The minimum air volume kept in diving Adélie penguins: evidence for regulation of air volume in the respiratory system

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Abstract — Penguins are outstanding divers. Particularly intriguing is the observation that they seem to dive on inspiration, which contributes to increasing oxygen stores but which increases their buoyancy. It has been concluded that buoyancy is a major factor in 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 the variation in the total air volume is caused by the variation in the air volume in the respiratory system or in plumage. In the present study, underwater weights of restrained Adélie penguins Pygoscelis adeliae (n=27 birds) were continuously measured in a experimental tank. The birds lost much air from their feathers within 1–2 min of submergence. The maximum weights in the water were used to calculate the minimum air volumes that diving birds are expected to have in their body. These volumes were compared with estimated air volumes from two free-ranging Adélie penguins. Most estimated values of the free-ranging birds were larger than values from the restrained birds, which indicates that variation in the former air volume is likely caused by the 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: acceleration, buoyancy, data logger, biomechanics

Introduction

Breath-holding divers must divide their time into obtaining two important resources; oxygen located at the water surface and prey located at depth (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 exercise presumably lead to more rapid termination of dives as oxygen reserves are quickly depleted. Several studies have concluded that buoyancy is a major load for shallow-diving birds (Dehner 1946, Stephenson et al. 1989, Lovvorn et al. 1991, Lovvorn and Jones 1991ab, Wilson et al. 1992, Stephenson 1994). Buoyancy of 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). However, some penguins apparently dive on inspiration (Kooyman et al. 1971), which will enhance oxygen stores but increase buoyancy. Unfortunately, no means have 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 ascent, they stopped flipper beating, and took advantage of their natural buoyancy to glide back to the surface. Biomechanical calculations for data indicate that the air volume of the birds (respiratory system and feathers) can provide enough buoyancy for the passive ascent (Sato et al. 2002). Comparison of passive ascents for 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 less air volume reducing air volume so as to avoid buoyancy resistance during shallow dives and inhale much air volume increasing oxygen store in deep dives. According to the measurements of restrained penguins (Kooyman et al. 1973), it was assumed that most of their air (more than 90%) was kept in the respiratory system (Sato et al. 2002). However, to date, it has not been definitively shown that air volume is actually adjusted in the respiratory system. To elucidate whether the variation in the total air volume is caused by the variation in the air volume in the respiratory system or in plumage, we conducted an ad-
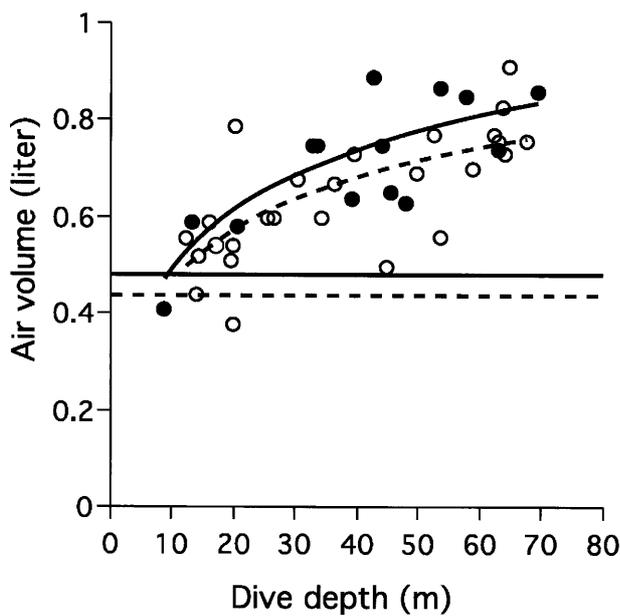
Fig. 1. Relationship between the maximum depths in dives and estimated air volume of a 4.0 kg penguin (open circles and a dotted curve) and a 4.5 kg penguin (closed circles and a solid curve). Redrawn and modified from Sato et al. (2002). Horizontal lines are calculated minimum air volumes for each bird (solid: 4.5 kg, dotted: 4.0 kg).

ditional experiment on Adélie penguins.

Materials and Methods

Underwater weights of Adélie penguins were measured at Hukuro Cove (60°00′S, 39°39′E) south of Syowa station in Antarctica during their breeding season from December 1999 to January 2000. Adult Adélie penguins ranging in body mass from 3.0 to 5.75 kg (n=27 birds) were used in the measurement. When penguins came back from foraging trips to their nests, they were captured using a hand net before feeding to their chicks. In each case, the penguins were attached to 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 the bird calm and the feet were fixed with the toes pointing down (Fig. 2). Belts on the holder were used to restrain movements of the flippers, which were pinned close to the body. At first, the body weight (Ma) was measured in air. Then the bird was slowly submerged in a tank filled with seawater up to eye level with care taken to ensure that ventilation was not impaired. Bird weight in seawater (Mw) was continuously measured to the nearest 5 g until the value equilibrated using a digital balance (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
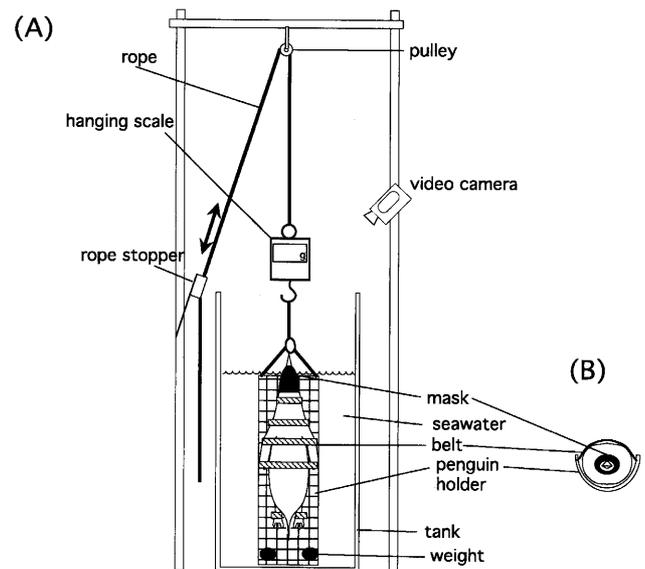

Fig. 2. Schematic diagram showing underwater mass measurements. (A) Side view and (B) view from above.

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 the measurements, 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;

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

where Va is air volume in penguin [m³], Ma is weight in air [kg], Mw is weight in water [kg], ρ_w is sea water density [kg m⁻³] which was measured using a hydrometer, ρ_t is density of penguin tissue ($=1.02\times10^3$ [kg m⁻³], Wilson et al. 1992).

Results

Figure 3 shows an example of the continuous measurement of the underwater weight of a bird. The total weight in the water increased rapidly at first when small bubbles came from feathers (indicated as a horizontal grey bar in Fig. 3). After 1–2 min, the base line of the weight seemed 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 separated by apneas. The mean frequency of breathing counted from video records ranged from 12.0 to 25.3 breaths/min (n=24 birds).
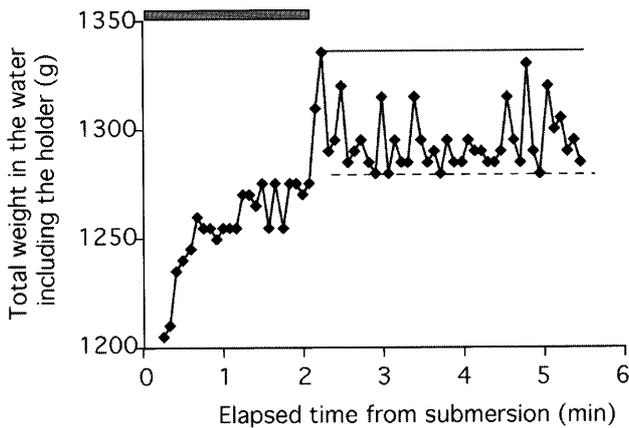
Fig. 3. An example of underwater weight measurements in one bird. A solid horizontal line corresponds with maximum and a dotted line corresponds with minimum values. Grey horizontal bar indicates duration when a penguin lost air in the plumage.
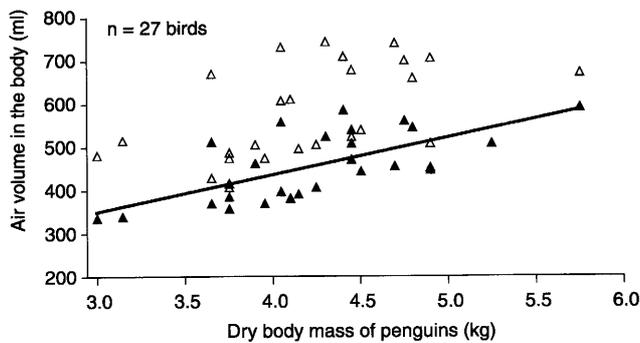

Fig. 4. Relationship between dry body weight and air volume (minimum: closed triangle, maximum: open triangle). A regression line was calculated for minimum air volume.

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 the body weight in air Ma and the minimum air volume Va was

$$Va = 87.3Ma + 86.0$$
$$(R^2 = 0.455, \quad n = 27, \quad F = 20.8, \quad P < 0.0001)$$

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).

Discussion

According to the underwater weight measurements (Fig. 3) and video observation, penguins apparently lost much air in their plumage within 1–2 min of submergence. We consider that a diving penguin actively stroking its flippers under natural conditions would lose most plumage air virtually immediately. Kooyman (1973) demonstrated that the plumage

air of restrained Adélie penguins was not more than 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 composed of both the air volume in the respiratory system and the residual plumage air volume. 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 the 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 maximum depths in dives rather than measured parameters having been due to plumage air volume or some other effect. We propose that when penguins make deep dives, they spend much of the dive time deeper than the critical depth at which the air is so compressed that the buoyancy is negligible. They can therefore have considerable amounts of air in their respiratory systems to increase their oxygen stores. Contrarily, shallow diving penguins reduce the volume of air in their respiratory system so as to avoid buoyancy. Biomechanical consideration, together with the data obtained from free-ranging penguins under natural condition, indicates that penguins may adapt their diving strategy to their own biomechanical and physiological constraints.

Acknowledgment

References

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.

Castellini, M. A., Murphy, B. J., Fedak, M. A., Ronald, K., Gofton, N. and Hochachka, P. W. 1985. Potentially conflicting metabolic demands of diving and exercise in seals. J. Appl. Physiol. 58: 392–399.

Dehner, E. W. 1946. An analysis of buoyancy in surface-feeding and diving ducks. Ph.D. thesis. Ithaca, NY: Cornell University.

Dunstone, N. and O'Connor, R. J. 1979. Optimal foraging in an amphibious mammal. I. The aqualung effect. Anim. Behav. 27: 1182–1194.

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.

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., 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.

Ross, R. K. 1976. Notes on the behavior of captive Great Cormorants. Wilson Bulletin 88: 143–145.

Sato, K., Naito, Y., Kato, A., Niizuma, Y., Watanuki, Y., Charrassin, J. B., Bost, C.-A., Handrich, Y. and Le Maho, Y. 2002. Buoyancy and maximal diving depth in penguins: do they control inhaling air volume? J. Exp. Biol. 205: 1189–1197.

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.

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

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.