The Journal of Experimental Biology 205, 1189–1197 (2002)
Printed in Great Britain © The Company of Biologists Limited 2002
JEB3913

Buoyancy and maximal diving depth in penguins: do they control inhaling air volume?

Katsufumi Sato[1,*], Y. Naito[1], A. Kato[1], Y. Niizuma[2,3], Y. Watanuki[2], J. B. Charrassin[4], C.-A. Bost[5], Y. Handrich[5] and Y. Le Maho[5]

[1]*National Institute of Polar Research, 1-9-10 Kaga, Itabashi, Tokyo 173-8515, Japan,* [2]*Laboratory of Applied Zoology, Faculty of Agriculture, Hokkaido University, Kita-9, Nishi-9, Kita-ku, Sapporo 060-8589, Japan,* [3]*Japan Science and Technology Corporation, Domestic Research Fellow, Hokkaido National Fisheries Research Institute, Katsurakoi 116, Kushiro-shi 085-0820, Japan,* [4]*Laboratoire d'Océanographie Physique, Muséum National d'Histoire Naturelle, 43 rue Cuvier, 75231 Paris Cédex 05, France* and [5]*Centre d'Ecologie et Physiologie Energétiques, Centre National de la Recherche Scientifique, 23 rue Becquerel, 67087 Strasbourg Cédex, France*

*e-mail: ksato@nipr.ac.jp

Accepted 12 February 2002

Summary

Using a newly developed data logger to measure acceleration, we demonstrate that free-ranging king and Adélie penguins only beat their flippers substantially during the first part of descent or when they were presumed to be chasing prey at the bottom of dives. Flipper beating stopped during the latter part of ascent: at 29±9 % (mean ± S.D.) of dive depth (mean dive depth=136.8±145.1 m, *N*=425 dives) in king penguins, and at 52±20 % of dive depth (mean dive depth=72.9±70.5 m, *N*=664 dives) in Adélie penguins. Propulsive swim speeds of both species were approximately 2 m s^{-1} during dives; however, a marked increase in speed, up to approximately 2.9 m s^{-1}, sometimes occurred in king penguins during the passive ascending periods. During the prolonged ascending, oblique ascent angle and slowdown near the surface may represent one way to avoid the potential risk of decompression sickness. Biomechanical calculations for data from free-ranging king and Adélie penguins indicate that the air volume of the birds (respiratory system and plumage) can provide enough buoyancy for the passive ascent. When comparing the passive ascents for shallow and deep dives, there is a positive correlation between air volume and the depth of the dive. This suggests that penguins regulate their air volume to optimize the costs and benefits of buoyancy.

Key words: king penguin, *Aptenodytes patagonicus*, Adélie penguin, *Pygoscelis adeliae*, buoyancy, diving, dive depth, data logger, acceleration, biomechanics.

Introduction

Penguins are outstanding breath-hold divers. Despite their small body mass, Adélie penguins *Pygoscelis adeliae* (4–5 kg) dive up to 180 m depth and may remain submerged for 4 min (Naito et al., 1990; Watanuki et al., 1997) and king penguins *Aptenodytes patagonicus* (10–12 kg) dive to over 300 m and for up to 7 min (Kooyman et al., 1992). Particularly intriguing is the observation that penguins seem to dive on inspiration (Kooyman et al., 1971), which no doubt contributes to increasing oxygen stores but obviously increases buoyant resistance at shallow depths and risk of decompression sickness. Air in the body makes divers buoyant. Several studies have concluded that buoyant force is a major load for shallow diving birds (Dehner, 1946; Stephenson et al., 1989; Lovvorn et al., 1991; Lovvorn and Jones, 1991a,b; Wilson et al., 1992; Stephenson, 1994). Air volume in the body is difficult to measure in free diving animals. Stephenson (1994) measured buoyancy in unrestrained shallow diving birds in a tank. However, this method is impossible to use for deep-diving birds such as penguins. Furthermore, buoyancy should change with ambient pressure at each depth, and work against buoyancy is expected to vary throughout diving. Metabolic rate in the locomotory muscles, which affects oxygen store depletion, is indirectly dependent on swim speed and directly dependent on flipper stroke effort (Kooyman and Ponganis, 1998), but no method has been devised for measuring their flipper movements under natural conditions. Detailed studies on underwater movement of penguins have remained limited to observations of birds close to the sea surface (Kooyman et al., 1971) or in aquaria (Clark and Bemis, 1979).

For swimming penguins, the periodic alternation of up- and down-strokes of the flippers induce oscillations of the body. This involves acceleration and deceleration with each propulsive stroke (Clark and Bemis, 1979; Bannasch, 1995). To investigate the fine-scale movements of penguins in unrestrained dives under natural conditions, we developed an acceleration data logger (Yoda et al., 1999). Propulsive beating of the flippers, depth and swim speed were recorded every second from Adélie and king penguins diving at sea. Using these data, we first determined some diving characteristics of penguins, especially of their flipper movements. Secondly, air volume in the body was estimated for each dive of Adélie and king penguins using a biomechanical model. Finally, the results are discussed in terms of biomechanical and physiological constraints on optimal diving strategies.

Materials and methods

Data loggers

The detailed behaviors of penguins were monitored using a data logger with 8-bit resolution that recorded depth and acceleration once every second (NIPR-400D2G: 42.7 g, 19 mm diameter, 90 mm length; Little Leonardo, Tokyo, Japan). Depth resolution was 1.56 m. The logger has a piezo-resistive accelerometer (Model 3031, IC Sensors) with filtering of the analog sensor signal by a band-pass filter of 0.53–64 Hz. The amplitude of accelerations was stored as an integrated value during the sampling interval of 1 s. The measuring range of the device was 0–11.8 m s^{-2}. The logger was attached to the back of a penguin to record the deceleration component of movements together with the long axis of the body. According to our investigations in aquaria using the acceleration data logger attached to captive penguins, the measured deceleration of gliding birds is lower than 0.098 m s^{-2}; we used this value to define the threshold for cessation of flipper beating.

Swim speed and depth were measured using a 12-bit resolution speed/depth/temperature (PDT) data logger (UWE-200PDT for Adélie: 59.2 g, 20 or 23 mm diameter at the thickest part, 120 mm length; KS-400PDT for king: 81.5 g, 25 or 32 mm diameter at the thickest part, 110 mm length; sampling interval 1 s; Little Leonardo, Tokyo, Japan). The depth ranges were 0–200 m (resolution 0.05 m, for UWE-200PDT) or 0–400 m (resolution 0.1 m, for KS-400PDT). Any recorded pressure values exceeding 2 m in depth were considered to constitute a dive. Maximum depth during a dive was represented as a dive depth. Swim speed was measured by counting the revolutions of a propeller (RPS; revs s^{-1}) and converting to speed using depth *versus* RPS calibration data collected from the same animals (see Blackwell et al., 1999; Yoda et al., 1999). The calibration lines were obtained from each logger with coefficients of determination higher than 0.97 within a speed range of 1.2–2.8 m s^{-1} for two king penguins and 0.6–2.2 m s^{-1} for two Adélie penguins. RPS values were not converted to speed when they were lower than the stall RPS (0.3 m s^{-1}) of the instrument, as determined experimentally.

Field experiments

The studies were carried out on Possession Island (46.4 °S, 51.8 °E, Crozet Archipelago) during part of the breeding season of king penguin *Aptenodytes patagonicu* (Miller) (February–March, 1996) and on Ile des Pétrels, Dumont d'Urville station, Adélie Land (66.7 °S, 140.0 °E) during the Adélie penguin *Pygoscelis adeliae* (Hombron and Jacquinot) breeding season (December, 1996–February, 1997).

The loggers were attached caudally to the back to minimize drag (Bannasch et al., 1994; Culik et al., 1994a), using plastic cable ties and adhesive at Dumont d'Urville and Tesa tape at Crozet. On removal of the loggers, the cable ties and tape were also removed from the birds. The remaining adhesive would fall off with the feathers at molt. Five king penguins were equipped with both PDT and D2G loggers, of which two sets were recovered with reliable data (see Ropert-Coudert et al., 2000 for detailed information). Seven Adélie penguins were equipped with D2G loggers, and other three birds were equipped with both PDT and D2G loggers. Adélie penguins were caught following their return from foraging trips, and the loggers were retrieved (see Yoda et al., 1999, for detailed information).

Biomechanical model

The data obtained from free-ranging penguins were analyzed using a biomechanical model, which was modified from a model used for flying birds (Azuma, 1997). Three forces act on an ascending, gliding penguin when flipper beating has ceased (Fig. 1). At ascent angle θ, changes in speed U along the swimming path are determined by the difference between the drag F_D and the component of the buoyancy F_B parallel to the path of swimming ($F_B\sin\theta$) (Fig. 1). Changes in ascent angle θ are determined by the difference between the downward lift F_L and the component of the buoyancy F_B perpendicular to the path of swimming ($F_B\cos\theta$) (Fig. 1). These relationships are described by the following equations.

$$m\left(\frac{\mathrm{d}U}{\mathrm{d}t}\right) = F_B\sin\theta - F_D\,, \tag{1}$$

and

$$mU\left(\frac{\mathrm{d}\theta}{\mathrm{d}t}\right) = F_B\cos\theta - F_L\,, \tag{2}$$

where m is the measured body mass (kg) of the birds and t is the time (s). The added mass (Daniel, 1984; Vogel, 1994) was not included with the body mass, assuming a quasi-steady flow around the gliding penguin, in which swimming motions are absent and changes in speed are not abrupt. The ascent angle θ was calculated from measured swim speed and vertical speed, the latter variable being calculated from the rate of change of depth. In model calculations, buoyancy F_B was adjusted for the compression of air spaces with depth using the following equation, which is modified from Wilson et al. (1992):

$$F_B = \boldsymbol{g}\left\{\rho_w\left[\frac{m}{\rho_t} + \frac{V_{a0}(P_S + \rho_w\boldsymbol{g}D_0)}{P_S + \rho_w\boldsymbol{g}D}\right] - m\right\}\,, \tag{3}$$

where $\boldsymbol{g}$ is the gravitational constant (9.807 m s^{-2}), ρ_w is the density of the sea water (1.027×10^3 kg m^{-3} at 10 °C; Kooyman, 1989), ρ_t is the density of penguin body tissue (1.02×10^3 kg m^{-3}; Wilson et al., 1992), V_{a0} is the initial air

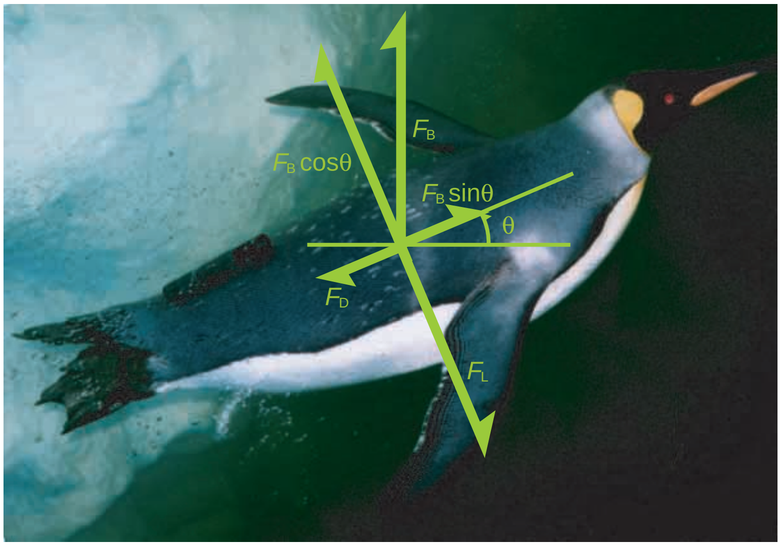

Fig. 1 Schematic diagram showing ascending angle (θ), buoyancy (F_B), drag (F_D) and downward lift (F_L) acting on an ascending, gliding king penguin with a data logger attached. This photograph was taken at an aquarium.

volume (m^3) kept in the respiratory system and trapped in feathers at depth D_0, the point at which the penguins cease flipper beating, P_s is atmospheric pressure at the surface (1.013×10^5 Pa; 1 atm) and D is depth. The total drag F_D increases with speed and was calculated using following equation:

$$F_D = \frac{1}{2}(\rho_w S U^2 C_D) + \frac{1}{2}\left[\rho_w S_w U^2 \left(\frac{{C_L}^2}{\pi A\!\!R}\right)\right], \qquad (4)$$

where S is a reference area and C_D is the drag coefficient. In the model calculation, the estimated wetted surface area ($0.3269\,m^2$) and C_D (0.003; Clark and Bemis, 1979) are used for king penguins. For Adélie penguins, we used $C_D=0.0368$ (Culik et al., 1994b) and the cross-sectional area of the body at its widest point, which was calculated from the measured girth of each bird. The first term on the right in equation 4 is the drag, including the parasite drag of the body and the profile drag of the wings. The drag coefficients C_D of both species were derived from decelerative gliding or swim canal measurements using living penguins (Clark and Bemis, 1979; Culik et al., 1994b). In the model calculation, C_D was assumed to be constant (discussed below). The second term on the right is the induced drag, which arises when the wings produce lift. Downward lift F_L was assumed to be generated by the outstretched flippers at negative angle of attack. Lift on the body itself was not considered. When S_W is taken to be the wing area ($8.71\times10^{-3}\,m^2$ for Adélie, $20.28\times10^{-3}\,m^2$ for king; Osa, 1994), C_L the lift coefficient, which varies with angle of attack of the flipper, and $A\!\!R$ the effective aspect ratio (7.28 for Adélie, 9.66 for king; Osa, 1994), the downward lift F_L was calculated using the equation:

$$F_L = \frac{1}{2}(\rho_w S_w U^2 C_L)\,. \qquad (5)$$

Substituting each force (F_B, F_D, F_L) in equations 1 and 2 by equations 3–5, respectively, gives two equations with two unknown variables, U and C_L. The model simulation was conducted for each dive under several values of initial air volume V_{a0}. The simulated speeds were then compared with measured speed to select an appropriate value of the initial air volume for each dive.

Results are presented as means ± S.D. Correlations between variables were tested using the Spearman rank correlation coefficient. Results were considered significant at $P<0.05$.

Results

The equipped king penguins conducted multiple deep dives with mean dive depth being 50.3±76.4 m (N=1428 dives, 2 birds) and maximum dive depths being 283.8 m for the 9.7 kg bird and 318.4 m for the 11.5 kg bird. Mean dive duration was 144.0±126.2 s (N=1428 dives, 2 birds) and maximum dive durations were 449 s for the 9.7 kg bird and 453 s for the 11.5 kg bird. Adélie penguins had a mean mass of 4.6 kg (10 birds; range 4.0–5.1 kg). The total number of dives recorded was 4067. Mean dive depth was 37.3±32.0 m and maximum dive depth for each bird varied from 65.6 m for a 4.0 kg bird to 145.9 m for a 4.8 kg bird. Mean dive duration was 80.7±46.6 s and maximum dive duration varied from 121 s for a 4.2 kg bird to 206 s for a 4.5 kg bird.

According to the acceleration data, flipper movements were substantial during the early descent in every dive made by the penguins (Fig. 2). However, birds stopped beating their flippers during the final stages of the ascent (Fig. 2). Although there was apparently some active propulsion in the late ascent of some dives, which could be attributed to pursuit of prey, all penguins exhibited cessation of flipper beating during the ascent (N=664 dives, 10 Adélies; N=425 dives, 2 kings). The depth at which this occurred differed between dives and individuals. Fig. 2A illustrates the V-shaped dives of an Adélie penguin, which stopped beating its flippers at a depth of 50 m after having descended to approximately 120 m. Fig. 2B shows a second Adélie penguin that stopped beating its flippers at around 30 m depth, i.e. close to the bottom of its trapezoid-shaped dives. The mean depth at which Adélie penguins stopped beating their flippers corresponded to an average of 52±20 % of the dive depth (10 birds, 664 dives, mean dive depth=72.9±70.5 m). Fig. 2C shows dives of a king penguin. King penguins stopped beating their flippers at an average of 29±9 % of dive depth (2 birds, 425 dives, mean dive depth=136.8±145.1 m). Fig. 3 shows the relationships between dive depth and the depth of flipper beat cessation. The ten Adélie penguins tended to cease their flipper beating closer to the dive bottom than did the two king penguins (Fig. 3A). The depths of flipper beat cessation expressed as a percentage of dive depth were significantly, but weakly, related to dive depth in both Adélie (Spearman r=–0.08,

$P<0.05$) and king penguins (Spearman $r=–0.46$, $P<0.0001$) (Fig. 3B).

The propulsive swim speeds of king and Adélie penguins were about 2 m s^{-1} during dives. For all deep dives (i.e. over 50 m depth; $N=181$ dives) of the king penguin, a marked increase in speed, up to approx. 2.9 m s^{-1} in the most extreme case, occurred after flipper beating stopped (Fig. 2C). This increase in speed occurred for both king penguins (2 birds, 317 dives). In case of another king penguin, where acceleration data were not obtained because the memory of D2G logger was full, the depths at which the bird ceased flipper beating were determined from the increase in swim speed. When Adélie penguins stopped beating their flippers their speed also sometimes increased (26 times in 1454 dives), but less markedly than for king penguins. In the most extreme case, swim speed increased from 1.8 to 2.3 m s^{-1}.

The model simulation analysis was conducted for the

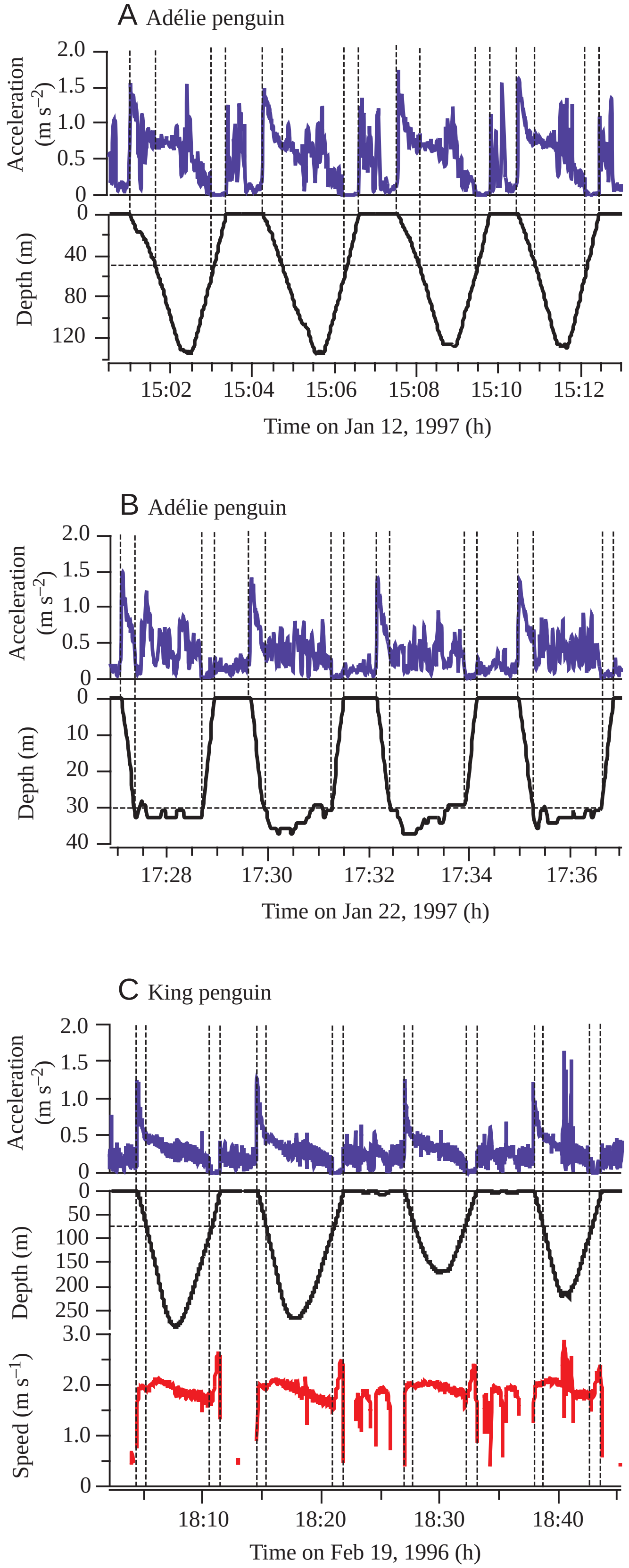

Fig. 2. Flipper beating (blue line) and dive profile (black line) for two Adélie penguins (A,B) and a king penguin (C). Swim speed is shown as a red line in C.

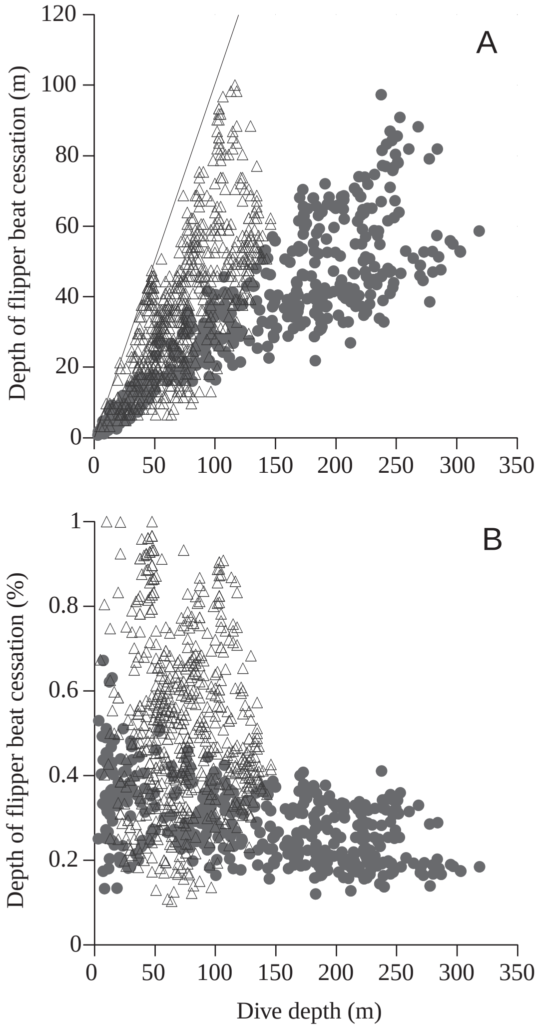

Fig. 3. Relationships between dive depth and depth of flipper beat cessation in two king penguins (filled circles) and ten Adélie penguins (open triangles). Depths of flipper beat cessation are plotted as absolute depth (A) and as a percentage of dive depth (B).

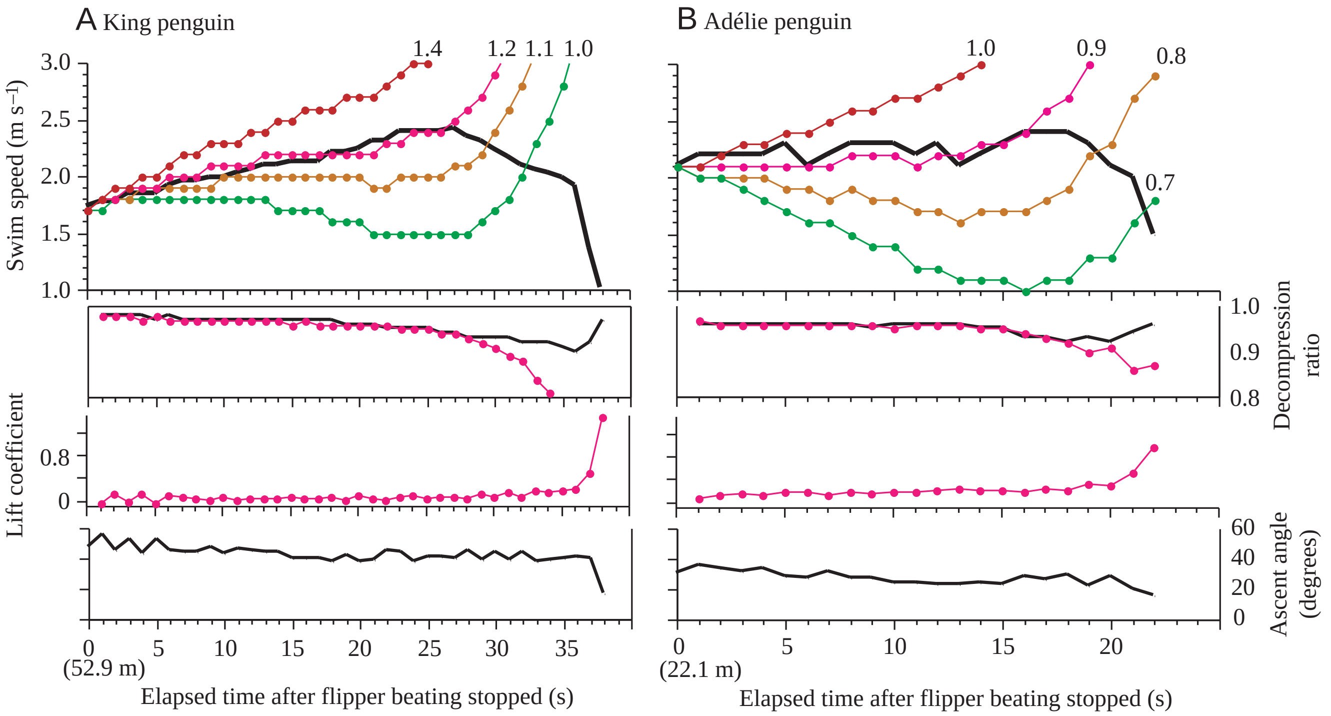

Fig. 4. Relationship between measured speed (thick black line) and simulated speed (colored dots and lines) during the passive ascent periods of a king penguin (A) and an Adélie penguin (B). Values beside the lines are air volume (l) that might be kept by birds ascending passively (1 atm) used in the model simulation. Measured decompression ratio and ascent angles are shown as thick black lines. Simulated decompression ratios and lift coefficients are also shown (colored dots and lines), assuming that each bird had 1.2 (A) or 0.9 litres (B) of air (1 atm). The depths at which the birds stopped flipper beating are indicated.

passive ascent periods of two king penguins and two Adélie penguins, from which a reliable swim speed was recorded. An example of the simulation results for a king penguin is shown in Fig. 4A. The simulated speed under the condition of V_{a0}=0.2 l initial air volume at 52.9 m depth (6.3 atm; 1 atm=1.013×10^5 Pa), when the bird stopped flipper beating, accords well with the measured speed (Fig. 4A). The initial air volume V_{a0} is the equivalent of 1.2 l at the surface (1 atm). It indicates that the king penguin could ascend passively if 1.2 l (1 atm) of air was retained in the body. Indeed, the simulated speed fits well with the measured speed in every dive, except for the final part of the ascent. Here, the simulated speed becomes much higher than the measured speed. The measured decompression ratio (P_t/P_{t-1}; the ambient pressure at time *t* divided by the pressure 1 s before) never went lower than 0.8 in any dive of either species. But simulated decompressions are rapid near the surface because of the increase in simulated swim speed (Fig. 4). Calculated lift coefficients C_L were nearly constant throughout the passive ascent periods in both species, except for the final parts (Fig. 4). Fig. 4B is one example of the model simulations for an Adélie penguin. An appropriate value of the initial air volume is the equivalent of 0.9 l at the sea surface (1 atm) for the dive in question (Fig. 4B), with the model simulation indicating that the bird could ascend passively if 0.9 l (1 atm) of air was kept in the body.

The air volumes kept by penguins were estimated for each dive (*N*=74 dives, 2 king penguins; *N*=40 dives, 2 Adélie

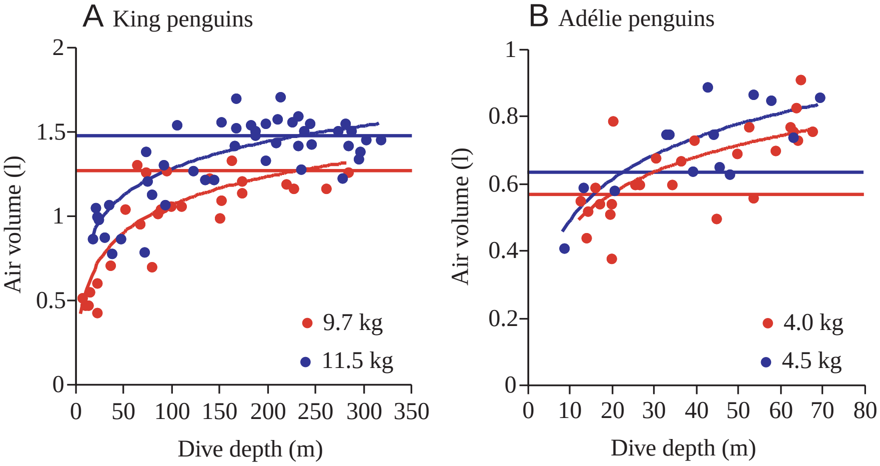

Fig. 5. Relationship between dive depth and estimated air volume of two king penguins (A) and two Adélie penguins (B). Horizontal lines, calculated from body mass using a equation in Lasiewski and Calder (1971), indicate the expected air volumes of the respiratory system for each penguin.

Table 1. *Relationships between dive depth and estimated air volume*

Bird	Body mass (kg)	Spearman *r*	*N*	*P*
King PF141	9.7	0.718	28	<0.001
King PF161	11.5	0.604	46	<0.0001
Adélie S10	4.0	0.738	26	<0.001
Adélie S15	4.5	0.594	14	<0.05

penguins). Their estimated air volumes range from 0.43 to 1.71 l for king penguins and from 0.38 to 0.91 l for Adélie penguins, respectively. There are significant positive relationships ($P<0.05$) between dive depth and the estimated air volume for each bird (Fig. 5, Table 1).

Discussion

Wing beat and passive ascending

The initial vigorous flipper beating of descending penguins demonstrates hard work against positive buoyancy at shallow depths. Conversely, cessation of flipper beating during the latter part of ascent indicates that penguins then ascend passively. Thus, diving behavior is clearly affected by buoyancy. Buoyancy can act as a resistance to downward movement but contributes to save energy when ascending. Swimming penguins glide between strokes to reduce drag costs (Clark and Bemis, 1979) because drag associated with thrust motion is several times greater than would be expected for the gliding phase (Lighthill, 1971). A passive ascent with prolonged gliding could be expected to reduce drag costs.

A passive ascent has been observed in shallow-diving birds such as the great cormorant *Phalacrocorax c. carbo*, canvasback *Aythya valisineria*, lesser scaup *Aythya affinis* and ruddy duck *Oxyura jamaicensis* (Ross, 1976; Tome and Wrubleski, 1988; Stephenson et al., 1989; Lovvorn, 1994). Lovvorn et al. (1999) assumed in their model that guillemots *Uria lomvia* would stop upward swimming to minimize total cost. Wilson and Wilson (1995) suspected that African penguins *Spheniscus demersus* may partly surface passively because of the increase in their measured swim speed. However, there has been no direct measurement of flipper movement in deep-diving penguins under natural conditions. The present study is a first report of extended periods of gliding in ascending penguins.

Slowdown near the surface

The propulsive swim speed was approximately 2 m s^{-1} during dives, independent of dive depth and species. This is consistent with the speed of king penguins measured using another type of data logger (Kooyman et al., 1992), and accords well with the optimal speed for minimum cost of transport found in each species (1.8–2.2 m s^{-1} for king, Culik et al., 1996; 1.7–2.3 m s^{-1} for Adélie, Culik and Wilson, 1991). When ascending, both penguins stopped beating their flippers and swim speed sometimes increased beyond the optimal speed.

Biomechanical calculations, together with data obtained from free-ranging penguins, yield important insights into the movements of these birds during the passive ascent periods. The model simulations indicate that the passive ascent of penguins can be attributed to increased buoyancy from the expanding air volume in the body. From Fig. 4A, the simulated speed matches the measured speed up to 27 s, after which it becomes much higher than the measured speed. Similar results were obtained from all other simulations in both species. The discrepancy suggests that the penguins actually decelerated speed by some means, possibly correlated to an increase in the profile drag of the flippers or parasite drag of the body. Fig. 4 indicates that the calculated lift coefficients suddenly increase during the final part of ascent, suggesting that penguins might increase the attack angle of their flippers, and thus increase the profile drag coefficient (Vogel, 1994). Except for the final part, lift coefficients were nearly constant throughout the ascent (Fig. 4), supporting the assumption that the drag coefficient (including profile drag) remains constant during most of the passive ascent. Penguins could also increase the parasite drag of the body. As has been observed for an emperor penguin *Aptenodytes forsteri* coming to the surface, the feet can be turned down into the normal standing posture to act as a brake (Kooyman et al., 1971). Penguins might also reduce speed by exhaling the air to decrease buoyancy, as can be seen in a photograph of a surfacing Adélie penguin (Kooyman, 1975).

Oblique ascent angle

Ascent angles were not vertical and became shallower the closer the bird was to the surface (Fig. 4). According to equation 2, ascent angle is affected by buoyancy and downward lift. Penguins can control the ascent angle *via* the lift coefficient mediated by the attack angle of their flippers. If penguins kept the ascent angle steep and did not brake near the surface, then buoyancy would take them rapidly to the surface without flipper stroke effort. For example, the king penguin in Fig. 4A could reduce the 38 s ascent duration by 13 s by ascending vertically. Therefore, the oblique ascent angle and braking near the surface seem to be energetically expensive and do not accord with optimal diving theory predicting that animals maximize the proportion of time spent at the foraging depth (Kramer, 1988; Ydenberg and Clark, 1989). Why then might the birds delay a prompt return to the surface?

Wilson et al. (1996) hypothesized that an oblique ascent angle allows the birds to search both the vertical and horizontal components of the water column. Results showing that ascent angles during feeding dives were greater than during non-feeding dives in Adélie penguins support the searching hypothesis (Ropert-Coudert et al., 2001b). However, the ascent angles became shallower nearer to the surface (Ropert-Coudert et al., 2001b), where the probability of prey acquisition should be low because ingestion events (detected as abrupt decreases in oesophageal temperature) were mostly observed at depths greater than than 40 m (Ropert-Coudert et al., 2001a). Hence, it seems unlikely that searching for prey can explain the oblique ascent angle.

Table 2. *Magnitude and distribution of oxygen stores in penguins*

Bird	Respiratory volume ($ml\,kg^{-1}$)	Total body oxygen ($ml\,O_2\,kg^{-1}$)	Respiratory system (%)	Blood (%)	Muscle (%)	Measuring condition	Source
King penguin	69*	45	23	30	47	Restrained	Ponganis et al. (1999)
King penguin	125*	54	35	25	40	Free-ranging	Present study
Adélie penguin	165*	55	45	29	26	Restrained	Kooyman et al. (1973), Kooyman and Ponganis (1998)
Adélie penguin	200*	61	50	26	24	Free-ranging	Present study

*No correction for air in feathers. Kooyman et al. (1973) demonstrated that plumage air of restrained Adélie penguins was not more than 10 % of the total air volume.

There may be physiological reasons why the penguins delay their ascent time. Seals are known to exhale air before diving, and the free-swimming Weddell seal *Leptonychotes weddellii* protects itself from nitrogen narcosis and decompression sickness by limiting blood nitrogen uptake through alveolar collapse (Falke et al., 1985), but how deep-diving birds avoid the bends is not clear (Kooyman and Ponganis, 1997). The bird's lung may not collapse during a dive; blood nitrogen tensions in Adélie penguins during simulated dives to 68 m rose to levels that were borderline for decompression sickness (Kooyman et al., 1973), leading the authors to suggest that shallow-diving penguins such as Adélies and gentoos *Pygoscelis papua* avoid the risk of elevated partial pressure of dissolved nitrogen by making short, shallow dives. Ponganis et al. (1999) suggested that king penguins have adapted to deep diving by reducing their respiratory air volume compared to that in shallow-diving penguins. Indeed, the measured air volume (69 $ml\,kg^{-1}$; Ponganis et al., 1999), including respiratory and plumage air, of restrained king penguins during simulated dives of up to 136 m was much smaller than in shallow-diving Adélie penguins of similar body size (165 $ml\,kg^{-1}$; Kooyman et al., 1973). Similarly we found that the maximum mass-specific total air volume (125 $ml\,kg^{-1}$; calculated from Fig. 5A) of king penguins was smaller than that of Adélie penguins (200 $ml\,kg^{-1}$; calculated from Fig. 5B). It is still unclear how these birds avoid the risk of decompression sickness, because free-ranging king penguins frequently repeat dives that are deeper and longer than the simulated dives of 136 m depth. As indicated by Kooyman et al. (1973), use of short and shallow dives only may not completely avoid the hazards of inert gas absorption in Adélie penguins. It is known that symptoms characteristic of decompression sickness can occur in man even after repetitive breath-hold dives of short duration to shallow (15–20 m) depths (Paulev, 1965).

Thus, there still seems to be a potential risk of decompression sickness in free-ranging Adélie and king penguins. Fig. 4 shows that measured decompression was actually kept moderate because birds actively reduced their rate of change of depth. Therefore, the oblique ascent angle and slowdown near the surface could be one way to avoid potential decompression sickness; other hypothetical mechanisms include a reduced cardiac output or a pressure-induced restriction of pulmonary gas exchange (Ponganis et al., 1999), although there is no evidence to conclusively support any of these hypotheses at present.

Air volume in the body

Whether animals dive on inspiration or expiration is important because buoyant resistance is determined by the total air volume kept in the body. However, air volume is difficult to measure in freely diving birds in the laboratory (Stephenson, 1995), and no methods have been devised for measuring them in the field (Lovvorn et al., 1999). Stephenson (1994) first measured buoyancy in unrestrained shallow-diving lesser scaup *Aythya affinis*, using a 1.52 m deep tank. However, the same method is impossible to use for deep-diving birds such as penguins. In the present study we therefore estimated the total air volume (including respiratory system and feathers) using data on depth, speed and acceleration, these being the first data obtained from free-ranging penguins. The air volume of the respiratory system was calculated to be 0.57 and 0.63 l for 4.0 kg and 4.5 kg Adélie penguins, respectively, and 1.27 and 1.48 l for 9.7 kg and 11.5 kg king penguins, respectively, using the analysis of Lasiewski and Calder (1971). The estimated total air volume for each species was similar to the expected respiratory volumes for diving birds (Fig. 5), which suggests that the biomechanical simulations yield good estimates of respiratory air volume in the birds, although we did not have direct data of the amount of air present in the feathers.

Ponganis et al. (1999) calculated the distribution of oxygen stores in king penguins (Table 2) using their relatively small air volume of 69 $ml\,O_2\,kg^{-1}$, which was measured from restrained king penguins during simulated dives of up to 136 m. Kooyman and Ponganis (1998) calculated the distribution in Adélie penguins (Table 2), assuming that they had a respiratory volume of 165 $ml\,O_2\,kg^{-1}$ (Kooyman et al., 1973). In the present study, maximum air volume for each species was larger than in previous reports. Assuming that our estimated air volumes (125 $ml\,kg^{-1}$ for king; 200 $ml\,kg^{-1}$ for Adélie) represent their respiratory volumes, the total body oxygen and the distribution of oxygen stores are modified as shown in Table 2. These are maximum values for the respiratory oxygen stored when the birds carry the maximum air volume in their respiratory system. As noted by Ponganis et al. (1999) and Stephenson (1995), the air volume becomes greater during unrestrained conditions. To improve the accuracy of this approach, more research is required into several variables, including (1) the air volume trapped in the feathers; (2) the tidal volume for each species; (3) the anatomical volume of the respiratory system of penguins; (4) the amount of air lost from the respiratory system and plumage during dives.

Regulation of air volume

The positive relationship between dive depth and estimated air volume during the late phase of ascending in both species (Fig. 5) implies that penguins control their air volume. This could be acheived by alterations in inhaled air volume and in the volume of air trapped in plumage. Stephenson (1995) found that the increasing relative influence of the air in the respiratory system on buoyancy was due to the loss of 47 % of the air in the plumage layer during a dive (1.5 m depth, 11.9 s mean duration). In the present study, air volume was estimated using data obtained during the latter part of the ascent. The air volume trapped in the plumage is unknown; however, the positive relationship between air volume and dive depth suggests that penguins might control their inhaled air volume according to their intended dive depth.

The air associated with the body makes diving birds buoyant, so many species must use considerable energy to swim against this buoyancy in order to remain submerged (Stephenson et al., 1989; Lovvorn and Jones, 1991a,b; Lovvorn et al., 1991; Wilson et al., 1992; Stephenson, 1994). Some flying birds such as cormorants and ducks have been observed to dive following expiration (Ross, 1976; Butler and Woakes, 1979; Tome and Wrubleski, 1988), so as to reduce buoyant resistance during dives. However, some penguins have been observed to dive on inspiration (Kooyman et al., 1971) and the present study partly supports this observation at least for deep dives (Fig. 5). The behavioral difference between flying birds and penguins could be attributed to differences in dive depth and in plumage air volumes (Wilson et al., 1992). Penguins generally dive much deeper than flying birds, which means that they spend much of the dive deeper than the critical depth at which air volume is so compressed that the buoyant force is negligible. Deep-diving penguins were not affected by buoyancy in the vicinity of the dive bottom, which explains why deep diving penguins inhale much air at the beginning of the dive. The lower estimated air volume during shallower dives (Fig. 5) further supports this idea. Here, penguins reduce the volume of air so as to avoid buoyant resistance during shallow dives.

Loggerhead turtles *Caretta caretta* adjust their residence depth to the depth of neutral buoyancy, which varies with the air volume in the respiratory system in order to minimize cost (Minamikawa et al., 1997, 2000). In the case of harbor porpoises *Phocoena phocoena*, the deeper the dive depth the faster the initial descent rate, which suggests that porpoises anticipate the depth to which they will dive before initiating the dive itself (Otani et al., 1998). The same pattern was found in penguins (see Wilson, 1995, for a review). Importantly, the present study indicates that penguins control their inhaled air volume according to the intended dive depth. This means that diving animals may adapt their diving strategy within their own biomechanical and physiological constraints.

We thank Y. Ropert-Coudert, G. Froget and the 1995/96 summer team in Crozet, and D. Rodary, W. Bonneau and the 1996/97 summer team in Dumont d’Urville French station, for their assistance in the field, T. Akamatsu, National Research Institute of Fisheries Engineering, for experiments to test the performance of the speed data loggers, and R. Wilson and two anonymous referees for reviewing the manuscript and their helpful suggestions. Aquarium investigations were done by permission of Tokyo Sea Life Park, Port of Nagoya Public Aquarium and Kamogawa Sea World. After approval by the ethics committee of the Institute Français pour la Recherche et la Technologie Polaires (IFRTP), this study was supported by grants from IFRTP, Centre National de la Recherche Scientifique (CNRS), Grants-in-Aid for International Scientific Research from the Ministry of Education, Science, Sports and Culture, and by the Japan Society for Promotion of the Science for Young Scientists. This study was conducted through the SIPENS (Sea Ice and Penguin Study) program.

References

Azuma, A. (1997). *Seibutsu no Ugoki no Jiten* (in Japanese). Tokyo: Asakura Syoten. 266pp.

Bannasch, R., Wilson, R. P. and Culik, B. (1994). Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J. Exp. Biol.* **194**, 83–96.

Bannasch, R. (1995). Hydrodynamics of penguins – an experimental approach. In *The Penguins* (ed. P. Dann, I. Norman and P. Reilly), pp. 141–176. Sydney: Surrey Beatty & Sons.

Blackwell, S. B., Haverl, C. A., LeBoeuf, B. J. and Costa, D. P. (1999). A method for calibrating swim-speed recorders. *Mar. Mamm. Sci.* **15**, 894–905.

Butler, P. J. and Woakes, A. J. (1979). Changes in heart rate and respiratory frequency during natural behaviour of ducks, with particular reference to diving. *J. Exp. Biol.* **79**, 283–300.

Clark, B. D. and Bemis, W. (1979). Kinematics of swimming of penguins at the Detroit Zoo. *J. Zool., Lond.* **188**, 411–428.

Culik, B. M. and Wilson, R. P. (1991). Energetics of under-water swimming in Adélie penguins (*Pygoscelis adeliae*). *J. Comp. Physiol. B* **161**, 285–291.

Culik, B. M., Bannasch, R. and Wilson, R. P. (1994a). External devices on penguins: how important is shape? *Mar. Biol.* **118**, 353–357.

Culik, B. M., Pütz, K., Wilson, R. P., Allers, D., Lage, J., Bost, C. A. and Le Maho, Y. (1996). Diving energetics in king penguins (*Aptenodytes patagonicus*). *J. Exp. Biol.* **199**, 973–983.

Culik, B. M., Wilson, R. P. and Bannasch, R. (1994b). Underwater swimming at low energetic cost by Pygoscelid penguins. *J. Exp. Biol.* **197**, 65–78.

Daniel, T. L. (1984). Unsteady aspect of aquatic locomotion. *Amer. Zool*. **24**, 121–134.

Dehner, E. W. (1946). An analysis of buoyancy in surface-feeding and diving ducks. PhD thesis, Cornell University, Ithaca, NY, USA.

Falke, K., Hill, R. D., Qvist, J., Schneider, R. C., Guppy, M., Liggins, G. C., Hochachka, P. W., Elliott R. E. and Zapol, W. M. (1985). Seal lungs collapse during free diving: evidence from arterial nitrogen tensions. *Science* **229**, 556–558.

Kooyman, G. L. (1975). Behaviour and physiology of diving. In *The Biology of Penguins* (ed. B. Stonehouse), pp. 115–137. London: Macmillan.

Kooyman, G. L. (1989). *Diverse Divers.* Berlin: Springer-Verlag. 200pp.

Kooyman, G. L. and Ponganis, P. J. (1997). The challenges of diving to depth. *Am. Scientist*. **85**, 530–539.

Kooyman, G. L. and Ponganis, P. J. (1998). The physiological basis of diving to depth: birds and mammals. *Annu. Rev. Physiol*. **60**, 19–32.

Kooyman, G. L., Cherel, Y., Le Maho, Y., Croxall, J. P., Thorson, P. H., Ridoux, V. and Kooyman, C. A. (1992). Diving behavior and energetics during foraging cycles in king penguins. *Ecol. Monogr*. **62**, 143–163.

Kooyman, G. L., Drabek, C. M., Elsner, R. and Campbell, W. B. (1971). Diving behavior of the Emperor penguin, *Aptenodytes forsteri*. *Auk* **88**, 775–795.

Kooyman, G. L., Schroeder, J. P., Greene, D. G. and Smith, V. A. (1973). Gas exchange in penguins during simulated dives to 30 and 68 m. *Am. J. Physiol*. **225**, 1467–1471.

Kramer, D. L. (1988). The behavioral ecology of air breathing by aquatic animals. *Can. J. Zool.* **66**, 89–94.

Lasiewski, R. C. and Calder, W. A. (1971). A preliminary allometric analysis of respiratory variables in resting birds. *Respir. Physiol*. **11**, 152–166.

Lighthill, M. J. (1971). Large-amplitude elongated-body theory of fish locomotion. *Proc. R. Soc. Lond. B* **179**, 125–138.

Lovvorn, J. R. (1994). Biomechanics and foraging profitability: an approach to assessing trophic needs and impacts of diving ducks. *Hydrobiologia* **279/280**, 223–233.

Lovvorn, J. R. and Jones, D. R. (1991a). Effects of body size, body fat, and change in pressure with depth on buoyancy and costs of diving in ducks (*Aythya* spp.). *Can. J. Zool.* **69**, 2879–2887.

Lovvorn, J. R. and Jones, D. R. (1991b). Body mass, volume, and buoyancy of some aquatic birds, and their relation to locomotor strategies. *Can. J. Zool.* **69**, 2888–2892.

Lovvorn, J. R., Croll, D. A. and Liggins, G. A. (1999). Mechanical versus physiological determinants of swimming speeds in diving Brünnich's guillemots. *J. Exp. Biol.* **202**, 1741–1752.

Lovvorn, J. R., Jones, D. R. and Blake, R. W. (1991). Mechanics of underwater locomotion in diving ducks: drag, buoyancy and acceleration in a size gradient of species. *J. Exp. Biol.* **159**, 89–108.

Minamikawa, S., Naito, Y. and Uchida, I. (1997). Buoyancy control in diving behavior of the loggerhead turtle, *Caretta caretta*. *J. Ethol.* **15**, 109–118.

Minamikawa, S., Naito, Y., Sato, K., Matsuzawa, Y., Bando, T. and Sakamoto, W. (2000). Maintenance of neutral buoyancy by depth selection in the loggerhead turtle *Caretta caretta*. *J. Exp. Biol.* **203**, 2967–2975.

Naito, Y., Asaga, T. and Ohyama, Y. (1990). Diving behavior of Adélie penguins determined by time-depth recorder. *Condor.* **92**, 582–586.

Osa, Y. (1994). Study of functional morphology for swimming- and/or flying seabirds. PhD thesis, Tokyo Universiy of Fisheries, Tokyo.

Otani, S., Naito, Y., Kawamura, A., Kawasaki, M. and Kato, A. (1998). Diving behavior and performance of harbor porpoises, *Phocoena phocoena*, in Funka Bay, Hokkaido, Japan. *Mar. Mamm. Sci.* **14**, 209–220.

Paulev, P. (1965). Decompression sickness following repeated breath-hold dives. *J. Appl. Physiol.* **20**, 1028–1031.

Ponganis, P. J., Kooyman, G. L., van Dam, R. and Le Maho, Y. (1999). Physiological responses of king penguins during simulated diving to 136 m depth. *J. Exp. Biol.* **202**, 2819–2822.

Ropert-Coudert, Y., Sato, K., Kato, A., Charrassin, J.-B., Bost, C.-A., Le Maho, Y. and Naito, Y. (2000). Preliminary investigations of prey pursuit and capture by king penguins at sea. *Polar Biosci.* **13**, 101–112.

Ropert-Coudert, Y., Kato, A., Baudat, J., Bost, C.-A., Le Maho, Y. and Naito, Y. (2001a). Feeding strategies of free-ranging Adélie penguins *Pygoscelis adeliae* analysed by multiple data recording. *Polar Biol.* **24**, 460–466.

Ropert-Coudert, Y., Kato, A., Baudat, J., Bost, C.-A., Le Maho, Y. and Naito, Y. (2001b). Time/depth usage of Adélie penguins: an approach based on dive angles. *Polar Biol.* **24**, 467–470.

Ross, R. K. (1976). Notes on the behavior of captive Great Cormorants. *Wilson Bull.* **88**, 143–145.

Stephenson, R., Lovvorn, J. R., Heieis, M. R. A., Jones, D. R. and Blake, R. W. (1989). A hydromechanical estimate of the power requirements of diving and surface swimming in Lesser Scaup (*Aythya affinis*). *J. Exp. Biol.* **147**, 507–519.

Stephenson, R. (1994). Diving energetics in Lesser Scaup (*Aythyta affinis*, Eyton). *J. Exp. Biol.* **190**, 155–178.

Stephenson, R. (1995). Respiratory and plumage gas volumes in unrestrained diving ducks (*Aythya affinis*). *Respir. Physiol.* **100**, 129–137.

Tome, M. W. and Wrubleski, D. A. (1988). Underwater foraging behavior of Canvasbacks, Lesser Scaups, and Ruddy Ducks. *Condor* **90**, 168–172.

Vogel, S. (1994). *Life in Moving Fluids: The Physical Biology of Flow.* 2nd edition. Princeton: Princeton University Press. 467pp.

Watanuki, Y., Kato, A., Naito, Y., Robertson, G. and Robinson, S. (1997). Diving and foraging behaviour of Adélie penguins in areas with and without fast sea-ice. *Polar Biol.* **17**, 296–304.

Wilson, R. P. (1995). Foraging ecology. In *The Penguins* (ed. T. D. Williams), pp. 81–106. Oxford, New York and Tokyo: Oxford University Press.

Wilson, R. P., Hustler, K., Ryan, P. G., Burger, A. E. and Nöldeke, E. C. (1992). Diving birds in cold water: Do archimedes and boyle determine energetic costs? *Amer. Nat.* **140**, 179–200.

Wilson, R. P. and Wilson, M.-P. T. (1995). The foraging behaviour of the African penguin *Spheniscus demersus*. In *The Penguins* (ed. P. Dann, I. Norman and P. Reilly), pp. 244–265. Sydney: Surrey Beatty & Sons.

Wilson, R. P., Culik, B. M., Peters, G. and Bannasch, R. (1996). Diving behaviour of gentoo penguins, *Pygoscelis papua*; factors keeping dive profiles in shape. *Mar. Biol.* **126**, 153–162.

Ydenberg, R. C. and Clark, C. W. (1989). Aerobiosis and anaerobiosis during diving by Western Grebes: an optimal foraging approach. *J. theor. Biol.* **139**, 437–449.

Yoda, K., Sato, K., Niizuma, Y., Kurita, M., Bost, C.-A., Le Maho, Y. and Naito, Y. (1999). Precise monitoring of porpoising behaviour of Adélie penguins determined using acceleration data loggers. *J. Exp. Biol.* **202**, 3121–3126.