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Where do penguins go during the inter-breeding period? Using geolocation to track the winter dispersion of the macaroni penguin

C. A. Bost[1,*], **J. B. Thiebot**[1], **D. Pinaud**[1], **Y. Cherel**[1] **and P. N. Trathan**[2]

[1] *Centre d'Etudes Biologiques de Chizé, UPR 1934 du CNRS, 79360 Villiers-en-bois, France*
[2] *British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK*
**Author for correspondence* (*bost@cebc.cnrs.fr*).

Although penguins are key marine predators from the Southern Ocean, their migratory behaviour during the inter-nesting period remains widely unknown. Here, we report for the first time, to our knowledge, the winter foraging movements and feeding habits of a penguin species by using geolocation sensors fitted on penguins with a new attachment method. We focused on the macaroni penguin *Eudyptes chrysolophus* at Kerguelen, the single largest consumer of marine prey among all seabirds. Overall, macaroni penguins performed very long winter trips, remaining at sea during approximately six months within the limits of the Southern Ocean. They departed from Kerguelen in an eastward direction and distributed widely, over more than 3.10^6 km^2. The penguins spent most of their time in a previously unrecognized foraging area, i.e. a narrow latitudinal band (47–49° S) within the central Indian Ocean (70–110° E), corresponding oceanographically to the Polar Frontal Zone. There, their blood isotopic niche indicated that macaroni penguins preyed mainly upon crustaceans, but not on Antarctic krill *Euphausia superba*, which does not occur at these northern latitudes. Such winter information is a crucial step for a better integrative approach for the conservation of this species whose world population is known to be declining.

Keywords: foraging; wintering; penguins; Southern Ocean; stable isotopes; bio-logging

1. INTRODUCTION

Penguins constitute a key group of consumers in the Southern Ocean, where they number approximately 23.6 million breeding pairs, form more than 90 per cent of seabird biomass and consume approximately 18.1 million tonnes of marine resources per year (Woehler 1995). Many penguins are seasonal breeders that disperse far away from the colonies during the inter-nesting period (thereafter called winter). Current environmental changes, especially in winter, are known to affect seabird population numbers and demography (Barbraud & Weimerskirch 2003). Therefore, a major challenge is to identify the underlying biological mechanisms during winter, but this is currently limited by a lack of information on seabird distribution during this period. This is particularly relevant for penguins because the swimming and diving habits of these flightless predators complicate accurate visual identification at sea.

Here we report the complete wintering-at-sea distribution of a penguin species, the macaroni penguin *Eudyptes chrysolophus*, during its inter-breeding period by using miniaturized global location sensors (GLS) and stable isotopes. Breeding in summer on sub-Antarctic islands, macaroni penguins are the most numerous penguin species (Woehler 1995) and the seabird with the highest consumption of marine resources worldwide (de Brooke 2004). After they moult at the end of the breeding season, they leave their colonies, so that no birds are seen on land for over six months, throughout the winter. A major question therefore is: where do these penguins go, and what do they eat during winter?

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2. MATERIAL AND METHODS

Fieldwork was conducted at Kerguelen Islands (49.06° S, 70.30° E), in the southern Indian Ocean. The Kerguelen population of macaroni penguins comprises approximately 1.8×10^6 pairs, i.e. approximately 18 per cent of the world population (Woehler 1995). Our study birds were equipped with GLS (MK9, BAS) that weigh approximately 6 g in air. The loggers were attached to newly smooth plastic leg bands (designed at Centre d'Etudes Biologiques de Chize, Centre National de la Recherche Scientifique). All the instrumented penguins were first colour marked on the chest in December 2005 while on their nest to be sure of their breeding status. GLS were subsequently deployed on marked birds after their moult (March to April 2006), a few days before they left for their winter migration. Devices were retrieved at the beginning of the next breeding season (October 2006). According to Phillips *et al.* (2004), accuracy of the locations calculated from the loggers is expected to be approximately 180 km. GLS record ambient light (measured every minute, then the maximum value in any 10 min period is archived) and sea temperature (with an accuracy of ±0.5°C) (Phillips *et al.* 2004). Penguin locations were estimated using the 'TripEstimation' package (R Development Core Team 2008) improved by a sea-surface temperature matching protocol (see the electronic supplementary material). Sea-surface chlorophyll *a* concentration was extracted from monthly SeaWiFS Project images. Following Cherel *et al.* (2007), penguins were blood-sampled in spring to measure their isotopic niche, with blood δ^{13}C and δ^{15}N values reflecting the birds' foraging habitat and trophic position, respectively, at the end of the winter period. Values are mean ± s.d.

3. RESULTS

Loggers were deployed on 21 adult individuals in autumn, of which 14 (67%) were recaught at their colony the next spring, all (but one) with devices, of which 12 downloaded successfully. The mean body mass of males ($n = 7$) and females ($n = 5$) in spring was 5005 ± 267 and 3744 ± 140 g, respectively. Location analysis indicated that the penguins left the colony over 35 days (9 April to 15 May), were away for approximately six months (190 ± 14 days) and returned synchronously to the colony in October (24 October ± 6 days). Once at sea, birds moved quickly away from Kerguelen waters towards the east (figure 1). They overall performed a very long movement, the maximal foraging range (2416 ± 1008 km) being reached after approximately three months at sea (109 ± 34 days). The minimum

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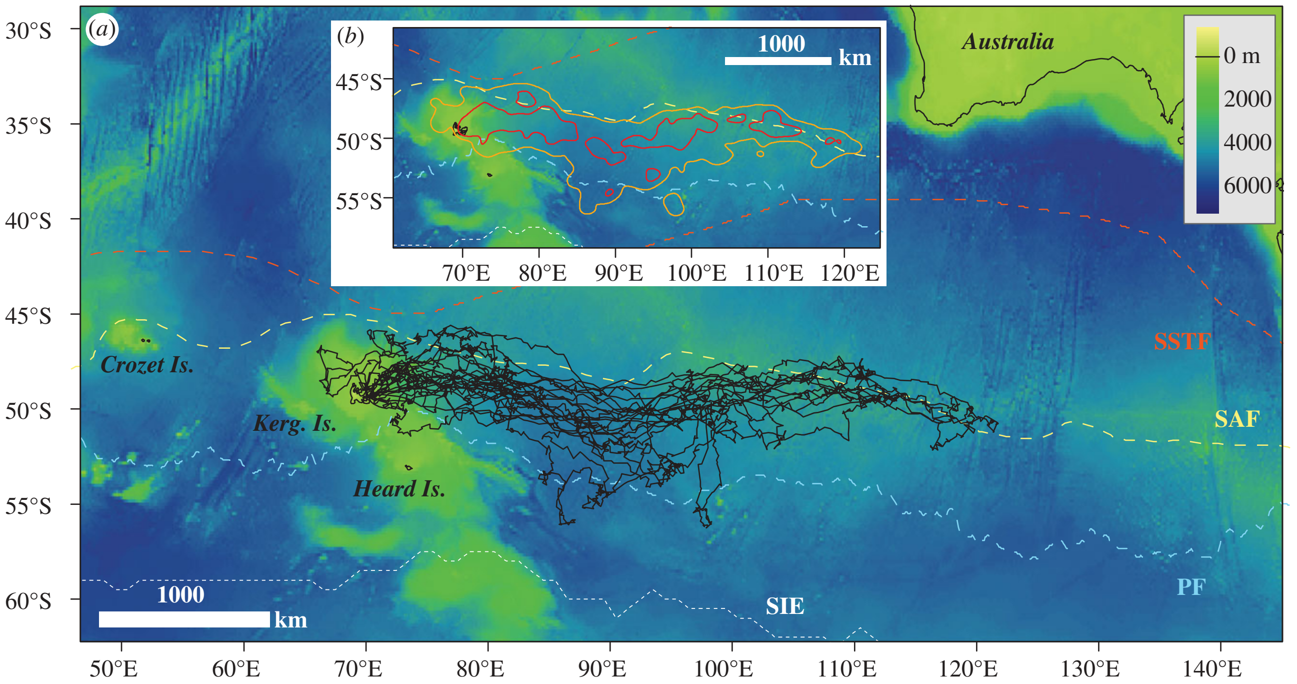

Figure 1. (*a*) Winter-at-sea movements of 12 macaroni penguins from Kerguelen tracked by GLS from April to October 2006. Bathymetric range is indicated in the right upper corner. SSTF, Subtropical Front; SAF, Sub-Antarctic Front; PF, Polar Front; SIE, maximal sea ice extent. (*b*) Kernel density distribution of penguins. The density contours encompass 50 (red) to 95 per cent (yellow) of the total distribution.

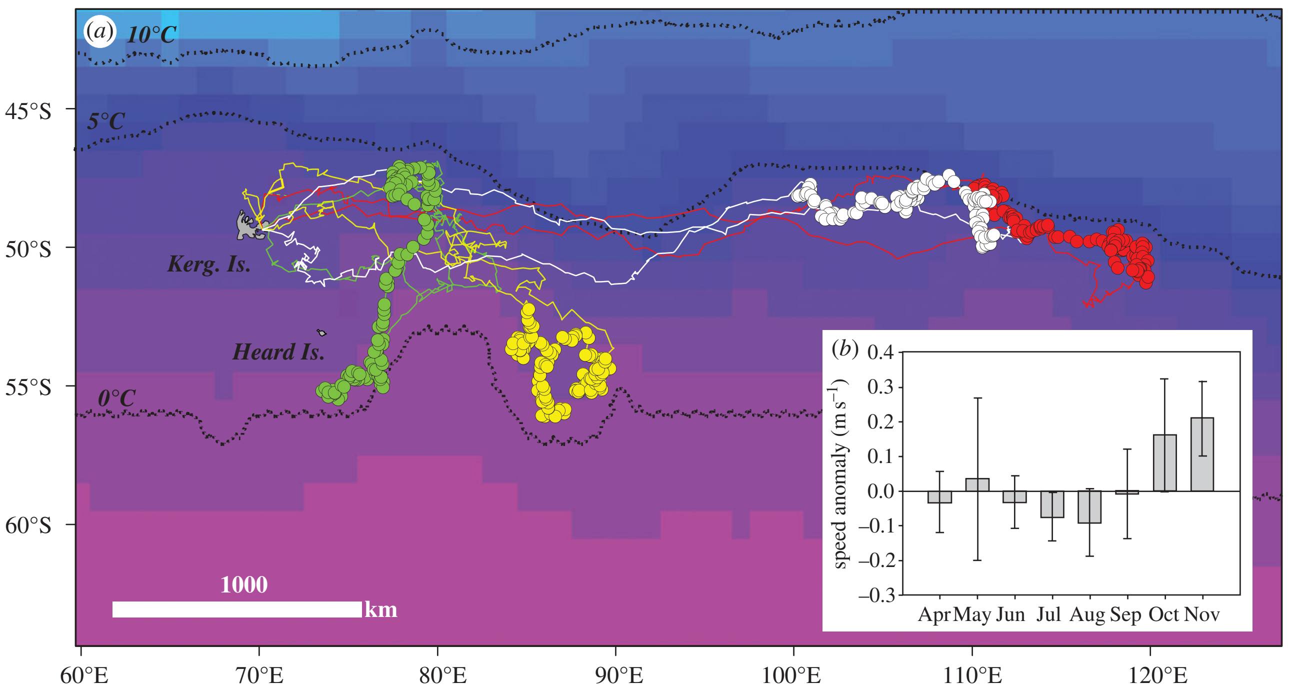

Figure 2. (*a*) Two distinctive at-sea distributions of macaroni penguins during winter (July to August 2006): direct paths towards Antarctic waters ($n = 2$, green and yellow circles) and long distance path in the Polar Frontal Zone (PFZ) ($n = 2$, white and red circles). The lines correspond to the routes taken by the same birds from their departure until their return. (*b*) (right corner) Distribution of speed anomalies of at-sea penguins (April to November 2006).

horizontal distance covered over the whole movement averaged 10 430 ± 1277 km. Monthly travelling speed varied during the winter (ANOVA, $F_7 = 4.65$, $p = 0.0002$). It reached its lowest values in July to August, and highest value in October (figure 2), during which birds swam back to Kerguelen and covered their greatest distance monthly (1743 ± 669 km).

Macaroni penguins distributed widely during winter, over more than 3.10^6 km^2. They spent most of the time in a narrow latitudinal band (47–49° S), within the central Indian Ocean (70–100° E) and further east (approx. 110° E). By far, the major targeted oceanic domain was the Polar Frontal Zone (PFZ), i.e. between the Polar Front and the Sub-Antarctic Front (81.9% of the time at sea), followed by the Sub-Antarctic Zone (11.5%), i.e. between the Sub-Antarctic Front and the South Subtropical Front, and the Antarctic Zone (south of Polar Front, 6.6%) (figure 1). Surface chlorophyll *a* concentration was low over the whole range of penguin distribution (0.17 ± 0.10 mg m^{-3}), and it did not differ between the main winter area used and Kerguelen shelf waters (0.16 ± 0.02 versus 0.17 ± 0.08 mg m^{-3}, Mann–Whitney, $U = 489$, $p = 0.379$).

No significant sexual differences were found in the number of days spent at sea, distance travelled, maximal foraging range, and mean and maximal travelling speeds (see the electronic supplementary material).

Two distinct movement patterns occurred according to the individuals (figure 2). Most penguins ($n = 7$) had an extended eastward foraging range, remaining all the time within the PFZ in waters with sea surface temperatures ranging from 2°C to 6°C. The others ($n = 5$) showed a shorter foraging range with a more southward migration towards colder tongues (1°C) of Antarctic waters. The blood δ^{13}C and δ^{15}N values of macaroni penguins in spring averaged -21.4 ± 0.3 and 7.6 ± 0.6 per cent, respectively, with no statistical differences between males and females or differences between eastward and southward birds (statistics not shown).

4. DISCUSSION

Here, we report for the first time, to our knowledge, the complete at-sea movements of a penguin species during the inter-breeding period, using miniaturized GLS. Our work shows it is now possible to investigate the at-sea movements of sensitive penguins during the winter. The recovered birds were healthy and in good condition as indicated by their body mass which was similar to usual values at the same stages (4685–5240 g for the males at arrival at colony, 3960 g for the females at the beginning of incubation; Williams 1995). A key methodological issue was that the loggers were fixed on a leg band that did not harm the birds over the long term. Our recovery rate (67%) is a minimal one as it is based on only three visits to the colony and the site fidelity is not absolute. Previous investigations using satellite tags prevented following the penguins' behaviour during the complete inter-breeding period because of the large device size and hydrodynamic drag induced by the antenna (Bost *et al.* 2004). Our attachment method is thus a crucial step allowing the investigation of the dispersion patterns of penguins, which have remained widely unknown until now.

A first major finding is that all birds exhibited the same migratory behaviour. Macaroni penguins dispersed from Kerguelen in an eastward direction. Birds neither crossed the northern limit of the Southern Ocean nor foraged in the pack-ice zone; instead, they remained mostly within the PFZ. None of the studied penguins came ashore during the winter, thus remaining consistently at sea during approximately six months, which is in agreement with winter diving data (Green *et al.* 2005).

A second major finding is that macaroni penguins showed unexpected large-scale dispersal over winter. To our knowledge, the study is the first to highlight the importance of a large oceanic zone in the central Indian Ocean (100–110° E, 47–49° S) for the nutrition of an apex predator. Macaroni penguins showed slower daily swimming speeds when they were closest to their farthest distance away from Kerguelen in mid-winter. Penguins slow down when increasing their foraging effort (Wilson 1995), thus suggesting that the central Indian Ocean is a favourable foraging ground. No specific oceanographic features were found in the area, which was characterized by a low phytoplankton concentration. However, low biological productivity in the habitat does not preclude abundant food sources for penguins in the PFZ in winter. Primary and secondary marine production can be spatially and temporally uncorrelated (Grémillet *et al.* 2008).

In winter, macaroni penguins from the southern Atlantic Ocean dive longer and to greater depths than in summer, suggesting either a change in location of the prey or even a change in prey type (Green *et al.* 2005). Blood δ^{15}N values of southern Indian Ocean birds in spring was low and identical to that of chicks that were fed with crustaceans in summer (7.5 ± 0.3‰; Cherel *et al.* 2007), thus indicating that they preyed mainly upon crustaceans in late winter. It is likely that they targeted the most abundant sub-Antarctic swarming macrozooplanktonic species (Cherel *et al.* 2007). Interestingly, their northern geographical range precluded feeding on Antarctic krill *Euphausia superba* in winter, and instead it indicates that birds from the southern Indian Ocean do not depend on this key Antarctic resource.

Macaroni penguins are sexually dimorphic (Williams 1995). Nevertheless, no sexual differences were found in the present work, indicating that males and females spent the austral winter in the same foraging grounds where they fed on the same prey. A recent isotopic investigation described two distinct winter strategies, with most macaroni penguins dispersing within the Sub-Antarctic/PFZ and a few individuals foraging in colder waters (Cherel *et al.* 2007). Indeed, our GLS data suggest two distinct dispersion strategies, with most birds showing an extended trip within the PFZ, and the remaining individuals performing shorter trips during which they foraged in part in cold Antarctic waters.

In conclusion, this work highlights the winter importance of the PFZ for migrating macaroni penguins, thus complementing previous investigations showing that this domain is a main foraging ground for other top consumers in summer. The world population of macaroni penguins has declined throughout its range over the last 20 years (BirdLife International 2008). Delineating the foraging areas during the inter-breeding period is a key step for a better understanding of predator biology and their conservation.

The Ethics Committee of IPEV approved the field procedure.

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