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S29-3 Evidence for regulation of air volume in the respiratory system of diving Adélie penguins, *Pygoscelis adelie*

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Abstract Penguins are outstanding divers. That they dive on inspiration is particularly intriguing because as it increases oxygen stores it also increases buoyancy. Buoyancy is a major factor determining the energetics of shallow diving birds, and there is a positive correlation between estimated air volume in the body (respiratory system and feathers) and the maximum depth in the dive of free-ranging penguins. However, it is not known whether variation in total air volume is caused by variation in the volume of air in the respiratory system or plumage. In the present study, underwater weights of restrained Adélie penguins *Pygoscelis adeliae* (*n*=27) were measured continuously. The birds lost much air from their feathers within 1–2 min of submergence. Maximum weights in the water were used to calculate the minimum air volumes that diving birds are expected to hold in the body. These volumes were compared with estimated air volumes from two free-ranging Adélie penguins. Most estimated values were larger than values in the restrained birds, which indicates that variation in total air volume is probably caused by variation in the air in the respiratory system. Penguins seem to adjust the volume of air inhaled to the maximum depths of their dives.

Key words Diving physiology, Buoyancy, Data logger, Biomechanics, Respiratory regulation

1 Introduction

Breath-holding diving birds must divide their time between obtaining two basic resources: oxygen at the surface and prey under water (Dunstone and O'Connor, 1979). When submerged, they must balance the energetic demands of movement with conservation of their limited oxygen store (Castellini et al., 1985). High levels of movement under water lead to shorter dives as oxygen reserves are depleted more rapidly. Several studies have shown that buoyancy 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). Buoyancy in birds is strongly affected by the volume of air in the respiratory system and plumage. 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). Yet penguins apparently dive on inspiration (Kooyman et al., 1971), which, although it enhances oxygen stores, also increases buoyancy. In 1971, however, no means had been devised for measuring either respiratory or plumage air volume in birds during natural, unrestrained dives (Lovvorn and Jones, 1991a).

Sato et al. (2002) used newly-developed acceleration data loggers on king (*Aptenodytes patagonicus*) and Adélie (*Pygoscelis adeliae*) penguins to monitor their flipper movements underwater. According to the data, the penguins flapped continuously as they descended, but after the first half of the re-ascent, stopped flipper beating and took advantage of natural buoyancy to glide back to the surface. Biomechanical calculations indicated that the air volume of the birds (respiratory system and feathers) could provide enough buoyancy for passive ascent.

Comparison of passive ascents from shallow and deep dives shows a positive correlation between estimated air volume and the maximum depth of the dive (Fig. 1). Sato et al. (2002) proposed that penguins inhale according to dive depth, reducing air volume so as to avoid buoyancy resistance during shallow dives. According to measurements of restrained penguins (Kooyman et al., 1973), it has been assumed that most of the air (more than 90 %) is held in the respiratory system (Sato et al., 2002). To date, however, it has not been shown definitively that air volume is actually adjusted in the respiratory system. To elucidate this, we conducted an additional experiment on Adélie penguins.

2 Materials and methods

The underwater weights of Adélie penguins were measured at Hukuro Cove (60°00'S, 39°39'E) south of Syowa station, Antarctica, during the 1999–2000 breeding season. Adult Adélie penguins ranging in body mass from 3.0 to 5.75 kg (*n* = 27 birds) were used. When penguins returned to nests from foraging trips, they were captured and caged in a penguin holder made of stainless steel mesh (Fig. 2). The head of the bird was covered with a mask of dark cloth to keep it calm, and the feet were fixed with the toes pointing down. Belts on the holder were used to restrain movements of the flippers, which were bound close to the body. Body weight (*Ma*) was first measured in air.

Then the bird was slowly submerged to eye-level in a tank filled with seawater, with care taken to ensure that ventilation was not impaired. Bird weight in seawater (*Mw*) was continuously measured to the nearest 5 g with a digital balance until the value equilibrated (Kansai Scale, KHS-7.5 kg). The bird could breathe through a hole at the top of the mask. Weight was attached to the holder to adjust the total weight of the system plus penguin in the water so that it was within the measuring range of the balance (from 0 to 7. 5 kg). The value displayed on the scale together with the appearance of the bird was recorded by a digital video camera (SONY DCR-PC1). After measurements were taken, all penguins were released near the breeding colony. They immediately returned to their own nests where normal interaction with their partners was observed. No birds abandoned their nests after the experiment.

After measurement, weight values were read every five seconds from the video records. Minimal and maximal values during the equilibrated period were used to calculate the total air volume in the body using following equation:

$$Va = (Ma - Mw)/\rho_w - Ma/\rho_t,$$

where *Va* is air volume in the penguin (m^3), *Ma* is the penguin weight in air (kg), *Mw* is the penguin weight in water (kg), ρ_w is sea water density (kg m^{-3}) which was measured using a hydrometer, and ρ_t is the density of penguin tissue ($= 1.02 \times 10^3$ (kg m^{-3})) (Wilson et al., 1992).

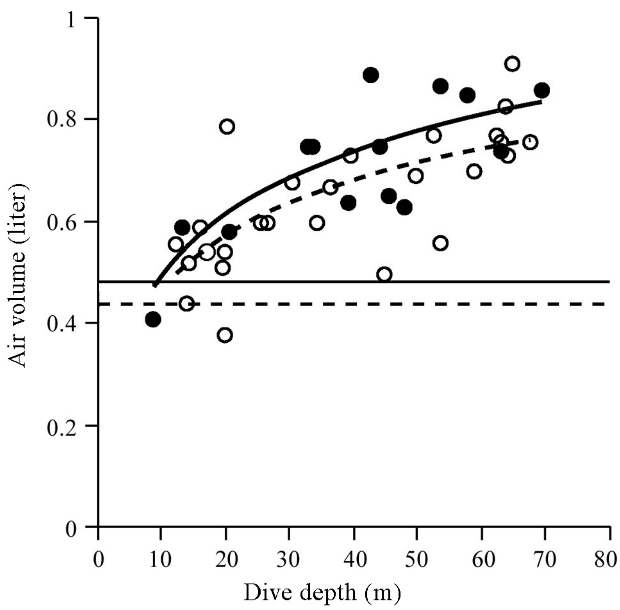

Fig. 1 Relationship between the maximum depths of dives and estimated air volume in the Adélie penguin
Open circles and dotted curve = 4.0 kg penguin; closed circles and solid curve = 4.5 kg penguin. Redrawn and modified from Sato et al. (2002). Horizontal lines are calculated minimum air volumes for each bird (solid = 4.5 kg, dotted = 4.0 kg).

3 Results

Fig. 3 illustrates continuous measurement of the underwater weight of a penguin. Total weight in the water increased rapidly at first when small bubbles came from feathers (Fig. 3). After 1–2 min, the base line of the weight began to equilibrate. During the period when the total weight was being equilibrated, abrupt increases in weight were recorded several times (Fig. 3). The video recordings indicated that these increments corresponded to breathing; rapid exhalation and subsequent inhalation were separated by apneas. The mean frequency of breathing counted from video records ranged from 12.0 to 25.3 breaths/min ($n = 24$ birds). The minimum air volume, which was calculated from the maximum weight in the water, ranged from 337.0 to 593. 2 ml in the studied penguins (Fig. 4). The relationship between body weight in air *Ma* and minimum air volume *Va* was

$$Va = 87.3\,Ma + 86.0$$

$$(R^2 = 0.455, n = 27, F = 20.8, P < 0.0001)$$

The maximum air volume, which was calculated from the minimum weight in the water, varied above the regression line for the minimum air volume (Fig. 4).

4 Discussion

According to the underwater weight measurements (Fig. 3) and video observations, penguins lost much of the air in their plumage within 1–2 min of submergence. We consider that a diving penguin actively stroking with its flippers under natural conditions would lose almost all plumage air immediately. Kooyman (1973) demonstrated that air in plumage of restrained Adélie penguins was not more than

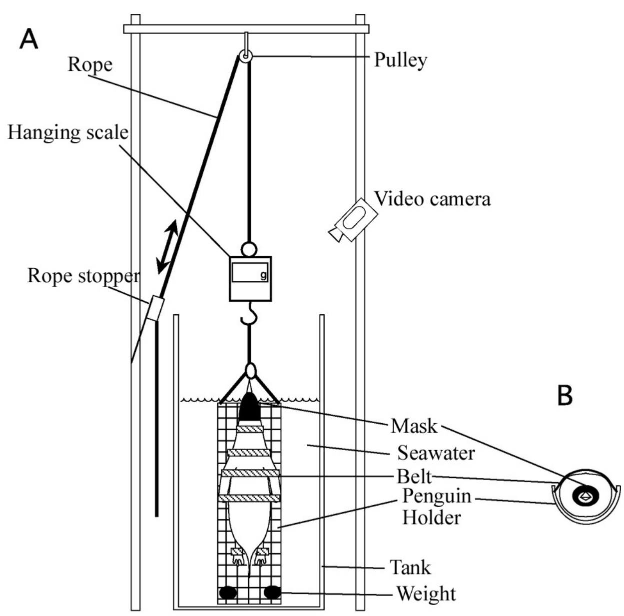

Fig. 2 Schematic diagram of construct for underwater mass measurements
A = side view, B = view from above.

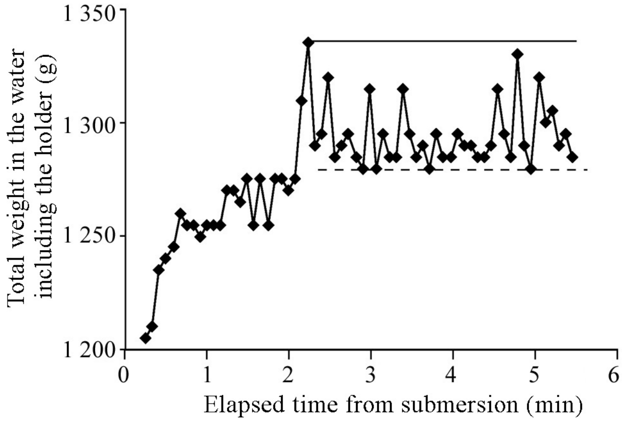

Fig. 3 Underwater weight measurements of an individual Adélie penguin
The solid horizontal line corresponds with maximum values and the dotted with minimum.

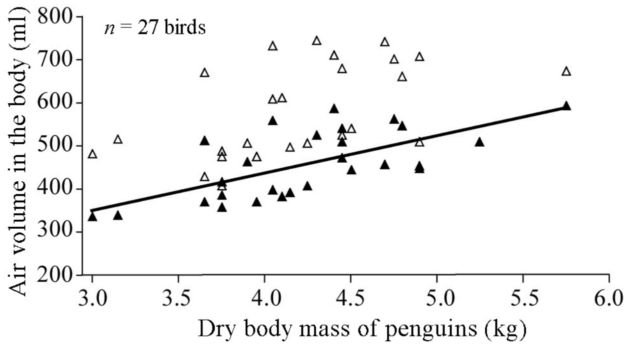

Fig. 4 Relationship between dry body weight and air volume
Minimum = closed triangles, maximum = open triangles. A regression line was calculated for minimum air volume.

10 % of the total air volume in the body, and Sato et al. (2002) assumed that most of the air (> 90%) at the end of dives would be in the respiratory system. This assumption seems acceptable under natural conditions.

The minimum air volume measured in our study incorporates both the air volume in the respiratory system and residual air in the plumage. The calculated minimum air volumes for two penguins (4.0 and 4.5 kg) are represented by horizontal lines in Fig. 1. Most estimated air volumes are larger than measured minimum volumes (Fig. 1), which indicates that variation above the lines was mainly caused by the variation in the air volume in the respiratory system. This means that the free-living penguins studied by Sato et al. (2002) are indeed likely to have adjusted their inhaled air volume in response to the depths of dives. We predict that when penguins make deep dives, they spend much of the dive time deeper than the critical depth at which air is so compressed that buoyancy is zero. They can therefore hold considerable amounts of air in their respiratory systems as oxygen stores. In contrast, shallow diving penguins reduce the volume of air in their respiratory system so as to avoid buoyancy. Biomechanical considerations, together with the data obtained from free-ranging penguins under natural conditions, indicates that penguins may adapt their diving strategy to their own biomechanical and physiological constraints.

If penguins indeed regulate inhaled air volume, how might this affect diving effort? To answer this question, swimming activity must be measured. Swim speed alone is a relatively poor indicator of aquatic effort, and may be inadequate for assessing energetic costs in diving animals because, in buoyant gliding penguins rising to the surface, it is sometimes faster than normal speed from flipper propulsion (approximately 2 m/s) (Sato et al., 2002). Although several studies have investigated the stroke pattern of diving birds (Clark and Bemis, 1979; Hui, 1988; Johansson and Aldrin, 2002), these experiments were conducted at shallow depths in aquaria, and it is unclear how reduced buoyancy at greater depths might affect force requirements (Johansson and Aldrin, 2002). This may yet be resolved by acceleration-measuring data loggers, which have already been used on a variety of free-ranging animals to monitor their behavior under natural conditions.

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