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Do Adélie penguins modify their foraging behaviour in pursuit of different prey?

Abstract We examined the question, does foraging behaviour of Adélie penguins, *Pygoscelis adeliae*, change in accord with the prey captured? To provide an answer, we attached instruments that record foraging behaviour to free-ranging Adélie penguins foraging, off Adélie Land, during the late breeding season 1997. Depth of foraging was recorded for nine birds whose diet ranged from krill only to predominantly fish. Previous studies suggested that penguins capturing fish dived to shallower depths, but this could not be verified in our study. Moreover, most other foraging parameters did not indicate any significantly different patterns relative to prey caught. Only swim speed in the commuting phase, but not in the undulatory, bottom phase of deep dives differed with respect to prey consumed. We conclude that Adélie penguins foraging in open waters may change their foraging behaviour only slightly depending on the prey. Under other conditions, these changes may become more significant.

Introduction

Most seabirds are generalists (Ashmole 1971; Ainley et al. 1992), on the basis of diet composition. This raises the question of whether they change their foraging behaviour in order to switch from one prey type to another. For instance, Antarctic krill, *Euphausia superba*, is one of the key species during summer for several Antarctic birds (e.g. Croxall et al. 1997), but krill abundance can vary locally (Nicol et al. 2000) leading to prey switching (Croxall et al. 1988; Boyd et al. 1994; Lunn et al. 1994).

A seasonal and interannual shift in the diet of Adélie penguins, *Pygoscelis adeliae*, has been observed in several instances, for example, off Syowa (Endo et al. 2000), Ross Island (Emison 1968; Ainley et al. 1998) and Adélie Land (Ridoux and Offredo 1989; Wienecke et al. 2000). At most of these sites, a diet dominated by krill (*E. superba* and *E. crystallorophias*) changed to one dominated by fish. Since *E. crystallorophias* is often associated with sea-ice (Stemacek et al. 1990; Eicken 1992), Ainley et al. (1998) suggested that diet changes may be related to changes in pack-ice cover. Accordingly, after separating penguins into krill and fish eaters, based on the percentage of composition of the diet, Endo et al. (2000) suggested that fish-eating individuals dive shallower than those eating krill.

Adélie Land is one area where a seasonal change in diet has been observed in Adélie penguins (Ridoux and Offredo 1989; Wienecke et al. 2000). This offered to us an opportunity to compare the foraging behaviour (depth and/or swim speed) of Adélie penguins having different diets during January 1997. The objective of our study was: (1) to determine if birds adopt a specific diving pattern and/or a specific swim speed in relation to the main type of prey captured and (2) to compare our results in Adélie Land with other localities.

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Materials and methods

The study was conducted on free-ranging Adélie penguins from a colony at Petrel Island (66.7°S; 140.0°E) in Adélie Land, Antarctica, during January 1997.

Birds were equipped with two different types of data loggers. We equipped nine birds with TDR loggers (MK5, Wildlife Computers, Washington, USA), which recorded depth data every 5 s. These devices measured 6.4×3.8×1.3 cm and weighed 50 g. The range of depth measured was set between 0 and 500 m, and the

resolution was 2.0 m (with an absolute accuracy of ±2 m). We equipped four other birds with loggers that record swim speed. These were 12-bit resolution, 16-Mbyte memory, three-channel UWE-PDT loggers (102×∅20 mm, 50 g); absolute accuracy for depth and speed was 0.5 m and 0.05 m s^{-1}, respectively (Little Leonardo, Tokyo, Japan). They recorded swim speed and depth every second. Birds fitted with UWE-PDT and TDR loggers were subsequently referred to as "PDT" and "TDR" birds, respectively. Loggers of both types were attached externally to the back of birds in a mid-line position, near to the tail in order to reduce drag (Bannasch et al. 1994). The TDR loggers were attached by Tesa tape (Wilson et al. 1997) and left on the birds for two consecutive foraging trips, although only depth data from the second foraging trip were analysed. The PDT loggers were attached with a combination of mastic and cable ties to a platform of glue spread on the feathers and were left on the bird for a single foraging trip. Upon return of birds to the colony, the loggers were removed and the data transferred to a computer.

All birds were flushed three times by stomach pumping as described by Wilson (1984). The samples obtained from TDR birds were preserved in alcohol and analysed in the laboratory. The samples of PDT birds were sorted according to the method described in Watanuki et al. (1994). If not too digested, prey items were separated into krill, fish and other elements. For TDR birds, frequency of occurrence, as well as the contribution by mass of each prey type was evaluated using the method of reconstructed mass for fish based on otolith size (North et al. 1984; Hecht 1987). For PDT birds, the items were sorted using the percentage of contribution by wet mass only.

Based on depth profile (Wilson 1995; Kirkwood and Robertson 1997), dives were separated into W- (feeding dives) and V- or U-shaped dives (probably prospecting dives). W-shaped dives were defined when two or more undulations (Wilson et al. 1996) with a magnitude >2 m were observed in the depth profile. In the subsequent analysis, the times spent descending or ascending the water column are defined as commuting, while the time spent performing an undulatory motion at the bottom phase of the dive was defined as hunting activity. In accordance with TDR resolution, dives with maximum depth ≤4 m were excluded from analysis. Therefore, information on porpoising and sub-surface travelling activities were lost (Wilson 1995; Yoda et al. 1999). Dives were grouped into dive bouts, the end of a bout being defined by a bout end criterion (see Gentry and Kooyman 1986, for calculation of the bout end criterion). Night extended from 2200 to 0200 hours local time, measured from the ephemeris of the Bureau des Longitudes de Paris, France (http://www.bdl.fr).

Speed, from PDT loggers, was calculated from the number of revolutions of a propeller per second, which was converted into flow speed (m s^{-1}) using a regression line obtained by calibration experiments. To confirm these results, the methods of Fletcher et al. (1993) and Blackwell et al. (1999) were used. Only dives >10 m were considered since the speed of dives <10 m might include speeds that correspond to porpoising and sub-surface travelling (Wilson 1995).

Finally, ten control birds, breeding at the same time as birds equipped with loggers were marked with picric acid on their breasts. These were used to test the effect of the externally attached logger on bird foraging trip duration.

To highlight differences statistically in foraging behaviour in accord with mass of krill eaten, Spearman rank correlation tests (non-parametric) were used (Zar 1984). The parameters investigated were: foraging trip duration (calculated between the first and the last dives >4 m recorded by the logger), number of bouts, the hourly dive rate (mean number of dives per hour), percentage of W-shaped dives, medians of the maximum dive depth and percentage of time spent commuting and hunting per foraging trip. Close attention was given also to dive depth (Endo et al. 2000). Proportions were tested using a Chi-squared test. Data were analysed with Statview (version 4.57, Abacus Concepts). For all statistical tests, the significance threshold was taken to be 5%.

Results

There were no statistically significant differences (Mann–Whitney, $Z=-1.46$, $P=0.14$) in the time spent away from the colony between birds equipped with loggers (42.0 ± 18.1 h, $N=13$) and control birds (31.9 ± 15.5 h, $N=15$).

Stomach contents were obtained from nine birds equipped with TDR loggers (numbered from 21 to 29) and four birds equipped with PDT loggers (numbered T3, T1, T42 and T24; Table 1). Krill was the predominant prey item in terms of frequency of occurrence, except for bird 22; *Euphausia superba* and *E. crystallorophias* were mixed in equal proportions. Proportions were not significantly different ($\chi^2_1=0.31$, $P=0.59$, $N=6$ birds). Fish identified as *Pleuragramma antarcticum* was the dominant prey in the diet of three TDR birds (birds 24, 26 and 23). In bird 22, all the fish were juveniles (~30 mm standard length, $N=231$), of a similar size to krill. Amphipods and small stones constituted a negligible portion of the diet of all birds (<1%). Birds equipped with PDT loggers were separated into birds that ate mainly krill (T3, T1) and birds with mixed diets (T42 and T24; Table 1).
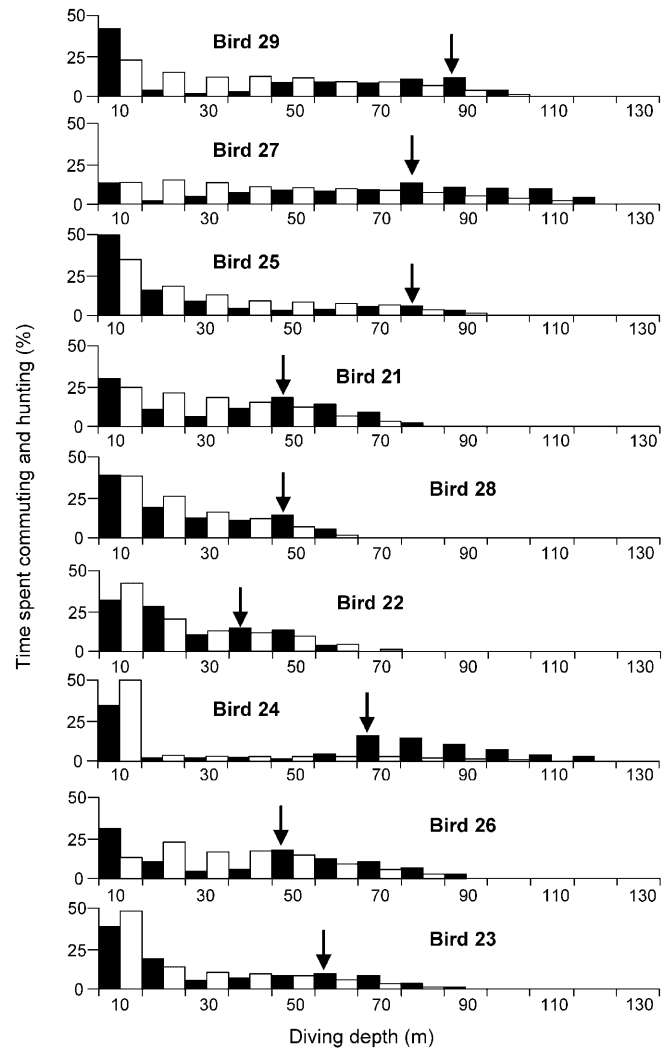
Table 1 *Pygoscelis adeliae.* Percent composition of diet by occurrence frequency and mass for free-ranging Adélie penguins. Birds are listed by decreasing percentage of krill to the diet; *Euphausia superba* was not separated from *E. crystallorophias*. The only fish species identified was *Pleuragramma antarcticum*; all were juvenile fish in bird 22

Bird no. (logger)	Foraging trip date	Occurrence (%)		Mass (%)		Stomach content mass (g)
		Krill	Fish (N)	Krill	Fish	
29 (TDR)	19 Jan	100	0 (0)	100	0	164
27 (TDR)	18–19 Jan	99.3	0.7 (2)	98	2	97
25 (TDR)	19–20 Jan	96.4	3.6 (10)	93	7	140
21 (TDR)	18–19 Jan	99.7	0.3 (2)	90	10	299
28 (TDR)	18–19 Jan	98.8	1.1 (2)	86	14	72
22 (TDR)	20–22 Jan	46.9	53.1 (231)	55	45	133
24 (TDR)	18–19 Jan	85.2	14.8 (38)	42	58	187
26 (TDR)	18–19 Jan	97.4	2.6 (3)	40	60	103
23 (TDR)	18–19 Jan	95.1	4.9 (3)	17	83	121
T3 (NIPR)	2–3 Jan	–		100	0	156
T1 (NIPR)	2–3 Jan	–		98	0	144
T42 (NIPR)	22–23 Jan	–		44	51	180
T24 (NIPR)	12–13 Jan	–		22	70	48

All the parameters of the foraging trip (Table 2) were independent of diet type (Spearman test): foraging trip duration (rho = –0.32, $Z = –0.90$, $P = 0.37$), number of bouts per trip (rho = –0.44, $Z = –1.24$, $P = 0.22$), hourly dive rate (rho = –0.12, $Z = –0.33$, $P = 0.74$), percentage of W-shaped dives (rho = –0.45, $Z = –1.27$, $P = 0.20$) and median of the maximum depth of foraging dives (rho = 0.24, $Z = 0.67$, $P = 0.51$). In addition, there was no significant relationship between diet and the percentage of commuting (rho = 0.08, $Z = 0.24$, $P = 0.81$) and hunting time per foraging trip (rho = –0.40, $Z = –1.1$, $P = 0.26$), although the frequency distribution of commuting and hunting times at different depths varied greatly from one bird to the next (Fig. 1). Commuting time followed a logarithmic-like decrease, whereas the time allocated to hunting followed a bimodal distribution. The first mode of the distribution of the hunting times (∼10 m) probably corresponds to both hunting and sub-surface travelling behaviour (Wilson 1995; Yoda et al. 1999), but the second mode likely was hunting. There were no statistically significant differences in the depth at which the second mode occurred (rho = 0.60, $Z = 1.69$, $P = 0.09$) between krill-eating birds (Fig. 1, birds 29, 27, 25) and birds having a mixed diet (birds 24, 28, 26, 23).

The analysis of speed was performed only on W-shaped dives, as these are feeding dives (Ropert-Coudert et al. 2001). In both groups, the frequency distribution of swim speed during descent (skewness = –0.07 and –0.27 for birds with a krill versus mixed diets, respectively) and during ascent (skewness = –0.22 and –0.22, respectively) was symmetrical (Fig. 2). During the undulatory phase, the speed distribution was symmetrical for krill feeders (skewness = –0.27), but was skewed to the left for those eating mixed diets (skewness = –0.73). Medians of the undulatory speed were not different between the two groups (Mann–Whitney, $Z = –0.99$, $P = 0.32$) and for both were slower than during commuting (Fig. 2). However, there were statistical differences in the commuting speeds between the two groups (descent: Mann–Whitney, $Z = –33.86$, $P < 0.0001$; ascent: Mann–Whitney, $Z = –47.19$, $P < 0.0001$). There were also differences between the descent and ascent within the two groups: krill-eating

Fig. 1 *Pygoscelis adeliae*. Percent time spent commuting (*open bars*) and hunting (*filled bars*) at different depths among free-ranging Adélie penguins. *Arrows* indicate the second mode of the bimodal distribution of the hunting times

Table 2 *Pygoscelis adeliae*. Comparison of foraging trip characteristics for free-ranging Adélie penguins

Bird no.	29	27	25	21	28	22	24	26	23
Foraging trip duration (h)	24.3	36.7	50.5	50.2	53.7	48.0	40.7	51.0	40.2
Number of bouts	20	14	10	37	39	65	14	41	21
Hourly dive rate	23.3 ± 10.1	16.7 ± 6.2	33.7 ± 14.3	19.9 ± 10.7	24.5 ± 13.1	20.0 ± 12.6	19.3 ± 7.2	21.1 ± 11.8	27.3 ± 8.0
W-shaped dives (%)	69.3	78.2	73.3	77.1	73.8	61.9	82.6	75.2	83.0
Commuting time/trip (%)	32.8	40.1	33.4	29.0	27.0	18.2	38.9	31.1	36.3
Hunting time/trip (%)	16.7	17.4	27.6	15.7	19.9	13.1	22.3	18.7	28.5
Median maximum depth (m)	52	74	14	34	18	20	66	44	18
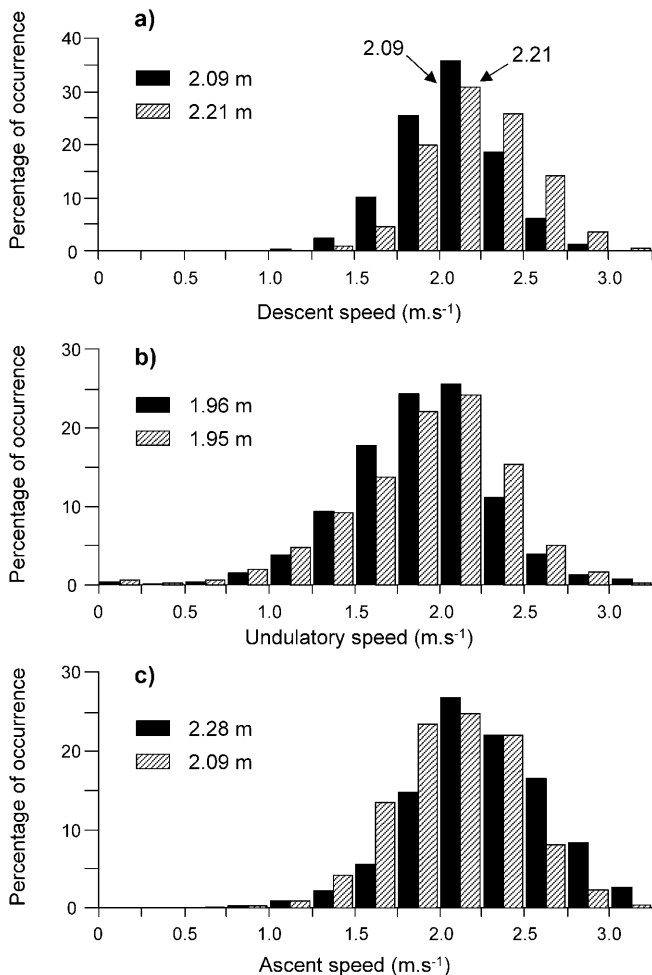
Fig. 2a–c *Pygoscelis adeliae*. Frequency distribution of: **a** descent, **b** undulatory and **c** ascent speeds of Adélie penguins, for individuals having a krill-based diet (*filled bars*) or a mixed (krill and fish) diet (*hatched bars*). For each distribution, the median values are indicated

penguins had faster ascents (2.29 ± 0.41 m s^{-1}, $N = 10{,}347$) than descents (2.10 ± 0.30 m s^{-1}, $N = 10{,}695$; Mann–Whitney, $Z = -39.59$, $P < 0.0001$). For mixed-diet birds, descent speeds (2.22 ± 0.30 m s^{-1}, $N = 24{,}887$) were significantly faster (Mann–Whitney, $Z = -45.16$, $P < 0.0001$) than ascent speeds (2.10 ± 0.35 m s^{-1}, $N = 27{,}397$).

Discussion

Experiments in water tanks showed that Adélie penguin energy expenditure might increase as a result of the increased drag caused by externally attached loggers (Wilson et al. 1986; Kooyman 1989; Wilson and Culik 1992; Bannasch 1995). In addition, it has been shown that externally attached TDR loggers (MK5) modify the diving behaviour of free-ranging King penguins, *Aptenodytes patagonicus* (Ropert-Coudert et al. 2000b), which are birds that have a larger frontal area than

Adélie penguins. Although the TDR loggers used in the present study were streamlined and attached caudally, we cannot exclude the possibility that the diving behaviour of birds might have been altered by the presence of loggers. However, since the diving parameters were only compared between birds equipped with TDR loggers similar in shape, mass and position of attachment, diving parameters should have been comparable between birds. This assumption can also be applied to birds equipped with PDT loggers, although the drag might have been proportionally higher as the propeller increased the frontal area of the logger by 2.2% of the bird's cross-sectional area.

Overall, in our study, Adélie penguins did not dramatically modify foraging behaviour with respect to prey type. No statistical differences in the foraging parameters could be found between birds with different diets. The absence of significant trends can be attributed to the small sample size or the considerable inter-individual variability (despite similar dates of foraging) in diet composition. It should also be noted that since prey capture might occur mainly during the central part of the foraging trip (Ropert-Coudert et al. 2001), an undefined proportion of these prey may not appear in the diet composition and/or a number of travelling dives may be integrated in the analysis. This could contribute to weaken a possible relationship between diet composition and diving activity. Indeed, TDR birds could not be grouped into typical krill versus fish feeders but, rather, showed a gradation from those that ate exclusively krill to those that fed primarily on juvenile fish.

Other explanations should not be overlooked. Adélie penguins eating predominantly fish did not dive less deep. This result bears some similarity with that obtained on free-ranging Gentoo penguins, *Pygoscelis papua*, at South Georgia, where birds that preyed on *Notothenia rossi* dived mainly between 59 and 136 m (Croxall et al. 1988), but differs from results obtained on Adélie penguins at Hukuro Cove, where it was suggested that the individuals that dived deeper ate more euphausids (Endo et al. 2000). Apart from inter-individual variability, birds in our study were foraging in open water, where the distribution of prey might differ drastically from that of ice-covered areas (Endo et al. 2000). In addition, the vertical distribution of *Pleuragramma antarcticum* can be extensive, spanning between 0 and 600 m or deeper (Kock et al. 1985; Ekau 1990).

Since the range of undulatory swim speed did not differ according to diet, this implies that krill and fish have a similar range of swimming speeds. Euphausids can swim at average speeds ranging 0.13–0.15 m s^{-1} (Kanda et al. 1982) up to 1 m s^{-1} when being pursued (Hamner 1984; O'Brien 1987). The range of swim speeds of nototheniid fish has been estimated to be 0.1–1.3 m s^{-1} (Eastman 1993). However, it is unlikely that the observed significant differences in descent speed were related to prey hunting since <5% of prey ingestion occurred during this phase (Ropert-Coudert et al. 2001).

Regardless of diet, descent speed corresponded to that incurring the minimum cost of transport (for definition see Schmidt-Nielsen 1972). The latter, calculated to be around 2.2 m s^{-1} for captive Adélie penguins in a swim canal (Culik and Wilson 1991a,b; Culik et al. 1991, 1994), was similar to values measured in free-ranging birds (Ropert-Coudert et al. 2001). On the other hand, although only 22% of prey may be caught during the ascent (Ropert-Coudert et al. 2001), we cannot at this time exclude the possibility that the reduced ascent speed of fish eaters might indicate that fish capture occurred predominantly during this phase of the dive.

In summary, this study revealed the difficulty in quantifying the foraging behaviour of penguins without direct observation. Besides a larger sample size, future studies should perhaps consider the number of prey caught as a relevant parameter, rather than the percent of contribution by mass of each prey type. Indeed when prey are large, fewer need to be caught. It appears crucial to be able to distinguish when and what type of prey are being captured during the course of the foraging trip. Currently, this can be done only by using technologies such as oesophagus temperature loggers (Ancel et al. 1997; Ropert-Coudert et al. 2000a) that could allow us to determine which dive is characteristic of fish or krill capture.

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