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Why do macaroni penguins choose shallow body angles that result in longer descent and ascent durations?

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Summary

It is generally assumed that air-breathing aquatic animals always choose the shortest route to minimize duration for transit between the surface and foraging depth in order to maximize the proportion of time spent foraging. However, empirical data indicate that the body angles of some diving animals are rarely vertical during descent and ascent. Why do they choose shallower body angles that result in longer descent and ascent durations? To investigate this question, we attached acceleration data loggers to eight female macaroni penguins, breeding on the Kerguelen Islands (48°45′–50°00′ S, 68°45′–70°58′ E; South Indian Ocean), to record depth, two-dimensional acceleration (stroke cycle frequency and body angle) and temperature. We investigated how they controlled body angle and allocated their submerged time. The instrumented females performed multiple dives (*N*=6952) with a mean dive depth for each bird ranging from 24.5±28.5 m to 56.4±75.1 m. Mean body angles during descent and ascent were not vertical. There was large variation in mean descent and ascent angles for a given dive depth, which, in turn, caused large variation in descent and ascent duration. Body angles were significantly correlated with time spent at the bottom-phase of the dive. Birds that spent long periods at the bottom exhibited steep body angles during ascent and subsequent descent. By contrast, they adopted shallow body angles after they had short or no bottom phases. Our results suggest that macaroni penguins stay at the bottom longer after encountering a good prey patch and then travel to the surface at steep body angles. If they do not encounter prey, they discontinue the dive, without staying at the bottom, ascend at shallow body angles and descend at shallow body angles in a subsequent dive. A shallow body angle can increase the horizontal distance covered during a dive, contributing to the move into a more profitable area in the following dive. During the ascent, in particular, macaroni penguins stopped beating their flippers. The buoyantly gliding penguins can move horizontally with minimum stroking effort before reaching the surface.

Key words: dive, acceleration, data logger, stroke, buoyancy, gliding, horizontal transit, penguin, *Eudyptes chrysolophus*.

Introduction

Air-breathing aquatic animals that forage underwater must divide their time between periods spent underwater seeking food and intervals at the surface, where gas exchange takes place (Kooyman, 1989). Using time-depth recorders, the time budgets of various diving animals have been documented, including the relationship between time spent at the surface relative to dive duration (e.g. Kooyman et al., 1992; Williams et al., 1992) and the proportions of time spent underwater at particular depths (e.g. Le Boeuf et al., 1988; Wilson et al., 1991, 1996; Croxall et al., 1993). Theoretical models generally assume that air-breathing aquatic animals always choose the shortest possible route to minimize duration for transit between the surface and foraging depth in order to maximize their foraging efficiency, which is defined as the proportion of time spent foraging (Houston and Carbone, 1992; Thompson and Fedak, 2001). A long transit time between the surface and foraging depth caused by non-vertical body angle is therefore not beneficial in terms of foraging efficiency. However, the calculated body angles based on swimming speed and vertical speed of most diving animals are not vertical during descent and ascent (Wilson, 1995; Wilson and Wilson, 1995; Wilson et al., 1996; Boyd et al., 1997; Otani et al., 2000; Ropert-

Coudert et al., 2001; Akamatsu et al., 2002; Sato et al., 2002). Why do these animals choose shallower body angles that result in longer descent and ascent durations?

Physiological factors, such as the potential risk of decompression sickness, may prevent air-breathing divers from using vertical transit (Sato et al., 2002). If this idea is true, then penguins would be expected to adopt shallow body angles to prolong their ascent durations after having spent relatively long periods at deep depths. A second explanation may be linked to the concept of optimal foraging behaviour. It has been proposed that predators remain longer at depths that have a higher prey density (Mori, 1998). If the diver encounters a good prey patch, it can prolong the time spent at the bottom and then adopt a steep body angle during its ascent, because it must return quickly to the surface to breathe. If this hypothesis is true, we would expect a positive relationship between the bottom-phase duration and body angle during the ascent.

The use of miniaturized acceleration data loggers allows for fine-scale monitoring of movements during diving (Sato et al., 2003). Low-frequency components of surging acceleration along the long axis of the body provide information on body angles during dives. Stroke frequency can be detected from high-frequency components of acceleration data. In the present study, small acceleration data loggers (depth, 2-D acceleration and temperature) were attached to macaroni penguins (*Eudyptes chrysolophus*). Here, we examine body angles during descent and ascent in relation to the bottom-phase duration of dives. Our aim was to test the hypothesis that mid-size penguins adjust their body angles during the transit phases in relation to their feeding success at the bottom phase of dives. We discuss our findings in terms of behavioural strategies based on physiological and environmental conditions during diving.

Materials and methods

Field study

The field study was carried out during the austral summer from 27 November to 13 December 2002 at the Cape Cotter Colony, Courbet Peninsula on the eastern side of the Kerguelen Archipelago (48°45′–50°00′ S, 68°45′–70°58′ E, South Indian Ocean). Approximately 300 000 pairs of macaroni penguins (*Eudyptes chrysolophus* Brandt 1837) breed in this locality (Weimerskirch et al., 1988), and the study was conducted during their incubation period. At this time, most female macaroni penguins forage at sea, while fasting males incubate the eggs. Study birds were selected randomly from nests located at the periphery of the colony to minimize disturbance to breeding birds. Eight females were captured at their nests, just as they were about to go to sea after switching incubating duties with their partner. The females were selected from a breeding pair on the basis of their smaller body size in relation to the male (Williams, 1995). Captured birds were weighed to the nearest 50 g (body mass ranging from 3.0 to 3.8 kg) and fitted with the data loggers. The attachment procedure took 7–16 min in total, after which the penguins were released close to their nest sites. Maximum care was taken to reduce stress to the birds, e.g. by covering the birds' eyes during handling and by moving carefully. The eight females immediately returned to their nests after being released and then departed voluntarily for their foraging trip within 1–21 h.

All instrumented birds returned from their foraging trips, with trip durations ranging from 12 to 15 days (mean ± S.D. = 13.6±1.1 days). The trip durations recorded in this study were slightly longer than the mean of 11.0 days reported for females studied at Bird Island (Williams and Croxall, 1991) and Crozet (Stahl et al., 1985). Upon their return, birds were recaptured at their nest and all loggers were retrieved. Body mass, bill length and bill depth were measured, and the sex of the instrumented birds was confirmed based on bill length and depth (Williams, 1995). All equipped birds appeared to have gained weight (by 0.50–0.95 kg), and no nest was abandoned through the experiment.

Data loggers

The detailed behaviour of diving penguins was studied using acceleration data loggers (M190-D2GT; Little Leonardo Ltd, Tokyo, Japan). Each instrument was 15 mm in diameter and 60 mm in length, with a mass of 16 g in air, corresponding to <0.5% of the body mass of a bird. The cross-sectional area of the instrument was <1.1% of the maximal cross-sectional area of a bird; therefore, we estimated the drag impact on swimming behaviour to be minimal (Wilson et al., 1986). The data logger was attached to the lower medial portion of the back using waterproof Tesa tape (Wilson and Wilson, 1989) and plastic cable ties.

The loggers recorded depth every second (±1 m accuracy and 0.05 m resolution), 2-D acceleration at 16 or 32 Hz *via* an accelerometer sensor (model ADXL202E; Analog Device, Inc., Norwood, MA, USA) and sea temperature at 30-s intervals. The measuring range of the accelerometer was ±29.4 m s^{-2} with a resolution of 0.0196 m s^{-2}. The logger recorded tail-to-head (surge) and ventral-to-dorsal (heave) accelerations. The loggers were programmed to start recording one or two days (four birds each) after departure in order to record data during the middle period of the foraging trip.

Data analyses

Data were analyzed using a custom-written macro program in Igor Pro (Wave Metrics, Inc., Lake Oswego, OR, USA). We defined dives as bird movements to depths greater than 1 m. As indicated in Fig. 1, a dive was divided into a descent (continuous descent from the initiation of the dive), a bottom phase (the time between the start and end of the time when birds showed a depth change of 0 m) and an ascent (continuous ascent to the end of the dive).

The accelerometer was able to measure both dynamic acceleration (such as propulsive activities) and static acceleration (such as gravity). Values recorded by loggers were converted into acceleration with linear regression equations. To obtain the calibration equations, values recorded by each logger set at 90° and –90° from the horizon in 4°C waters (corresponding to mean ambient water temperatures) were regressed on the corresponding acceleration (9.8 m s^{-2} and –9.8 m s^{-2}, respectively). We used high-frequency components of heave and surge accelerations to count stroke cycle frequency. A single stroke cycle included both an upstroke and a downstroke. Mean stroke cycle frequencies (Hz) during descent, bottom phase and ascent were calculated from the total number of stroke cycles divided by the duration of each phase for each dive.

The acceleration sensor along the longitudinal body axis measured the surging accelerations, which are affected by both the forward movements of the animal and gravity (Yoda et al., 2001; Tanaka et al., 2001; Sato et al., 2003). High-frequency components of the surging accelerations, which are caused by flipper movements, were filtered out using 1-Hz low-pass filters (IFDL version 3.1; Wave Matrics, Inc.). Low-frequency components of the surging acceleration were then used to calculate the body angle of the animals (for details, see Sato et al., 2003). Descending body angles are represented as negative values. When an animal descends or ascends vertically, its body angle is close to –90° or 90° ('steep' body angle) whereas when an animal swims horizontally, the body angle is close to 0° ('shallow' body angle). As described by Watanuki et al. (2003) and Sato et al. (2003), the loggers were not exactly parallel to the longitudinal axes of the animals because they were attached to the lower back of each animal to diminish hydrodynamic drag (Bannasch et al., 1994). In this position, each logger had an attachment angle. To measure the attachment angle for each bird, we arbitrarily selected five samples of 3-s surge acceleration when birds were at the water surface between dives; their trunks were assumed to be horizontal while at the surface. The mean surging acceleration during these surface periods was used to calculate the attachment angle. The estimated attachment angle for each bird, which ranged from 5.2° to 11.6°, was taken into consideration when calculating body angles.

Data were analyzed statistically using StatView (version 5.0, SAS, Cary, NC, USA) software. Values are presented as means ± S.D., with significance set at the $P<0.05$ level. Mean values were calculated for each bird, and correlations were examined individually.

Results

Diving performances

The eight instrumented macaroni penguins performed a total of 6952 dives, with mean dive depth for each bird ranging from 24.5±28.5 m to 56.4±75.1 m and maximum dive depth ranging from 74.7 m to 99.2 m. Mean dive duration for each bird ranged from 63.2±64.9 s to 123.4±64.0 s, and maximum dive durations ranged from 158 s to 190 s (Table 1).

Dives typically had either a V-, U- or W-shaped profile when depth was plotted against time. A typical dive cycle of a macaroni penguin is presented in Fig. 1. Based on acceleration data, the penguin stroked continuously during the descent, stopped stroking during the middle of the ascent and completed the ascent with a prolonged glide (Fig. 1). Small amplitudes and aperiodic fluctuations in acceleration indicated that penguins did not swim during surface intervals (Fig. 1). Porpoising behaviour was observed close to the coast (C.A.B. and K.S., personal observations), but recorded data did not cover the first and last few days of the foraging trip. For each dive, the mean stroke cycle frequency during the descent, bottom phase and ascent was plotted against dive depth (Fig. 2). Each penguin descended with a mean stroke cycle frequency ranging from 2.0 to 2.6 Hz (Fig. 2A; Table 2). Ascending penguins had lower mean stroke cycle frequencies (Fig. 2C; Table 2), and the distribution of the mean stroke cycle frequency during the bottom phase was intermediate between descent and ascent values (Fig. 2B; Table 2). Mean stroke cycle frequencies between the dive phases differed significantly at each dive depth range: <20 m (Scheffé's test: $N_1=N_3=1510$, $N_2=1311$, $P<0.0001$), 20–40 m (Scheffé's test: $N_1=N_3=1258$, $N_2=1212$, $P<0.0001$), 40–60 m (Scheffé's test: $N_1=N_3=1514$, $N_2=1464$, $P<0.0001$), >60 m (Scheffé's test: $N_1=N_3=1069$, $N_2=1040$, $P<0.0001$).

Time allocation during dives

Dive duration was positively correlated with dive depth (Fig. 3), and this relationship was significant for each bird (Table 3). Descent and ascent durations were significantly correlated with the depths at the beginning and at the end of the bottom phase, respectively (Fig. 4; Table 4). However,

Table 1. *Characteristics of diving behaviour of eight female macaroni penguins*

			Dive depth (m)		Dive duration (s)	
Bird	Body mass (kg)	Number of dives	Mean ± S.D.	Maximum	Mean ± S.D.	Maximum
MK1	3.8	1398	29.0±19.3	83.6	83.5±37.9	158
MK2	3.4	1147	32.2±26.9	99.1	88.5±53.3	163
MK3	3.0	11*	56.4±75.1	80.1	123.4±64.0	169
MK4	3.2	277*	37.0±15.8	74.7	120.6±34.9	181
MK5	3.0	1279	24.9±22.7	78.6	79.9±57.5	165
MK6	3.1	1559	24.5±28.5	89.3	63.2±64.9	188
MK7	3.6	619	36.3±29.4	99.2	101.1±62.3	190
MK8	3.3	662	38.6±22.1	82.1	105.3±38.0	167

*Data length was short because of battery failure.

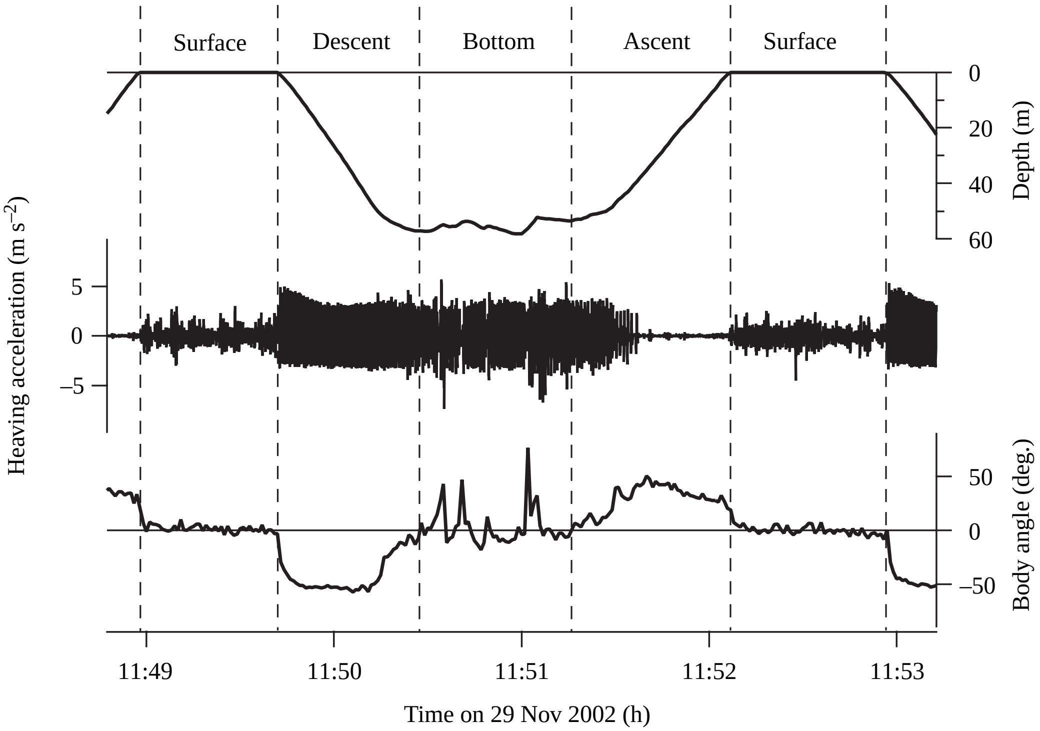

Fig. 1. Typical dive cycle of a macaroni penguin (MK8). The vertical broken lines delineate the separation of the dive into three phases: descent, bottom phase and ascent.

descent and ascent durations at a given depth showed a large range of variation (Fig. 4). For example, the time necessary to reach the surface from a 60-m depth ranged from 27.5 s to 90 s (Fig. 4B). As shown in Fig. 5 (bird MK1), descent and ascent durations recorded during the different dives were significantly affected by mean body angle during each dive, with descent durations decreasing with steeper descent body angles at each depth range: <20 m (Spearman R=0.437, N=470, P<0.0001), 20–40 m (Spearman R=0.820, N=478, P<0.0001), 40–60 m (Spearman R=0.893, N=255, P<0.0001), >60 m (Spearman R=0.767, N=79, P<0.0001). Similarly, ascent durations decreased with steeper ascent body angles in each depth range deeper than 20 m: <20 m (Spearman R=–0.002, N=544, P=0.958), 20–40 m (Spearman R=–0.763, N=475, P<0.0001), 40–60 m (Spearman R=–0.891, N=194, P<0.0001), >60 m (Spearman R=–0.912, N=69, P<0.0001). This tendency was significant for all birds except bird MK3, for which only a small number of dives were recorded. The significance of body angle and duration of the eight birds at each depth range is summarized in Table 5.

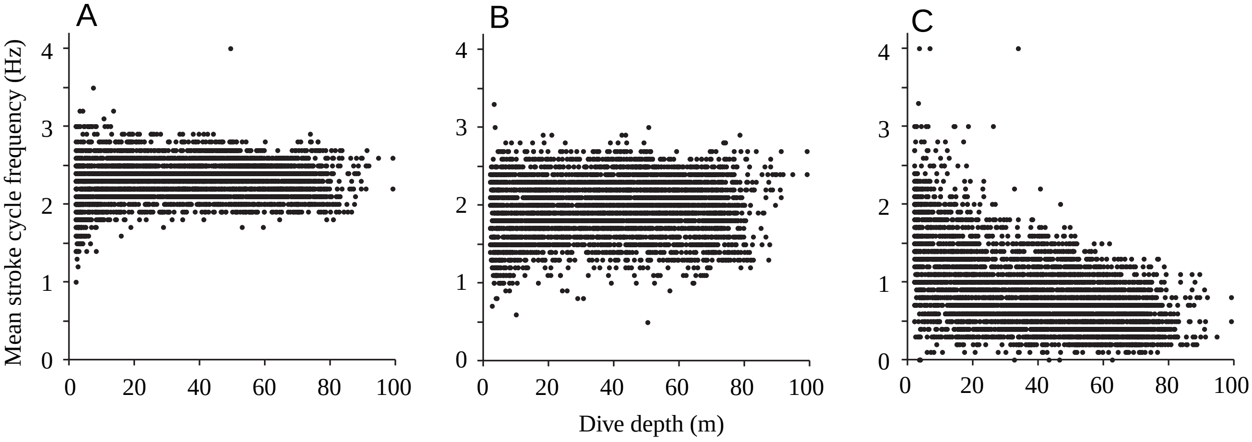

Fig. 2. Relationships between dive depth and mean stroke cycle frequency during (A) descent, (B) bottom phase and (C) ascent. Data from all birds are represented (N=5351 for A and C; N=5027 for B).

Body angles during descent and ascent

Mean body angles during descent and ascent were not vertical (Table 6). Mean descent angles ranged from –23.7° to –42.6° among birds. Mean ascent angles ranged from 24.4° to 32.1°, and the maximum angles were shallower than 70° in most dives (Table 6). The large S.D. indicates that, for a given bird, body angles were highly variable among dives. Body angles were significantly correlated with time spent at the bottom, and significant regression lines for ascent and subsequent descent were obtained for each depth range (Table 7). Significant regression lines were obtained for all birds except birds MK3 and MK4, for which only a small number of dives were recorded. A typical example of this relationship is shown in Fig. 6, with data from bird MK1. When birds spent long periods at the bottom, they adopted steep body angles during ascent and subsequent descent. By contrast, they maintained shallow body angles after they had short or no bottom phases.

Table 2. *Stroke cycle frequencies (mean ± S.D.) of eight female macaroni penguins*

	Mean stroke cycle frequency (Hz)		
Bird	Descent	Bottom	Ascent
MK1	2.2±0.2	1.7±0.2	0.7±0.4
MK2	2.6±0.2	2.3±0.2	1.1±0.6
MK3	2.3±0.2	1.9±0.2	0.7±0.4
MK4	2.4±0.1	2.1±0.3	0.9±0.5
MK5	2.4±0.2	2.1±0.2	1.1±0.5
MK6	2.2±0.2	1.7±0.3	0.6±0.4
MK7	2.0±0.2	1.7±0.4	0.7±0.4
MK8	2.2±0.1	2.1±0.3	0.9±0.5

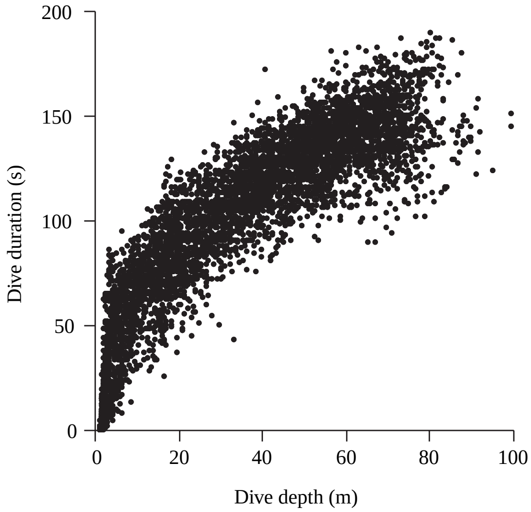

Fig. 3. Relationship between dive duration and depth for all dives (N=6952) made by eight macaroni penguins.

Table 3. *Relationship between depth and duration of dives for each bird*

Bird	*N*	Spearman *R*	*P*
MK1	1398	0.912	<0.0001
MK2	1147	0.944	<0.0001
MK3	11	0.945	<0.01
MK4	277	0.883	<0.0001
MK5	1279	0.962	<0.0001
MK6	1559	0.945	<0.0001
MK7	619	0.947	<0.0001
MK8	662	0.902	<0.0001

Discussion

The present study indicates that macaroni penguins exhibited steep body angles during ascent and subsequent descent after they had a long bottom phase and that they maintained shallow body angles after a short or no bottom-phase duration. In the absence of contemporaneous data on prey distribution, theoretical models validated with empirical data can help to clarify the significance of time allocation during a dive. A positive correlation between patch quality and patch residence time has been predicted, such that a diver should stay longer in a better patch (Mori, 1998). This prediction is supported by data from guillemots and Antarctic fur seals (Mori et al., 2002; Mori and Boyd, 2004). Thus, if we apply this model to our data, macaroni penguins should stay at the bottom for a relatively long period when they encounter a good prey patch. In Adélie penguins, most feeding events detected by drops in oesophagus temperature occurred during the bottom phase (Ropert-Coudert et al., 2001). In that study, angles of descent and ascent during feeding dives were greater than during non-feeding dives (Ropert-Coudert et al., 2001).

Therefore, if we consider that long bottom-phase durations indicate foraging success, as compared with short bottom-phase periods, two main hypotheses could help explain the steep body angle that is related to more time spent at the bottom. First, steeper ascent angles presumably occur when birds have depleted their oxygen stores and must return to the surface more quickly to breathe (Wilson and Wilson, 1995). Second, when a dive is successful, as suggested by a long bottom-phase duration, and, if we assume that penguins will try to relocate the same prey patch, steep ascent and subsequent descent angles will increase the probability of encountering the patch in the following dive because the horizontal component of the dive will be minimized (Wilson and Wilson, 1995). However, even when they ascended at a steeper angle after a long bottom-phase duration, the ascent angles in macaroni penguins were not vertical (Table 6).

Several factors may explain the oblique body angles. First, it is possible that penguins ascended obliquely to prolong their ascent time and thereby avoid decompression sickness (Sato et al., 2002). However, there are no data to support this idea, as yet. Although we expected penguins to delay their ascent after they stayed longer at deep depths, they actually ascended relatively quickly after spending long periods in the bottom

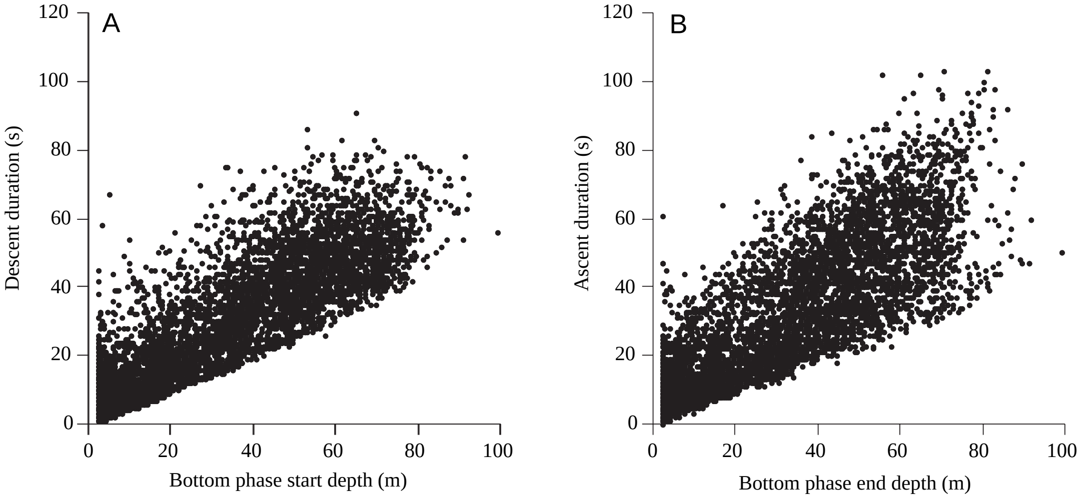

Fig. 4. Relationships between (A) descent duration and bottom phase start depth and (B) ascent duration and bottom phase end depth. Data from all birds are represented (*N*=5352).

Table 4. *Relationship between depth and travelling time for each bird*

Bird	*N**	Descent		Ascent	
		Spearman *R*	*P*	Spearman *R*	*P*
MK1	1282	0.858	<0.0001	0.831	<0.0001
MK2	921	0.828	<0.0001	0.814	<0.0001
MK3	10	0.770	<0.05	0.948	<0.01
MK4	277	0.844	<0.0001	0.829	<0.0001
MK5	893	0.752	<0.0001	0.684	<0.0001
MK6	831	0.803	<0.0001	0.763	<0.0001
MK7	486	0.882	<0.0001	0.852	<0.0001
MK8	652	0.931	<0.0001	0.898	<0.0001

*Dives deeper than 2 m were used for this analysis.

phase (W-shaped dives) and prolonged their ascent duration in dives with a short or no bottom phase (V-shaped dives).

Second, shallow angles during ascent and subsequent descent might help the penguins to scan the water column horizontally to locate a new patch of prey. This hypothesis was first proposed by Wilson et al. (1996) and Peters et al. (1998), who suggested that scanning the water during the ascent and descent phases is probably essential for optimal exploration of the water column, with the horizontal scanning of the habitat being favoured by shallow angles. However, it is hard to believe that such scanning could be the main reason for the shallow body angles. Body angles of macaroni penguins became shallower as they approached the surface (Fig. 1). Adélie and king penguins also ascended similarly (Ropert-

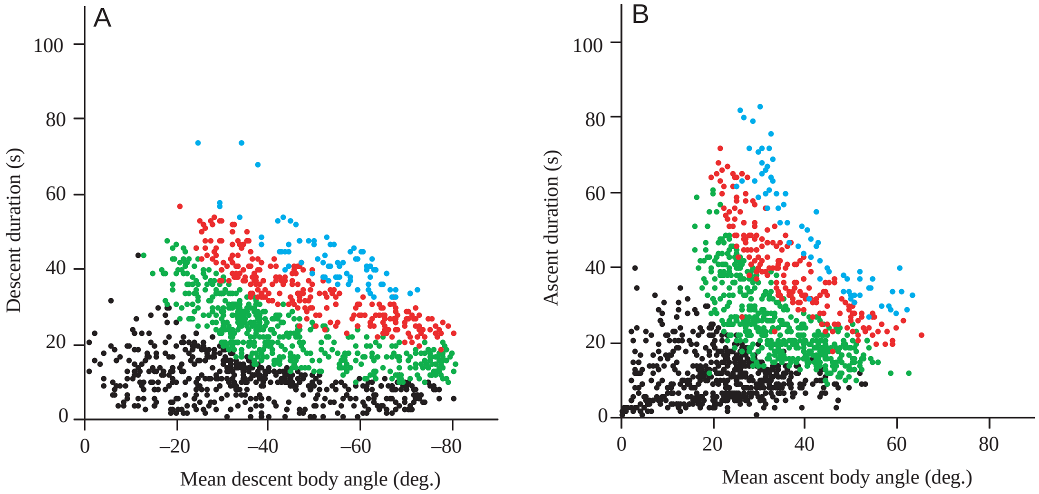

Fig. 5. Relationships between (A) mean descent body angle and duration and (B) mean ascent body angle and duration of a macaroni penguin (MK1). Colours of plots represent ranges of bottom-phase start or end depths (black for <20 m, green for 20–40 m, red for 40–60 m, blue for >60 m).

Coudert et al., 2001; Sato et al., 2002). As indicated by Wilson and Wilson (1995) and Ropert-Coudert et al. (2001), shallower body angles result in a longer time spent per metre depth. It is improbable that penguins would spend more time searching near the surface, where the probability of prey acquisition should be lower.

Third, a shallow body angle can contribute towards increased horizontal distances travelled during the descent and ascent. Indeed, female macaroni penguins travelled long distances during incubation, averaging 376 km at Bird Island (Barlow and Croxall, 2002), but our study shows that they did not swim actively while at the surface between dives (Fig. 1). Shallow and short dives are generally considered to be travelling dives, while deep and long dives are considered foraging dives (Wilson, 1995). Here, we propose that all dives (including deep foraging ones) contribute to horizontal transit, because very shallow body angles were observed during the last part of the ascent in the case of deep foraging dives (Fig. 1). The shallow body angle would contribute to horizontal transit at any depth (Fig. 7) and therefore would permit penguins to move into a more profitable area for the following dive, assuming that they do not alter their directions (compass heading) during the descent and ascent. Particularly in the case of the ascent, macaroni penguins stopped beating their flippers after the first part of the ascent (Fig. 1), as has also been observed in Adélie and king penguins (Sato et al., 2002), and they were able to reach the surface using buoyancy, without any stroking effort. Body angle can be controlled using outstretched wings (Sato et al., 2002; see fig. 1 in Takahashi et al., 2004), so penguins can optimize their ascent

Table 5. *Relationships between body angle and duration during descent and ascent for each depth range of eight macaroni penguins*

Depth range	Spearman *R*	*N**	*P*
Descent			
<20 m	0.397	1700	<0.0001
20–40 m	0.851	1297	<0.0001
40–60 m	0.850	1434	<0.0001
>60 m	0.871	921	<0.0001
Ascent			
<20 m	–0.048	1822	<0.05
20–40 m	–0.810	1364	<0.0001
40–60 m	–0.839	1412	<0.0001
>60 m	–0.861	754	<0.0001

*Dives deeper than 2 m were used for this analysis.

Table 6. *Descent and ascent body angles of eight macaroni penguins*

		Descent (deg.)		Ascent (deg.)	
Bird	*N**	Mean ± S.D.	Maximum	Mean ± S.D.	Maximum
MK1	1282	–42.6±18.3	–80.6	29.4±12.8	65.1
MK2	921	–32.5±19.7	–81.6	29.0±15.5	66.4
MK3	10	–30.5±13.6	–44.2	24.4±9.6	35.0
MK4	277	–41.4±17.0	–80.6	26.1±11.7	56.9
MK5	893	–23.7±14.7	–61.6	26.7±12.2	62.1
MK6	831	–32.9±16.2	–72.3	29.1±12.5	61.3
MK7	486	–27.2±15.1	–70.9	32.1±10.8	71.4
MK8	652	–34.4±12.2	–68.8	28.7±11.8	62.6

*Dives deeper than 2 m were used for this analysis.

Table 7. *Relationships between body angle and bottom-phase duration for each depth range of eight macaroni penguins*

Depth range	Equation	R^2	*F*	*N**	*P*
Ascent of *N*th dive					
<20 m	y=8.0+0.3x	0.370	1071.1	1821	<0.0001
20–40 m	y=17.1+0.3x	0.428	1022.6	1363	<0.0001
40–60 m	y=21.7+0.3x	0.434	1082.8	1411	<0.0001
>60 m	y=28.6+0.3x	0.286	302.3	753	<0.0001
Descent of (*N*+1) dive					
<20 m	y=–13.0–0.4x	0.187	370.8	1614	<0.0001
20–40 m	y=–20.1–0.3x	0.225	383.7	1316	<0.0001
40–60 m	y=–24.3–0.3x	0.214	360.9	1324	<0.0001
>60 m	y=–30.6–0.3x	0.202	180.3	710	<0.0001

x, bottom-phase duration of *N*th dive (s); y, mean ascent or descent angle (deg.).
*Dives deeper than 2 m were used for this analysis.

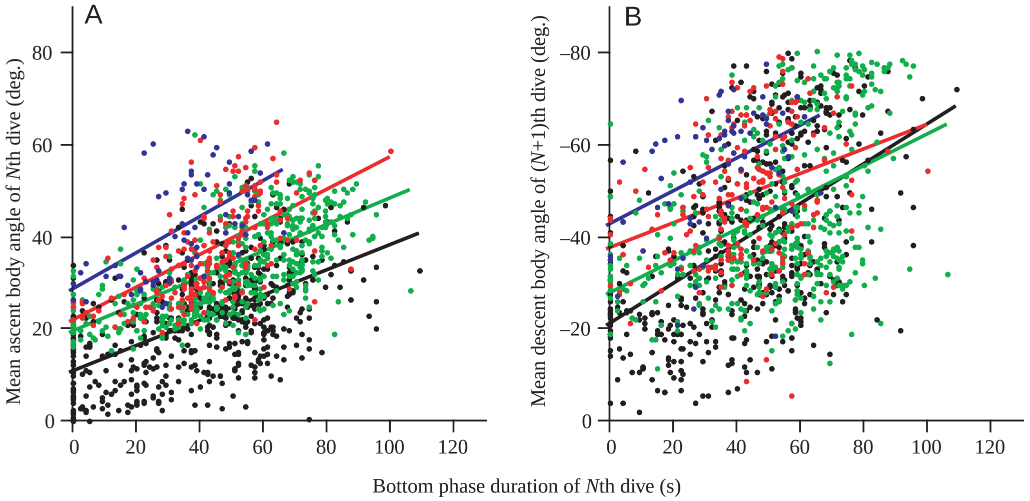

Fig. 6. Relationships between (A) bottom-phase duration and mean ascent body angle within a dive and (B) bottom-phase duration of a dive and mean descent body angle of a subsequent dive in a macaroni penguin (MK1). Colours of plots represent ranges of bottom-phase start or end depth (black for <20 m, green for 20–40 m, red for 40–60 m, blue for >60 m). Regression lines are for each depth range.

angle to move horizontally. Decreasing the ascent angle makes sense because buoyancy increases with ascent. If penguins decreased their body angles during the ascent, the effect of buoyancy parallel to the longitudinal axis of a penguin was sufficient against the drag. Thus, penguins can adopt shallower body angles to move longer horizontal distance using the increasing buoyancy.

It has been observed that terrestrial animals make the decision to remain in a prey patch or to leave according to the prey richness of the patch. For example, pipistrelle bats (*Pipistrellus pipistrellus*) spent a greater proportion of their time foraging in higher-density patches and searched for less than 1 min when local prey densities were below a threshold value (Racey and Swift, 1985). In the case of air-breathing aquatic animals, time-depth recorders have been used to monitor their behaviour, as it is difficult to observe animals foraging underwater. As a result, time-based models have been developed, and empirical data have been used to test predictions derived from the models (Boyd et al., 1995; Carbone et al., 1996; Thompson and Fedak, 2001; Mori et al., 2002; Mori and Boyd, 2004). Longer transit times between the surface and the foraging depth are not beneficial in terms of time efficiency, but a longer transit time does allow birds to move horizontally. If they fail to locate prey, they can shorten the proportion of the dive spent at the bottom and ascend, keeping their body angle shallow in order to move horizontally so that they can reach a more profitable area for the following dive.

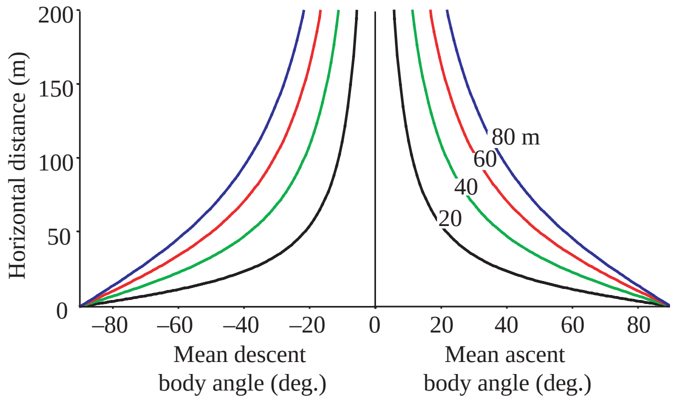

Fig. 7. The maximum horizontal distance (H) travelled during the descent and ascent, which is calculated from depth (D) and body angle (θ) using the equation $H=D/|\tan\theta|$. Colours of lines and values on lines represent the depth of bottom-phase start (descent) or end (ascent).

In conclusion, macaroni penguins modify the time spent at the bottom in accordance with the conditions, both physiological and environmental, that occur during the course of the bottom phase of the dive. If penguins encounter prey, they can prolong the bottom duration of the dive and then adopt steep body angles during the ascent, as they have depleted their oxygen stores and must return to the surface quickly to breathe. If they fail to locate prey on one dive, they can shorten the bottom duration and benefit from travelling horizontally for some distance before reaching the surface. Using increasing buoyancy during the ascent, gliding penguins can move horizontally with minimum stroking effort.

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