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ORIGINAL PAPER

Foraging behavior of Adélie penguins during incubation period in Lützow-Holm Bay

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Abstract The diving behavior of Adélie penguins *Pygoscelis adeliae* was investigated using time–depth recorders during the incubation period in the fast sea-ice area of Lützow-Holm Bay, Antarctica. Dive profiles and activity/time allocation suggested that penguins were obligated to walk on the fast-ice for 90–100 km until a polynya, which they used as an access to the pack-ice zone. Dive depth did not differ between males and females, though males' dive duration was longer than that of females. Dive depth was slightly shallower and dive duration was shorter during the incubation than during the chick-rearing phase. Birds dove throughout the day, although less frequently around midnight, and there was no clear diel change in dive depth. This daily dive pattern during incubation period was similar to that previously observed during the chick-rearing period in a fast sea-ice area, but differed from that observed in sea-ice-free area. Variations in diving behavior resulted from different environmental conditions, such as foraging area with different sea-ice condition, as well as from different life history strategies.

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Introduction

As central place foragers, seabirds commute between an on-land breeding site and an at-sea foraging area (Stephens and Krebs 1986). In the case of Antarctic penguins, they sometimes need to walk long distances on the sea-ice between breeding sites and open waters (Pinshow et al. 1977). In this regard, extensive sea-ice in winter has been regarded as a limitation to the distribution range of Adélie penguin *Pygoscelis adeliae*'s breeding colonies, as suggested by the absence of colonies between the east coast region of the Lützow-Holm Bay and the Antarctic Peninsula (Ainley 2002). In Lützow-Holm Bay, sea-ice develops far off-shore in winter and remains in the bay even during the summer (Kato et al. 2003); this is a unique feature for an Adélie penguin's breeding site. The biology of Adélie penguins being closely associated with sea-ice, modifications in sea-ice conditions are known to affect the birds' foraging behavior and, consequently, their breeding success (Watanuki et al. 1997; Rodary et al. 2000).

In Lützow-Holm Bay, Adélie penguins start to arrive at the breeding colonies in late October (Watanuki and Naito 1992). After laying eggs in mid- to late November, females go to sea for about 12–14 days to replenish their body reserves. Upon the return of the females, males, having fasted for about a month, leave for the second foraging trip of the pair, which will last about 10–12 days. After this, females perform another trip for 5–6 days, followed by several 1–2 days long rotations between mates until chicks hatch. From the incubation to the chick-rearing period, sea-ice condition changes drastically. Although it is known that

incubating birds generally display a more extensive foraging range (Clarke et al. 2006) and swim more (Chappell et al. 1993a) than chick-rearing ones, information on the foraging behavior of incubating Adélie penguins remains very limited. Yet, this is a crucial period in terms of ecological trade-offs, as, for instance, it has been shown that wandering albatrosses *Diomedea exulans* maximize time at sea and minimize foraging energy costs during incubation, while doing the reverse during brooding, i.e. minimizing time at sea to maximize food delivery rate to chicks (Shaffer et al. 2003). Changes in adult body condition and offspring demand have been suspected as the principal drivers of this situation. We hypothesized that Adélie penguins also adopt different foraging strategies between incubating and brooding periods in relation to specific intrinsic and extrinsic factors.

In this article, we investigated the diving behavior of Adélie penguins using bird-attached time–depth recorders during the incubation period and compared diving parameters of incubating birds with those of chick-rearing ones in literature. We discuss how foraging strategies may be related to life history, energy demand and environment.

Materials and methods

The study was conducted at the Adélie penguin colony of Hukuro Cove in Lützow-Holm Bay (69°00′S, 39°39′E, Fig. 1) between November and December 1999. Diving behavior of incubating parents were recorded by miniature data loggers (NIPR-DT, Little Leonardo, Tokyo). The loggers were cylindrical, 14 (diameter) × 84 mm, weighed 26 g in the air (including battery) and had a flash memory of 394 KB, in which depth data were stored with 8-bit resolution, giving depth range of 0–119 m and absolute and relative accuracies of 1 and 0.5 m, respectively. Depth was recorded at 3-s intervals for up to 25 days.

Five females leaving their nest after egg-laying and five males—belonging to different nests—leaving their nest after the return of the females from their first trip were caught on 16 November 1999 and 2 December 1999, respectively. A data logger was attached to the lower back of the penguins using waterproof TESA tape (Wilson and Wilson 1989). Birds were weighed and then released at the vicinity of the colony. All birds were recaptured on 20 December 1999 or 21 December 1999, and both data loggers and tape were retrieved.

Data were downloaded onto a PC and analyzed using a custom-written macro-program in IGOR Pro (WaveMetrics, Version 5.03 J). Maximum dive depth and dive duration were calculated for each dive that was >1 m. Dive parameters were log-transformed for normality before being investigated using a General Linear Model with bird as random factor.

Sea-ice distribution and concentration off Lützow-Holm Bay were obtained from satellite imagery data collected via DMSP SSM/I (http://www.ngdc.noaa.gov/dmsp/) and NOAA/AVHRR (http://noaasis.noaa.gov/NOAASIS/ml/avhrr.html), and distances from the breeding colony to the fast-ice edge and to the pack-ice edge were calculated on 20 November 1999, and 6 and 20 December 1999.

Results

All birds continued breeding normally after the deployment. Diving data for the complete incubation trips of five males and five females were successfully collected, leading to a total of 71,971 dives being analyzed (see Table 1 for a

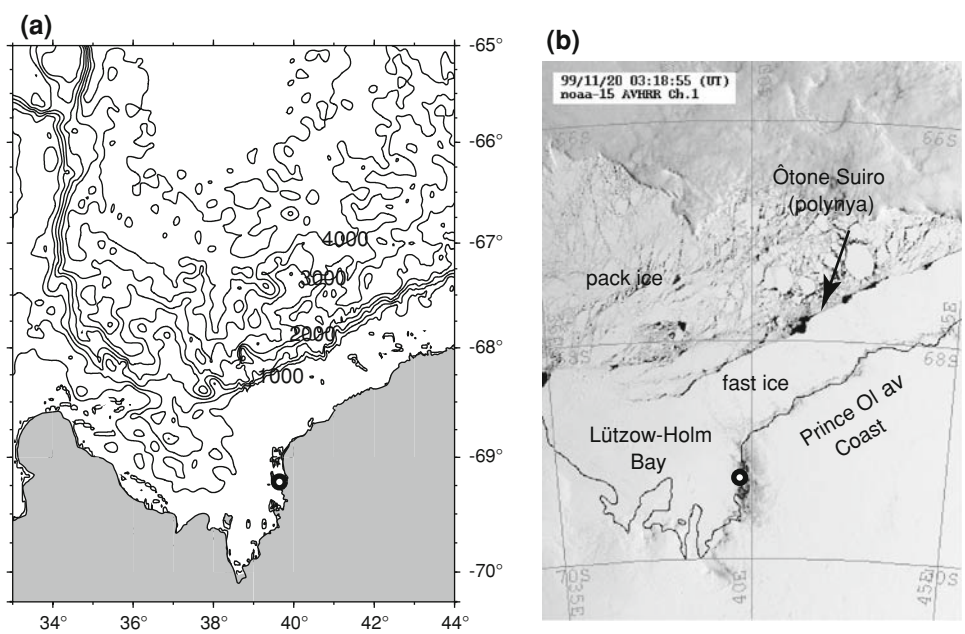

Fig. 1 (**a**) Bathymetry off Lützow-Holm Bay area, Antarctica, and (**b**) sea-ice distribution on 20 November 1999 (NOAA AVHRR sensor). *Circles* show the location of the study colony

Table 1 Diving data of five female and five male Adélie penguins during incubation period and chick-rearing period (Takahashi 2001)

	Incubation				Chick-rearing[a]	
	Female	Male	*F*	*P*	Female	Male
Mean initial body mass (kg)	4.04 ± 0.40	4.19 ± 0.42	0.34	0.58	4.32	4.83
Time from first to last dive (h)	321.8 ± 69.0	373.4 ± 25.0	2.5	0.15	–	–
Number of dives recorded	8,495 ± 1866	5,899 ± 2959	2.8	0.14	–	–
Total daily dive time (h/day)	5.46 ± 0.72	4.40 ± 1.78	1.5	0.25	4.68	4.07
Mean dive depth (m)	8.9 ± 2.0	11.0 ± 2.7	2.8	0.13	16.8	15.9
Mean dive duration (s)	30.9 ± 2.8	45.5 ± 9.3	12.9	<0.01	67.6	66.9

Values are presented as grand mean ± SD of individuals. Differences between females and males were tested by GLM

[a] Values are grand means of five seasons from 1995/1996 to 1999/2000

summary of the diving activity). Females started to dive between 18 November 1999 and 25 November 1999, i.e. 96.4 ± 68.4 h (range 50–216 h) after their release, and stopped diving between 28 November 1999 and 6 December 1999. Males started diving between 3 December 1999 and 5 December 1999, i.e. 46.1 ± 14.7 h (range 34–71 h) after their release, and stopped between 18 December 1999 and 20 December 1999. During the incubation trips, females dove everyday while some males interrupted their diving activity for >24 h toward the end of trips (Fig. 2).

The majority of the dives were shallower than 5 m (Fig. 3), with the distribution being skewed to the right (Fig. 4). Maximum dive depth of females was 96.0 m and two dives of one male were deeper than the depth range of the loggers (>119 m). Though the mean dive depth of males and females was not statistically different, the mean dive duration tended to be slightly shorter for females than for males (Table 1). All other dive parameters did not show any sex-specific differences. Birds dove throughout the day, although less frequently around midnight, and there was no clear diel change in dive depth (Fig. 5). At Syowa Station (69°00′S, 39°35′E), about 25 km north of the colony, midnight sun was observed from 22 November 1999 until the end of the study period.

The sea was covered by fast-ice along the coast and by pack-ice off shore. An open water zone situated between the fast-ice and the pack-ice zones, the "Ôtone Suiro" polynya, was observed along the continental slope area from mid-November to mid-January, i.e. from the incubation to the guard period (Fig. 1). Though the pack-ice area was drastically reduced during the breeding season, the location of the fast-ice edge did not change throughout the incubation period, from mid-November to mid-December. Then, fast-ice started to decrease gradually from the east side, along the Prince Olav Coast, but did not decrease much off the Lützow-Holm Bay until mid-January. The shortest distance from the breeding colony to the ice edge was about 800, 700 and 550 km on 20 November 1999, 6 December 1999 and 20 December 1999, respectively, while that to the edge of the fast sea-ice was about 99 km on 20 November 1999 and about 93 km on 6 December 1999 and 20 December 1999.

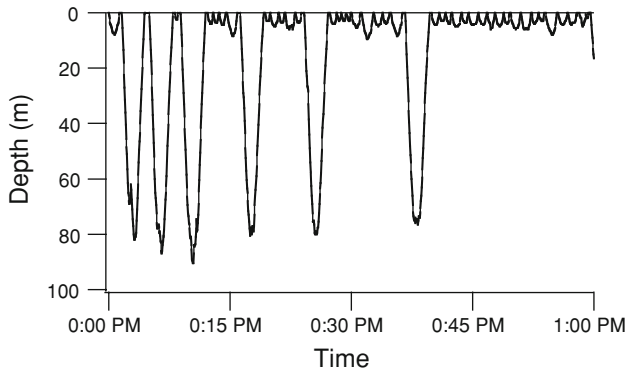

Fig. 3 Typical dive profiles of an Adélie penguin during incubation

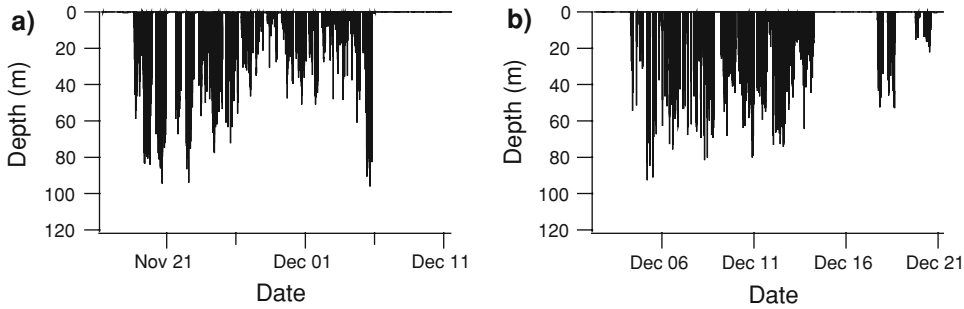

Fig. 2 Diving record of one female (**a**) and one male (**b**) Adélie penguins during incubation

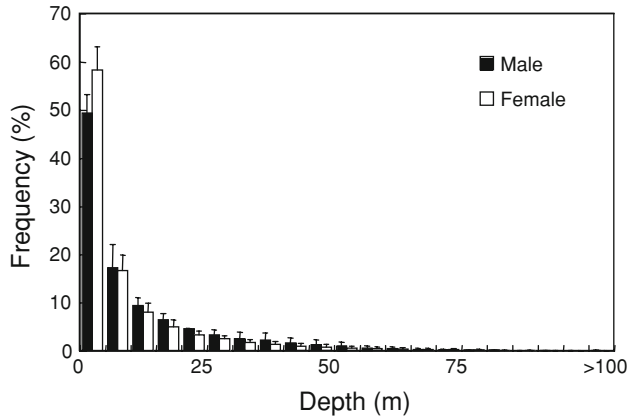

Fig. 4 Dive depth distribution of female and male Adélie penguins during incubation

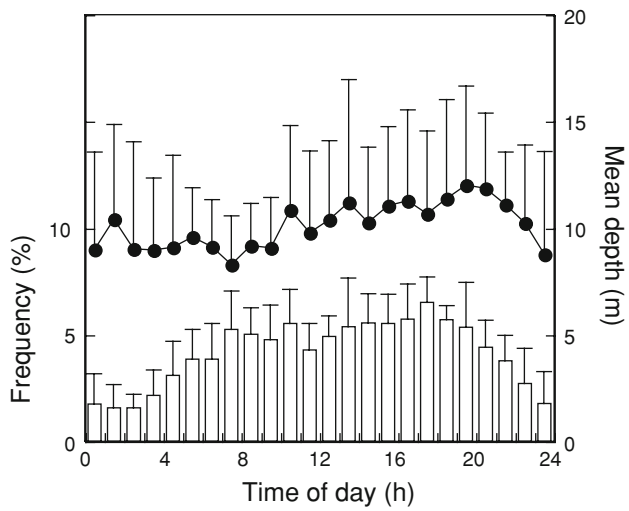

Fig. 5 Daily pattern of dive frequency (*bar*) and dive depth (*dot*) of Adélie penguins during incubation. *Values* are grand mean of all individuals (+SD)

Discussion

Foraging area

The durations of the first (females) and second foraging trips (males) of incubating Adélie penguins from Lützow-Holm Bay were much longer than those during chick-rearing (14–36 h, Kato et al. 2003). In this regard, we can expect that birds went on to forage at greater distances from the colony during incubation. Adélie penguins rearing chicks at Hukuro Cove colony feed in small areas of open water along the shore or around icebergs and islets in fast sea-ice area within 5 km from the colony (Kato et al. 2003; Watanuki et al. 2003). During the incubation period, however, open water is rare and not available near the colony. At this time of the breeding cycle, penguins are often seen walking on the sea-ice, while there are very few observations of diving penguins near the colony (K. Sato, personal observation). "Ôtone Suiro" polynya is recurrently observed along the continental slope area (500–1,500 m depth) off Lützow-Holm Bay throughout the year (Ushio et al. 1993). In our study, the distance to the polynya from the breeding colony was about 90–100 km. As penguins walk on fast sea-ice at about 1.9 km/h (Watanuki et al. 1999), it would take approximately 50 h for penguins to reach the open water from the breeding colony. This accords well with our observation that Adélie penguins from Lützow-Holm Bay started diving 34–216 h after instrumentation with data-loggers.

Adélie penguins breeding along the Mawson Coast traveled to the edge of the continental shelf (80 ± 120 km from the colony) to feed (Clarke et al. 1998), and although they use a polynya to access the water, they show a preference for foraging amongst the pack-ice rather than in the open water of the polynya (Clarke et al. 2006). More than 95% of the diet of the penguins in the study colony during the following chick-rearing period (end of December to mid January) consisted of Antarctic krill *Euphausia superba* (Takahashi 2001), though the diet during incubation period has never been thoroughly investigated. Antarctic krill is abundant near the southerly positioned pack-ice edge and the continental break (Ichii 1990), as the under-ice environment is considered to be an important habitat for this crustacean (krill densities under the ice, 1–13 km south of the ice edge, are fivefold greater than that in open water, Brierley et al. 2002).

Dive profiles during incubation (Fig. 3) were different from those of penguins feeding under fast-ice whose dives often present a slow ascending phase during which birds search for an access to the surface from under the ice (Watanuki et al. 1999). Incubating birds performed many shallow dives (Fig. 4), which are generally regarded as traveling dives (Chappell et al. 1993a). Penguins feeding in fast-ice area, however, walk on ice between foraging areas and shallow traveling dives are rarely observed (Kato et al. 2003). This suggests that incubating penguins use the polynya only as an access to the foraging area, and feed in the pack-ice zone, where prey availability is high.

Comparison between sexes and seasons

Incubating males and females need to replenish their body reserves after long fasting periods on the egg. In this part of the breeding cycle, all the energy ingested at sea is thus allocated to body maintenance. This contrasts with the chick-rearing phase in which parents must allocate energy to both the chicks and themselves. Yet, the foraging effort of incubating birds is similar to that of chick-rearing birds and also did not differ between males and females (Table 1). During chick-guard phase, females foraged

longer at sea and males, being more aggressive, spent longer time at the nest to defend the chick (Clarke et al. 1998; Takahashi 2001). In contrast, predatory pressure and nest defense against intruders is generally less acute during the incubation than during the chick-rearing phase. In fact, there was no loss of eggs of study birds and the colony was quieter during the incubation than during the chick-rearing periods, because of less attack by predators or intruders (A. Kato, personal observation). This should allow birds to concentrate on the replenishment of their body reserves following the extended fasting periods spent mating and on the eggs. While males are generally slightly larger (Williams 1995) and heavier than females during the chick-rearing period (Watanuki et al. 2004), we found no differences in the body mass of incubating males and females in the present study. This could be due to the fact that incubating males fasted longer than females before foraging.

Though Takahashi (2001) did not find sex-specific differences in either diving depth or duration in birds from the same colony during five chick-rearing seasons (1995/1996 to 1999/2000), our incubating males had longer dive duration than females (Table 1). In addition, dive depth and duration were slightly shallower and shorter, respectively, during incubation than during chick-rearing phase (Table 1). This probably resulted from the birds foraging in contrasted environments during these two phases of the breeding cycle. As incubating males foraged later in the season than females, they would thus encounter slightly different sea-ice condition, prey availability and prey distribution than females did. Adélie penguins breeding at Hukuro Cove colony foraged in coastal area with a fast-ice-covered sea during chick-rearing and the proportion of shallow dives increased when birds dove in deeper waters (Kato et al. 2003). This is consistent with our observation that incubating birds dove shallower, as they are supposed to exploit deeper waters in the shelf break area, than chick-rearing ones. Daily dive pattern closely resembled that of chick-rearing birds in this area but differed from those observed in sea-ice-free areas (Watanuki et al. 1997; Takahashi 2001).

During incubation, Adélie penguins (Clarke et al. 2006), wandering albatrosses (Shaffer et al. 2003) and little penguins *Eudyptula minor* (Kato et al. in press) travel farther and stay at sea for longer periods than during chick-rearing. It has been shown that Adélie penguins from the Antarctic Peninsula region, as well as wandering albatrosses, spent less energy during incubation than during brooding (Chappell et al. 1993b; Shaffer et al. 2003). Although we do not have any information for the energy consumption of Adélie penguins in the present study, we could expect that they would also save energy by commuting less often between the breeding and the distant foraging sites. This is especially likely since penguins in this study walked long distance on the fast-ice to reach the foraging area.

Adélie penguins breeding in fast-ice area applied a similar foraging trip strategy to the Adélie penguins breeding in open-sea area and other species during incubation. However, there are variations in behavior, which essentially result from the birds exploiting different environments (different foraging areas with different sea-ice conditions) and having specific life history strategies. The latter would proceed from an evolutionary adaptation of Adélie penguins to past sea-ice condition in Antarctica, since their ecology is known to be highly associated with sea-ice (Ainley 2002). In this context, we can expect the current climate change to profoundly modify the relationship between the birds and its environment. Changes in sea-ice distribution will—or probably already—affect breeding, population and survival of this species, as Adélie penguin populations have been declining over the last few decades in the Antarctic Peninsula region (Fraser and Patterson 1997), where a drastic decrease in sea-ice extent has been reported (Stammerjohn and Smith 1997). In contrast, populations of Adélie penguins are increasing in the Lützow-Holm Bay region, where frequent sea-ice break-ups have occurred recently (Kato and Ropert-Coudert 2006). Although the situation seems not as alarming in Lützow-Holm Bay as in other regions, careful long-term monitoring is more than ever needed.

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