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RESEARCH ARTICLE

Temporal changes in activity budgets of chick-rearing Adélie penguins

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Abstract Changes in sea-ice conditions can affect locomotion on land, diving behavior, and corresponding foraging success of penguins. In this study, locomotion on land and diving behavior were compared between early and late stages of the guard phase with different sea-ice conditions using miniaturized time-depth-acceleration data loggers for Adélie penguins *Pygoscelis adeliae* from 18 December 2001 to 11 January 2002 in Dumont d'Urville, Adélie Land (66.7°S, 140.0°E), Antarctica. Differences were found between early and late stages in the ratio of walking vs. tobogganing, proportion of time spent diving, diving depth as well as in the rate of parental tissue accumulation. In contrast, trip duration, distance traveled on land, and meal delivery rate to chicks did not differ between the stages. This study suggests that physical changes in sea-ice during the penguins' chick-rearing period may affect certain on-land and/or at-sea behaviors which, in turn, may affect how resources are allocated to self-maintenance or chick-provisioning.

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Introduction

In Antarctica, sea-ice condition and its associated variability, particularly due to global warming, may affect the behavior and foraging success of seabirds (reviewed by Croxall et al. 2002). This is especially true in the case of Adélie penguins, *Pygoscelis adeliae*, whose breeding success (Ainley et al. 1998; Irvine et al. 2000; Jenouvrier et al. 2006) and population dynamics (Wilson et al. 2001; Kato et al. 2002) depend greatly on sea-ice conditions (Ainley 2002). In addition, several studies showed that contrasting sea-ice conditions might also affect the diving behavior of penguins (e.g. Watanuki et al. 1997; Rodary et al. 2000). However, we still know relatively little about the influence of sea-ice conditions on penguin locomotory behavior on ice during foraging trips, i.e. how they switch from walking to tobogganing and vice versa. Tobogganing penguins lie on their belly and push themselves forwards with alternating foot movements (Williams 1995). This allows the birds to move more rapidly at a lower cost under most conditions (Wilson et al. 1991), but they may have difficulties tobogganing over irregular surfaces, such as broken ice. The choice between locomotory modes with different energy expenditures will affect not only time budget but also foraging success such as net energy intake rate (e.g. Bautista et al. 2001).

In this study, we used penguin-borne instruments (cf. Ropert-Coudert and Wilson 2005) to measure simultaneously the diving behavior and locomotion on land of Adélie penguins breeding in Dumont d'Urville, Adélie Land. This is a suitable location for testing the effect of different sea-ice conditions on the behavior of penguins given that sea ice is known to change drastically within just a few weeks during the chick guard stage (45–60 days in December and January, R.C. personal observation) in this location (Rodary et al. 2000). First, we evaluated how penguins adjusted their locomotion on land to contrasting sea-ice conditions. We expected penguins in our study to increasingly use walking rather than tobogganing as the ice gradually breaks up from early to late guard stage. To test this, we used acceleration data loggers to distinguish walking from tobogganing and determine which mode is preferentially used (see Yoda et al. 2001). Second, we monitored the diving activity of Adélie penguins, the parental mass accumulation and the mass delivered to the chicks under contrasting sea-ice conditions in the early and late guard phases to determine how foraging behavior was affected and how birds allocated food for self-maintenance.

Materials and methods

Study site and study birds

The study was conducted from 18 December 2001 to 11 January 2002 on breeding Adélie penguins in Dumont d'Urville, Adélie Land (66.7°S, 140.0°E), Antarctica. A total of 21 birds, brooding one or two small chicks during the guard phase, were equipped with two different types of data-loggers: three-channel W200-PDT loggers (102 mm × 22 mm, 50 g, Little Leonardo, Japan) which measured speed, depth, and temperature at 1 Hz; and four-channel M190-D2GT data loggers (53 mm × 15 mm, 17 g, Little Leonardo, Tokyo, Japan), which recorded depth, temperature (1 Hz), and acceleration (16 Hz) along the longitudinal (surging) and right-left (swaying) axes of the birds (see Yoda et al. 2001). Nine birds were equipped with D2GT loggers and 12 birds were equipped with PDT loggers (Table 1).

Ten birds were equipped early in the guard stage (between 18 and 24 December 2001) when the sea ice was stable and stretched to the horizon. At that stage, the sea ice was smooth, and the surface homogeneous (Fig. 1). Eleven birds were caught later in the guard stage (between 1 and 11 January 2002) when the sea ice had developed pressure ridges. At this time, penguins were occasionally seen jumping from floe to floe.

Following capture, birds and chicks were weighed to the nearest gram. Loggers were attached along the median line of their backs (Bannasch et al. 1994) using tesa tape (Tesa-Band®, Beiersdorf, Germany) as in Wilson et al. (1997). After one foraging trip, devices were removed and birds reweighed. The stomach contents of birds were collected using the water offloading technique (Wilson 1984) before the penguins fed their

Table 1 Penguin ID#, deployment date, sea-ice condition, trip duration, type of data logger, availability of dive data, and tobogganing vs. walking data for 21 chick-rearing Adelie penguins, *P. adeliae*, on the Adelie land in the early (18–24 December 2001) and late (1–11 January 2002) guard phases of chick-rearing

Penguin ID#	Deployment date	Sea-ice condition	Trip duration (h)	Type of data logger	Dive data available?	Walking and tobogganing data available?
1	18 December	Smooth	18.1	UME-D2GT	Yes	Yes
2	19 December	Smooth	43.5	UWE-PDT	Yes	No
3	19 December	Smooth	32.3	UWE-PDT	Yes	No
4	19 December	Smooth	47.5	UME-D2GT	Yes	Yes
5	22 December	Smooth	32.9	UME-D2GT	Yes	Yes
6	22 December	Smooth	32.9	UWE-PDT	Yes	No
7	22 December	Smooth	36.7	UWE-PDT	Yes	No
8	22 December	Smooth	20.8	UME-D2GT	Yes	Yes
9	22 December	Smooth	49.3	UME-D2GT	Yes	Yes
10	22 December	Smooth	42.8	UWE-PDT	Yes	No
11	1 January	Uneven	22.9	UME-D2GT	Yes	Yes
12	1 January	Uneven	34.4	UWE-PDT	Yes	No
13	1 January	Uneven	71.1	UME-D2GT	Yes[a]	Yes[a]
14	2 January	Uneven	28.3	UWE-PDT	Yes	No
15	2 January	Uneven	34.8	UWE-PDT	Yes	No
16	7 January	Uneven	105.5	UME-D2GT	Yes[a]	Yes[a]
17	7 January	Uneven	109.2	UWE-PDT	Yes	No
18	7 January	Uneven	76.8	UWE-PDT	Yes	No
19	7 January	Uneven	92.3	UME-D2GT	Yes[a]	Yes[a]
20	7 January	Uneven	78.0	UWE-PDT	Yes[a]	No
21	7 January	Uneven	66.5	UWE-PDT	Yes	No

[a] Full trip was not recorded due to a long foraging trip. We estimated the total amount of diving and locomotion on land by calculating twice of the data from the start of the trip to the middle of the trip

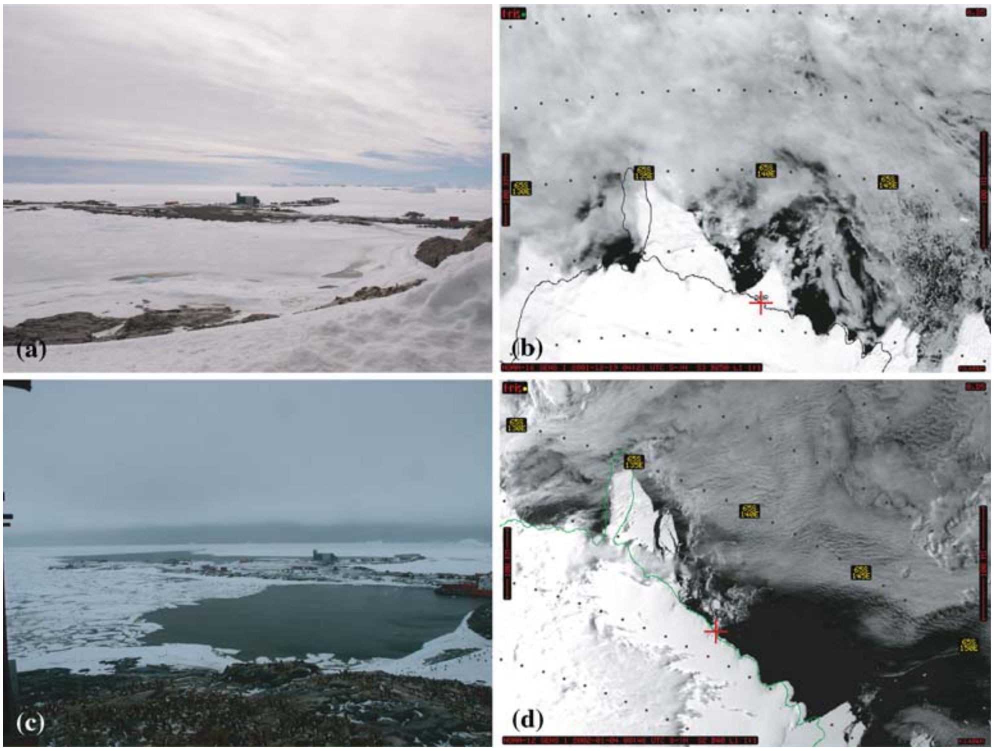

Fig. 1 Changes in sea-ice condition at Adélie Land, Antarctica on: **a** 18 December 2001, **b** 19 December 2001, **c** 14 January 2002, and **d** 4 January 2002. Experimental site was shown on the maps as a cross mark on (**b**) and (**d**)

chicks. This procedure was repeated at least three times until the water regurgitated by the bird came out clear. The stomach contents were drained before being weighed to the nearest gram. Birds were then fed with shrimps to account for their lost meal, before being released in the vicinity of their nest. The difference between the parental mass at departure and that at arrival (excluding the stomach contents) was taken to be the parental tissue accumulation (Watanuki et al. 2002).

Data were downloaded from the loggers into a computer and analyzed using Igor software (Wavemetrics, USA, Version 5.0). Only dives ≥1.0 m were included in the analysis.

The acceleration sensors measure the acceleration related to changes in the movements of birds as well as gravitational acceleration (9.8 m s^{-2}; Fig. 2). Thus, the amplitude of surging acceleration when the penguin was not moving represents the component of gravitational acceleration that changes in response to the posture of the bird (Fig. 2). To remove the high-frequency component (resulting from movements) from the acceleration signal, we filtered the surging acceleration using a two-band low-pass filter where the end of the

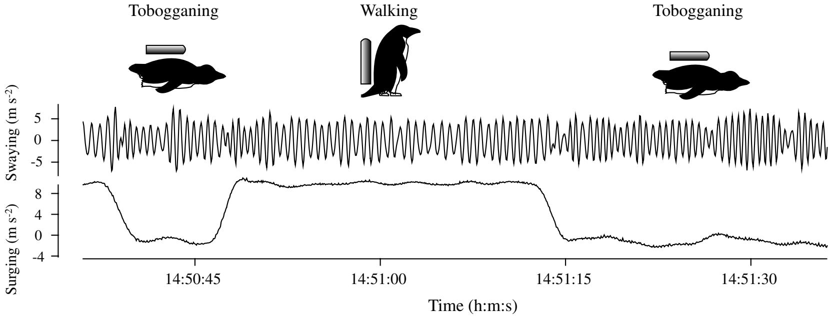

Fig. 2 Acceleration signals recorded along (*top*) the swaying axis and (*bottom*) the surging axis for tobogganing and walking Adélie penguin in Adélie land. Swaying is the acceleration recorded transversely crossing the penguin's body from right to left, while surging is along the longitudinal body axis. Surging acceleration was filtered to differentiate the two types of penguins' postures (lying and standing). Swaying acceleration was also filtered to extract clear peaks, each of which corresponded to one stride (foot movement) of walking and tobogganing

first band and the start of the second band were 0.1 and 0.5 Hz, respectively (Watanuki et al. 2005). We filtered the swaying acceleration using a three-band filter where the end of first band, the start of second band, the end of second band, and the start of third band were 0.6, 1.5, 2.5, and 3, respectively, which passes frequencies throughout the second band (IFDL Igor Pro, WaveMetrics, USA). As both the frequency of walking and tobogganing is 1.7 Hz (Yoda et al. 2001), we could easily extract the movement components of walking and tobogganing from the rest of the signal (Fig. 2) and distinguish between these two behaviors using the periodic swaying and posture properties of the surging acceleration signal (Fig. 2; Yoda et al. 2001).

Where diving and acceleration data for an entire trip could not be recorded due to memory limitations (four birds; Table 1), we assumed symmetry in foraging activity to reconstruct the data over a complete trip. Such an assumption is plausible since the foraging activity of Adélie penguins in Dumont d'Urville follows the pattern of a central-place foraging seabird (cf. Ropert-Coudert et al. 2004). We calculated the midpoint of the trip from the known return date of the penguin to its nest and multiplied dive duration, duration of tobogganing, and walking from the start of trip to the midpoint by two to give an entire trip's worth of data. To validate this technique, we also applied it to complete trips and compared the diving duration between the start to middle of the trip, and from the middle to end of a trip.

We calculated the distance traveled on land using the time spent commuting on land, as derived from the accelerometers signals, and multiplying it by the estimated speed of walking and tobogganing, i.e. 0.53 and 0.75 m s^{-1}, respectively (Wilson et al. 1991).

All dependent variables were log-transformed to normalize distributions. We used *t*-test to examine the effect of the stages of the guard phase on variables. As foraging trip duration might increase with brood mass (Williams and Rothery 1990), we tested the effect of sea ice on trip duration with brood mass as covariant.

Diving depth and duration were highly correlated (Spearman rank correlation: $r_s = 0.94$, $N = 26055$, $P < 0.001$). Therefore, we examined the effect of the stages of the guard phase on diving depth only, using a linear mixed model, including bird identity as a random factor. The significance of sea ice on diving depth was determined by a log-likelihood ratio test.

All statistical analyses were performed using the statistical package Statview Version 5.0 (SAS Institute Inc.) and R Version 2.4 (R Development Core Team 2005).

Results

We recovered all loggers and measured the brood mass, trip duration, meal mass delivered to the chick, and body mass accumulation in all 21 birds. The mean brood mass before a trip was 569 ± 451 g (mean ± SD) (range 74–1644 g, $N = 21$), while foraging trip duration for the penguins was on average 51.26 ± 27.64 h (range 18.1–109.2 h, $N = 21$). The meal mass delivered was 399 ± 231 g (range 10–968 g, $N = 21$). All birds fed exclusively on krill. The mean body tissue accumulation was −0.04 ± 0.22 kg (range −0.48 to 0.4 kg, $N = 21$).

We did not record a complete trip in four birds (bird nos. 13, 16, 19, and 20; Table 1). Based on dive records from penguins with complete trips, there was a strong relationship in total dive duration from the start of the trip to the midpoint (a) and from middle to the end of the trip (b) ($b = 1.05 \pm 0.06a$, $t = 17.3$, $P < 0.001$, $R^2 = 0.95$, $N = 17$). The 95% confidence interval of this slope was 0.92–1.18, which means that there was no significant difference from one in the slope. Therefore, we multiplied the behavioral parameters by two from the start to the midpoint of the trip to generate complete trip data for the four birds with incomplete trips.

Trip duration was not affected by the stages of the guard phase (ANCOVA: $F = 0.013$, $P = 0.91$, df = 1.17) nor brood mass ($F = 0.89$, $P = 0.36$, df = 1.17). The ratio of tobogganing was higher in the early stage when the ice was smooth than in the later stage of the guard phase when the ice was more fractured (*t*-test: $t = 2.86$, $P < 0.05$; Fig. 3a). The distance traveled from the colony did not differ between the stages of the guard phase (*t*-test: $t = 1.42$, $P = 0.20$; Fig. 3b).

The proportion of time spent diving during a trip was higher in the later stage than in the earlier stage of

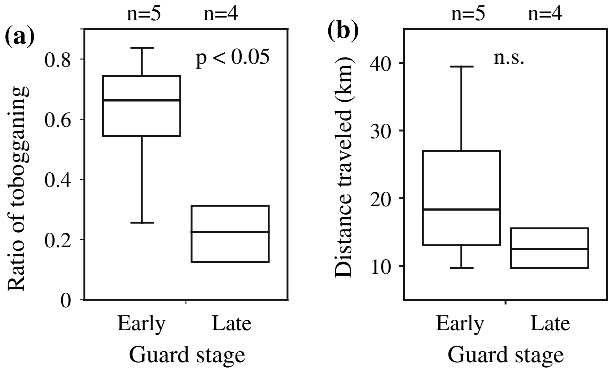

Fig. 3 **a** Ratio of tobogganing to locomotion on land, and **b** distance traveled of foraging trips made by nine chick-rearing Adélie penguins in the early and late stage of guard phase at Adélie Land in 2001/2002. The *centerline* through *each box* represents the median. See text for statistical tests

the guard phase (t-test: $t = -4.85$, $P < 0.001$; Fig. 4a). Meal delivery rate did not differ between the stages of the guard phase (t-test: $t = -0.74$, $p = 0.47$; Fig. 4b). Parental mass accumulation rate was lower in the early stage than in the later stage of the guard phase (t-test: $t = -2.96$, $P < 0.01$; Fig. 4c). Penguins dove shallower in the earlier guard stage and deeper in the later guard stage (log-likelihood = 36,377, df = 1, $P < 0.0001$).

Discussion

To our knowledge, this is the first study to record simultaneously three components of behavior during the chick-rearing phases of Adélie penguins, namely locomotion on land, diving, and resource allocation. From the early to the late chick-rearing phase, penguins shifted their on-land traveling behavior (using less and less tobogganing as a means of locomotion), had longer dives, and accumulated more energy. These results are based on a small sample size and should be viewed cautiously. In addition, sea ice is not the only factor that might explain the observed patterns. Seasonal effects could have also played a role in explaining the differences between the early and late chick-rearing phases, as sea-ice condition and season evolve concurrently. However, Rodary et al. (2000) showed that the diving behavior of Adélie penguins from Dumont d'Urville did not differ between the first and third weeks after hatching. This is contradictory to our results and, thus, suggests that despite sea ice and seasonal effect being intertwined, there is a change in the behavior of birds following a change in sea-ice conditions.

In this study, birds traveled the same distance despite different sea-ice conditions. This is a surprising result, especially since visual inspection of the images suggests that the bird's access to the ocean should have improved (Fig. 1b, d) and small holes appeared available for foraging in the later guard stages (Fig. 1a, c). However, prey availability in isolated holes in the ice may be limited and easily depleted, especially since many penguins may utilize them (Watanuki et al. 1997). Therefore, birds may meander from hole to hole to forage and travel to the ocean on a winding course. This, and the small sample size, might explain why the distance traveled on land by penguins did not change throughout the study period.

We found that Adélie penguins tobogganed more frequently in the early season than in the late season of their guard stage. This indicates that penguins can switch between different traveling modes depending on the condition of the ice as we predicted. We can predict this would lead to an increase in the cost of traveling due to changes in the surface sea ice, in turn, leading to an increase in foraging effort following optimal foraging theory (OFT; Charnov 1976). Actually, the stage of the guard phase affected the proportion of time devoted to diving, such that Adélie penguins spent a greater proportion of time diving in the later stage than in the early stage. Unfortunately, we do not have any available data on energy expenditure in tobogganing, although it is available for walking (Pinshow et al. 1977); so, this hypothesis could not be tested. Alternatively, food availability might decrease from the early to the late guard stage independent of sea-ice conditions through stock depletion by predators (Ainley et al. 2006) and this would fit with the fact that birds displayed deeper diving depth in the later stage in the present study. As noted previously, a study conducted at the same site but in a different year showed that diving depth did not differ between the stages of the chick-rearing season (Rodary et al. 2000), suggesting that the pattern of diving could vary from year to year. In this regard, a long-term monitoring study of the birds' activity at sea is needed to address the link between inter-annual variability in diving depth and food availability.

In our study, the rate of meal delivery to the chicks was not affected by the stage of guard phase, although parental tissue accumulation rate increased as the season progressed. Thus, penguins apparently devoted a

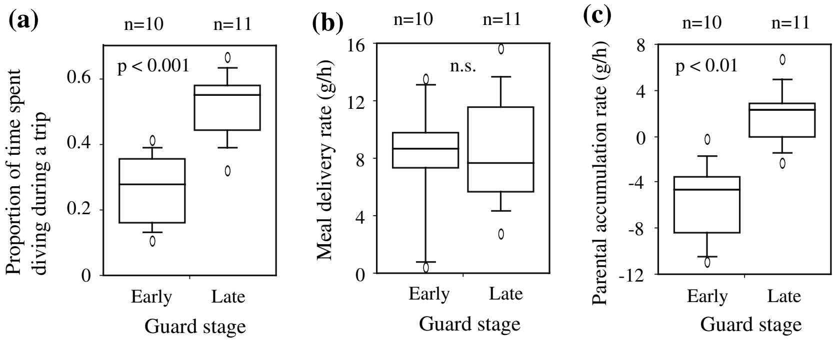

Fig. 4 **a** Proportion of time spent diving during a trip, **b** meal delivery rate, and **c** rate of parental tissue accumulation in the early and late stage of guard phase for 21 Adélie penguins on Adélie Land in 2001/2002. The *centerline* through *each box* represents the median. *Open circles* indicate possible outliers. See text for statistical tests

higher proportion of their foraging effort to food accumulation for self-maintenance than to chick-provisioning later in the season. One potential explanation for this is that penguins encountered lower prey availability later in the season. In general, long-lived seabirds are more likely to favor maintaining their body condition in relation to environmental change even if breeding success is negatively affected (Monaghan et al. 1989; Watanuki et al. 1993; Ainley et al. 1998). Alternatively, Adélie penguins overcompensated for the higher cost of locomotion on land caused by uneven sea-ice conditions in order to maintain a positive energy balance. This positive budget would provide insurance against the highly stochastic environmental variation (Dall and Johnstone 2002), such as sea-ice conditions.

Adélie penguins are known to be closely associated with sea ice. In the present study, Adélie penguins changed their behavior within a relatively short time as sea-ice conditions also changed. These penguins are apparently well adapted to living in pack-ice margins (Ainley 2002). In fact, late pack-ice break-off has been shown to result in lower reproductive success in chinstrap penguins *Pygoscelis antarctica*, while Adélie penguins were rather insensitive to this disturbance (Rombolá et al. 2003). Although it is a challenge to link the physical environment with predator behavior, the information provided from data-loggers will increase our understanding of seasonal changes in sea ice on animal behavior.

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