrates to the upper 0 to 200 m at night, providing most of the biomass of macrozooplankton and micronekton (56%), in contrast to *E. antarctica* (8.5%, Lancraft et al. 1991). Penguins would, therefore, be able to catch krill during their descent phase at dawn, when these prey are detectable.

During summer and autumn, the northern limit of the *Euphausia superba* distribution (59° S in the South Indian Ocean sector, Pakhomov 2000) is not accessible to the shorter foraging range of king penguins that feed chick (Charrassin & Bost 2001). No diet data are available for king penguins foraging in Antarctic waters. The congeneric Emperor penguin *Aptenodytes patagonicus* relies partly on krill when foraging in winter (Kirkwood & Robertson 1997) but whether or not king penguins rely partly on krill when foraging in Antarctic waters remains to be determined. The foraging distribution of king penguins during winter, as determined by satellite tracking, overlaps with that of juvenile emperor penguins that travel as far north as 57° S (Kooyman et al. 1996). The 2 species may thus forage for the same prey. However, the standing stocks of fish and euphausiid biomass in the MIZ are relatively high compared to other oceanic areas (Weddell and Scotia Sea regions) and vary little seasonally (Lancraft et al. 1991), preventing potential competition for the same food resource. To conclude, the strategy of travelling towards the MIZ during winter ensures that the king penguin has access to predictable feeding areas at a time when food availability is low in the polar frontal zone. Foraging studies based on the use of stable isotopes (Cherel et al. 2000) and feeding activity recorders on individually tracked penguins are still necessary to better identify the trophic niche of these subantarctic predators during winter.

Acknowledgements. This work was supported financially and logistically by the Institut Polaire Français (IPEV) and Terres Australes et Antarctiques Françaises. We are especially indebted to N. Lambert, M. Gauthier-Clerc, S. Drault, J. Menard, A. Rosinsky, E. Vallentini and S. Eudes for their help in the field with the fitting and recovery of the penguins. Special thanks also go to R. Ezraty (IFREMER) for providing sea ice data from CERSAT. A. Pape and 3 anonymous referees provided constructive suggestions that were greatly appreciated by the authors.

LITERATURE CITED

Aebischer NJ, Robertson PA, Kenward, RE (1993) Compositional analysis of habitat use from animal radio-tracking data. Ecology 74(5):1313–1325

Bannasch R, Wilson RP, Culik B (1994) Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. J Exp Biol 194:83–96

Bost CA, Georges JY, Guinet C, Cherel Y, Pütz K, Charrassin JB, 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

Bost CA, Zorn T, Le Maho Y, Duhamel G (2002) Feeding of diving predators and diel vertical migration of prey: king penguin diet versus trawl sampling at Kerguelen islands. Mar Ecol Prog Ser 227:51–61

Charrassin JB, Bost CA (2001) Utilisation of the oceanic habitat by king penguins over the annual cycle. Mar Ecol Prog Ser 221:285–297

Charrassin JB, Le Maho Y, Bost CA (2002) Seasonal changes in the diving parameters of king penguins. Mar Biol 141:581–589

Cherel Y, Verdon C, Ridoux V (1993) Seasonal importance of oceanic myctophids in king penguin diet at Crozet Islands. Polar Biol 13:355–357

Cherel Y, Hobson KA, Weimerskirch H (2000) Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. Oecologia 122:155–162

Croxall JP 1984 Seabirds and marine resources. In: Laws E (ed) Antarctic ecology. Academic Press, London, p 533–619

Croxall JP, Davis LS (1998) Penguins: paradoxes and patterns. Mar Ornithol 26:1–12

Culik BM, Wilson RP, Bannash R (1993) Flipper-bands on penguins: what is the cost of a life-long commitment? Mar Ecol Prog Ser 98:209–214

Davis LS, Harcourt RG, Bradshaw CJA (2001) The winter migration of Adelie penguins breeding in the Ross Sea sector of Antarctica. Polar Biol 24:593–597

Descamps S, Gauthier-Clerc M, Gendner JP, Le Maho Y (2002) The annual breeding cycle of unbanded king penguins *Aptenodytes patagonicus* on Possession Island (Crozet). Avian Sci 2:87–98

Duhamel G, Koubbi P, Ravier C (2000) Day and night mesopelagic fish assemblages off the Kerguelen islands (Southern ocean). Polar Biol 23:106–112
Guinet C, Cherel Y, Ridoux V, Jouventin P (1996) Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass 1962–85. Antarct Sci 8(1):23–30
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
Kirkwood R, Robertson G (1997) The foraging ecology of female emperor penguins in winter. Ecol Monogr 67:155–176
Knox GA (1994) The biology of the Southern Ocean. Cambridge University Press, Cambridge
Kooyman GL, Kooyman TG, Horning M, Kooyman CA (1996) Penguin dispersal after fledging. Nature 383:397
Kooyman GL, Hull C, Olsson O, Robertson G, Croxall J, Davies L (1999) Foraging patterns of polar penguins. In: Adams NJ, Slotow RH (eds) Proc 22nd Int Ornithol Congr. BirdLife South Africa, Johannesburg, p 2021–2039
Koslov AN, Shust KV, Zemsky AV (1991) Seasonal and interannual variability in the distribution of *Electrona carlsbergi* in the Southern Polar Front area. In: Selected scientific papers (SC-CAMLR-SSP/7), Committee Conservation Antarctic Living Resources, Hobart, p 337–367
Lancraft TM, Hopkins TL, Torres JJ, Donnelly J (1991) Oceanic micronektonic/macrozooplanktonic community structure and feeding in ice covered Antarctic waters during the winter (AMERIEZ 1988). Polar Biol 11:157–167
Moore GJ, Wienecke B, Robertson G (1999) Seasonal change in foraging areas and dive depths of breeding king penguins at Heard Island. Polar Biol 21:376–384
Pakhomov EA (2000) Demography and life cycle of antarctic krill *Euphausa superba*, in the Indian sector of the Southern Ocean: long-term comparison between coastal and open-ocean regions. Can J Fish Aquat Sci 57(Suppl 3):68–90
Pütz K, Ropert-Coudert Y, Charrassin JB, Wilson RP (1999) Foraging areas of king penguins (*Aptenodytes patagonicus*) breeding at Possession Island in the southern Indian Ocean. In: Cooper J (ed) Proc 3rd Int Penguin Conf, Cape Town, 2–6 Sep 1996, Mar Ornithol 27:77–84
Pütz K, Ingham R, Smith JG (2000) Satellite tracking of the winter migration of Magellanic penguins *Speniscus magellanicus* breeding in the Falkland Islands. Ibis 142:614–622
Torres JJ, Lancraft TM, Weigle BL, Hopkins TL (1984) Distribution and abundance of fishes and salps in relation to the marginal ice zone of the scotia sea, November and December 1983. Antarct J US XIX 5:117–119
Wilson RP, Culik B (1992) Package on penguins and devices-induced data. In: Priede IG, Swift SM (eds) Wildlife telemetry. Remote monitoring and tracking of animals. Ellis Horwood, New York, p 573–580
Wilson RP, Grant WS, Duffy DC (1986) Recording devices on free-ranging marine animals: does measurement affect foraging performance? Ecology 67:1091–1093
Wilson RP, Pütz K, Bost CA, Culik BM, Bannasch R, Reins T, Adelung D (1993) Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candlelight? Mar Ecol Prog Ser 94:101–104
Wilson RP, Alvarrez B, Latorre L, Adelung D, Culik B, Bannasch R (1998) The movements of gentoo penguins *Pygoscelis papua* from Ardley Island, Antarctica. Polar Biol 19: 407–413
Wingfield JC (1993) Modulation of the adrenocortical response to stress in birds. In: Davey KG, Peter RE, Tobe SS (eds) Perspectives in comparative endocrinology. National Research Council of Canada, Ottawa, p 520–528
Woehler EJ (1995) Consumption of southern ocean marine resources by penguins. In: Dann P, Norman I, Reilly P (eds) The penguins: ecology and management. Surrey Beaty & Sons, Chippington North, p 266–294

Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: August 22, 2003; Accepted: May 27, 2004
Proofs received from author(s): November 19, 2004