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SHORT NOTE

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Time/depth usage of Adélie penguins: an approach based on dive angles

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Abstract Data on the swim speed, dive depth and feeding rates of three Adélie penguins (*Pygoscelis adeliae*) foraging in summer 1998/1999 in Adélie Land, Antarctica were collected using dorsally-mounted loggers, in tandem with oesophageal temperature sensors. Swim speed could be integrated, together with the rate of change of depth, to determine dive and return-to-surface angles. Overall, birds increased rates of change of depth during commuting phases so that dive angles were steeper in dives terminating at greater depths. Angles of descent and ascent during feeding dives were greater than during non-feeding dives. Variation in the descent angle over time of particular dives was generally less than 10°, but the angles of the ascent phases varied more widely. The importance of selecting the optimum descent and ascent angles with respect to prey exploitation, oxygen stores and time gained in the feeding area over the course of a dive by diving at a steeper angle is discussed.

Introduction

Diving seabirds have to commute periodically from the surface where they replenish their oxygen stores to the depths at which prey are found. The profitability of each dive can be determined by the length of time that the birds can remain in the depth layer of the prey compared to that devoted to commuting between the surface and the point of maximum depth (Kooyman et al. 1992). The optimum strategy will thus be determined by the profitability of the various depths, the maximum dive duration and the rate at which birds move through the water column (Wilson et al. 1996). In addition, the speed at which seabirds and marine mammals choose to swim during the ascent and the descent phases of dives is generally physiologically dependent on the size of the animal (Wardle 1975), and is generally close to the values that determine the minimum cost of transport (for definition, see Schmidt-Nielsen 1972). Animals can optimise the commuting part of their dives only by modifying the angle of ascent and descent (Wilson et al. 1996).

Recently, loggers with fine resolution that measure simultaneously the rate of depth changes and the swim speed were deployed on free-ranging Adélie penguins (*Pygoscelis adeliae*), in tandem with oesophageal temperature recorders that detect the timing of prey ingestion (Ropert-Coudert et al., 2001). By simultaneously measuring the rate of depth changes and the swim speed, it is also possible to calculate precisely the values of dive angles adopted by birds and to relate them, through the use of the oesophageal temperature logger, to the timing of prey intake, enabling a separation between feeding dives and non-feeding dives. The present analysis uses some of the data obtained by Ropert-Coudert et al. (2001), but focuses exclusively on the analysis of the angle at which Adélie penguins dive in relation to a successful or unsuccessful encounter with prey. More precisely, we investigated: (1) the characteristics of dive angles in free-ranging penguins, and (2) whether these angles change subsequent to prey encounter.

Materials and methods

The study was conducted during summer 1998/1999, on 16 breeding Adélie penguins in Adélie Land, Antarctica (66.7°S,

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140.0°E). Swim speed and depth were measured every second with UWE-PDT loggers (absolute accuracy 0.5 m and 0.05 m s^{-1} for depth and speed, respectively; Little Leonardo, Tokyo, Japan), while oesophageal temperature was measured every second with a UME-TT logger (Ropert-Coudert et al. 2000b). Technical details about the loggers, as well as the method of attachment, can be found in Ropert-Coudert et al. (2000b).

After one foraging trip, birds were recaptured, the devices removed and data were downloaded into a computer. Dives were divided into descent, ascent and undulatory phases. Drops in oesophageal temperature, indicating prey ingestion (Wilson et al. 1992), were treated mathematically, using a method that counted the number of markedly decreasing events over the course of each dive (Ropert-Coudert et al. 2000a). This method of determination was successfully tested during feeding experiments performed on captive Adélie penguins (see details of the experiments in Ropert-Coudert et al., 2001). Based on the presence or absence of temperature drops, dives were further defined as feeding or non-feeding dives, respectively. Angles of descent and ascent in radians (θ) were calculated as follows:

$$\mathrm{Sin}(\theta) = \Delta D/\mathrm{Sp} \qquad (1)$$

where ΔD represents the absolute value of the depth changes calculated over 2-s intervals, and Sp the swim speed. As the accuracy of measurements of angles depends on descent or ascent duration, dives with short commuting phases (dives with a maximum depth < 20 m) were excluded from the analysis. Where data were normally distributed, one-way analyses of variance (ANOVA) and covariance (ANCOVA) were applied to the data (Sokal and Rohlf 1969). Proportions were tested by a χ^2 test. The data were statistically treated using Systat (version 7.0, SPSS, USA) and Statview (version 4.57, Abacus Concepts, USA) softwares. For all statistical tests, the threshold was 5%.

Results

Of the 16 free-ranging birds equipped, swim speed, depth utilisation and oesophageal temperature data were reliably logged for portions of the foraging trip of 3 birds, accounting for 100, 91.2 and 66% of the dives (details in Ropert-Coudert et al. 2001).

Two periods could be distinguished in the evolution of the angle during the descending phase of dives. Firstly, the descent angle remained constant or increased slightly during the main part of the descent (Fig. 1a). During this early period of the descent, variations in the angle were generally less than 10° in both feeding and non-feeding dives (Table 1). The descent angle increased with maximum depth and became steeper if a prey capture occurred in the previous dive (Fig. 2a). The slopes of the regression lines were not significantly different (ANCOVA $F_1 = 1.29$, $P = 0.26$) but the intercepts were (ANCOVA $F_1 = 111.9$, $P < 0.0001$ and $F_1 = 271.7$, $P < 0.0001$ for dive types and maximum depth, respectively). Secondly, towards the end of the descent phase, most dives abruptly changed in descent angle (Fig. 1a), which became more acute until the direction changed indicating the beginning of the undulatory phase. This abrupt point was observed in 68.5% of the cases but occurred significantly later in the descent phase of feeding dives (84.8 ± 13.4% of the descent time or at 81.2 ± 8.9% of the maximum depth) than for non-feeding dives (71.0 ± 15.7% of descent time ANOVA $F_1 = 75.6$, $P < 0.0001$; 75.7 ± 9.2% of maximum depth, ANOVA $F_1 = 29.2$, $P < 0.0001$).

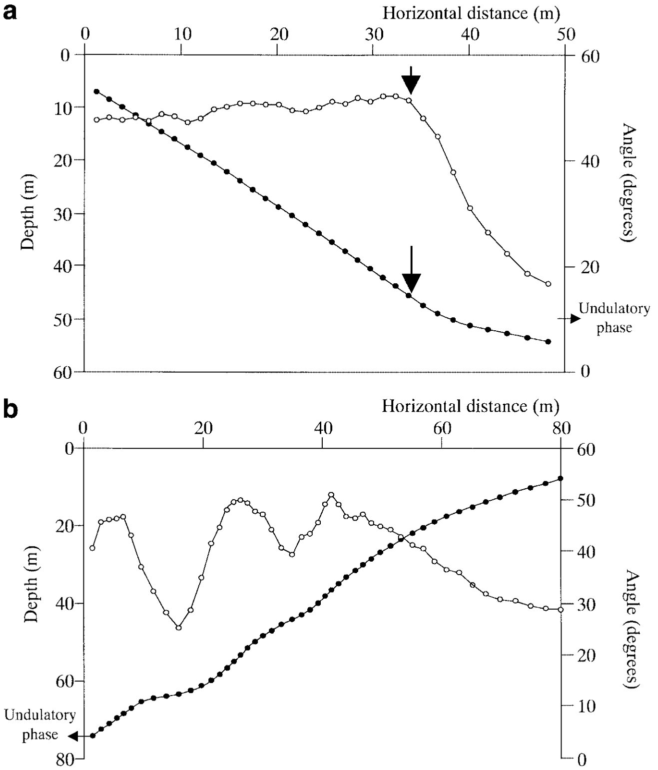

Fig. 1 **a** Descent angle (*unfilled circles*) and the corresponding profile of the distance travelled vertically and horizontally (*filled circles*) during the descent phase of a feeding dive. The *arrows* indicate the time when the angle abruptly changed from a constant value, decreasing sharply prior to the start of the undulatory phase. The maximum depth of this dive was 60 m. **b** Ascent angle (*unfilled circles*) and the corresponding profile of the distance travelled vertically and horizontally (*filled circles*) during the ascent phase of a feeding dive. The maximum depth of this dive was 73 m

Table 1 Profile of the descent angles of free-ranging Adélie penguins calculated for dives with a maximum depth > 20 m

Dive types	Angle constant (changes ≤ 10°)	Steady increase of angle (< 30°)	Irregular pattern
Feeding	69.0% ($N = 208$)	26.0% ($N = 77$)	5.0% ($N = 15$)
Non feeding	57.5% ($N = 81$)	17.0% ($N = 24$)	25.5% ($N = 36$)
Total	65.5% ($N = 289$)	23.0% ($N = 101$)	11.5% ($N = 51$)

Although 36% of the ascent angles of dives tended to have an oscillating pattern (Fig. 1b), the large proportion of angles with an irregular pattern made further classification difficult. The ascent angles were affected by the presence or absence of prey capture during the undulatory phase of the dive (Fig. 2b). Ascent angles of dives where no prey were encountered increased less quickly with maximum dive depth than angles of dives with prey capture (ANCOVA test of the homogeneities of the slope, $F_1 = 13.7$, $P < 0.0001$).

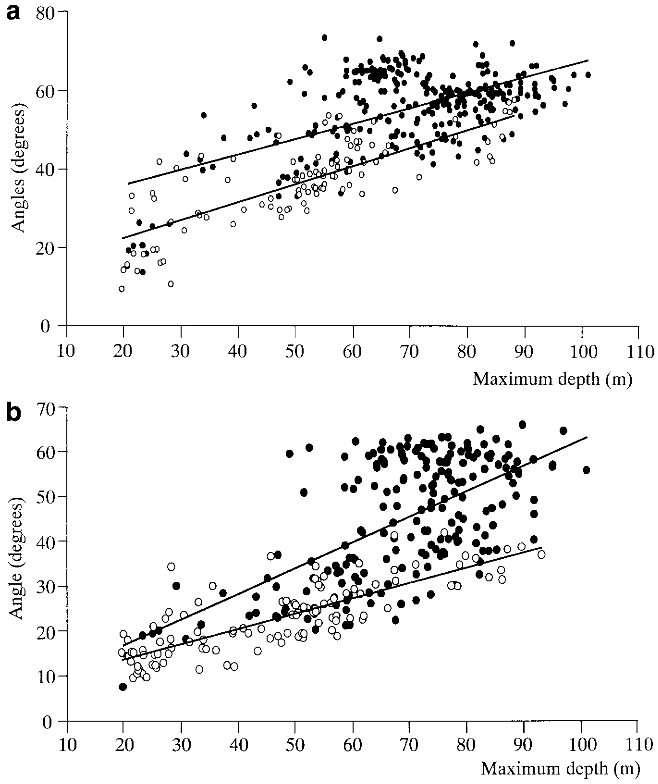

Fig. 2 **a** Descent angle in relation to the maximum depth (MD) of dives of free-ranging Adélie penguins according to the presence (*filled circles*) or absence of feeding events (*unfilled circles*) in the immediately preceding dive. The best fit regressions are $\text{Angle} = 0.40 * MD + 27.9$ ($R^2 = 0.36$, ANOVA $F_{279} = 152.8$, $P < 0.0001$) and $\text{Angle} = 0.46 * MD + 13.2$ ($R^2 = 0.61$, ANOVA $F_{98} = 150.0$, $P < 0.0001$), respectively. **b** Ascent angle in relation to the maximum depth (MD) of dives of free-ranging Adélie penguins according to the presence (*filled circles*) or absence of feeding events (*unfilled circles*) in the undulatory phase of the dive. The best fit regressions are $\text{Angle} = 0.60 * MD + 4.5$ ($R^2 = 0.38$, ANOVA $F_{112} = 214.3$, $P < 0.0001$) and $\text{Angle} = 0.30 * MD + 6.6$ ($R^2 = 0.66$, ANOVA $F_{200} = 120.7$, $P < 0.0001$), respectively

Discussion

During the descent phase of feeding dives, the angle was steeper if the bird encountered prey in the previous dive. A typical feeding dive may be summarised as follows: birds descend directly to the depth where prey are to be found at a steep angle until an abrupt change in the angle that corresponds either to pursuit of the first prey encountered or a rapid deceleration in order to reduce speed in the prey patch. An abrupt decrease in the angle would modify the orientation of the vector of the positive lift force, acting against negative buoyancy at these depths, and thus contribute to deceleration. In this case, the birds may pass through the depth zone where the patch is located and then invert their angle quickly to approach the patch from underneath. This pattern of hunting is similar to that observed in other species of marine seabirds and mammals using vision to catch prey in a relatively dark environment (Davis et al. 1999; Ropert-Coudert et al. 2000a).

Dive angle is a key parameter in determining the depths at which penguins invest foraging effort. To date, all penguins investigated appear to increase dive and return-to-the-surface angles with increasing maximum dive depth (see Wilson 1995 for review), which means that since swim speed remains virtually unchanged, as maximum dive depth increases so birds spend proportionately less time per unit depth. This strategy differs markedly from that of benthic-feeding birds where descent and ascent angles are always very steep, a strategy which allows the birds to move as quickly as possible between the surface and the foraging depth (see Wilson and Wilson 1988; Grémillet et al. 1999; Tremblay and Cherel 2000). This latter strategy is a consequence of minimising time spent in unprofitable zones. Penguin prey, however, are typically pelagic, and may occur at any depth. Thus, steep dive angles down to specific preferred depths tend to make the birds pass very quickly through the intermediate water layers and thus reduce the probability of prey encounter in these zones. It is to be expected, however, that the descent and ascent angles that penguins use may vary according to prey distribution in (1) taking the birds to the depths where prey encounter is most likely, and (2) ensuring, despite this, that an appropriate amount of time is dedicated to searching the upper water layers in case prey may occur there. This overall strategy should be tempered according to perceived circumstances. In particular, it is to be expected that where birds have located aggregating prey at depth, it might be advantageous for birds to descend quickly and repeatedly to that depth during subsequent dives because of the greater likelihood that prey will be relocated. Although changes in descent and ascent angles in relation to foraging success have rarely been documented (but see Wilson and Wilson 1995), our data show clearly this to be the case in Adélie penguins.

The exact amount of time invested per unit (m) depth can easily be calculated using the relationships between dive angle and depth both for dives where prey were ingested and non-successful dives. Here, the time spent per unit depth is given by

$$T = (1/(2.16 \sin \theta)) + (1/(2.06 \sin \varphi)) \tag{2}$$

where Θ and φ are the descent and ascent angles, respectively (Fig. 3), and 2.16 and 2.06 are the swim speeds adopted for the descent and ascent phases, respectively (Ropert-Coudert et al., 2001). This approach shows that during normal searching dives, where no prey are encountered, Adélie penguins spend 2.4 s travelling through each vertical metre for dives to 40 m and 1.35 s for dives to 100 m. Equivalent figures for birds during feeding dives are 1.68 and 1.04 s, respectively. Considered over the length of the dive, this means that during feeding dives birds concentrate ca. 23% more of their commuting time on the depths where they had encountered prey. If birds descended and ascended vertically, irrespective of maximum dive depth, they would spend less than 1 s per metre water depth, which would mean that they could allocate between 25 and 55% of their

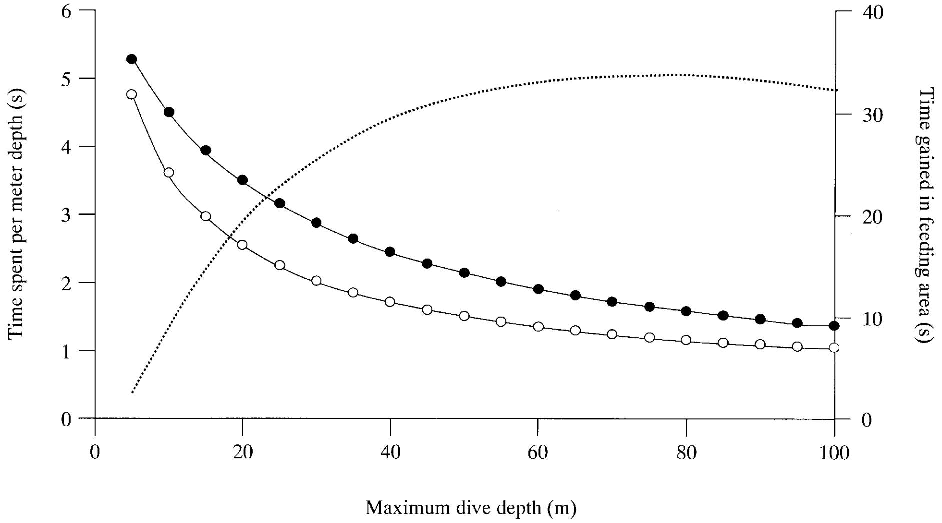

Fig. 3 Exact time spent per metre depth during the commuting processes of feeding (*filled circles*) and non-feeding dives (*unfilled circles*) and time gained at feeding depth (*dotted line*) by diving at steeper (feeding) angles in free-ranging Adélie penguins

commuting time to their preferred depths. The fact that they do not do this may be related to either the considerations detailed above, or perhaps to physiological or bio-mechanical reasons.

During the ascent, the angle of the swim path was less well defined than in descending birds. This may be because the birds might engage in minor pursuit movements to catch prey encountered, following the principle of "lost-opportunities" (Stephen and Krebs 1986). This principle states that even less profitable prey, e.g. an isolated prey, is worth catching if it occurs during the course of the commuting process and does not require an extra energy expenditure. During the ascent, the probability of perceiving a prey silhouetted against the brighter background (Clarke and Denton 1962) is increased.

To summarise, by increasing or reducing their dive angles, Adélie penguins optimise the feeding component of the bottom phase of their dive, or the searching component during the commuting phases.

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