DIFFERENTIAL AIR SAC PRESSURES IN DIVING TUFTED DUCKS *AYTHYA FULIGULA*

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Summary

The air in the respiratory system of diving birds contains a large proportion of the body oxygen stores, but it must be in the lungs for gas exchange with blood to occur. To test the hypothesis that locomotion induces mixing of air sac air with lung air during dives, we measured differential pressures between the interclavicular and posterior thoracic air sacs in five diving tufted ducks *Aythya fuligula*. The peak differential pressure between posterior thoracic and interclavicular air sacs, 0.49±0.13 kPa (mean ± S.D.), varied substantially during underwater paddling as indicated by gastrocnemius muscle activity. These data support the hypothesis that locomotion, perhaps through associated abdominal muscle activity, intermittently compresses the posterior air sacs more than the anterior ones. The result is differential pressure fluctuations that might induce the movement of air between air sacs and through the lungs during dives.

Key words: diving, air sac, avian respiratory system, air sac pressure, tufted duck, *Aythya fuligula*.

Introduction

There is evidence that aerobic metabolism is the major source of energy production during normal feeding dives in many aquatic birds (Butler and Jones, 1997). To accommodate that aerobic metabolism, diving birds must have large oxygen storage capacities as well as mechanisms to restrict oxygen delivery preferentially to those tissues most in need of it during the exercise of the diving bout (achieved through vasoconstriction in the skin and parts of the viscera; Bevan and Butler, 1992). Oxygen stores in diving species tend to be greater than those in their non-diving relatives, including a higher haemoglobin concentration in the blood, myoglobin concentration in the muscle and volume of the respiratory system. In both tufted ducks *A. fuligula*, (Keijer and Butler, 1982) and gentoo and Adélie penguins, *Pygoscelis papua* and *P. adeliae*, respectively (Kooyman *et al.* 1973), much of the total oxygen available during a dive is in the respiratory system (approximately 50 % in the tufted duck, 32 % in Adélie penguins; Culik *et al.* 1994). Air samples taken from the first exhalation upon surfacing in Humboldt penguins *Spheniscus humboldti* indicate that oxygen in the respiratory system had been used during the preceding dive and that carbon dioxide had been stored in the blood and tissues (as indicated by the low respiratory exchange ratio, Butler and Woakes, 1984).

Although tufted ducks (*Aythya fuligula*) exhale before diving, the effective volume of air in the respiratory system is in the range of measurements for various *Aythya* species of 0.165–0.335 l BTPS kg^{-1} (Dehner, 1946; Keijer and Butler, 1982; Stephenson *et al.* 1989; Stephenson, 1993, 1995). Much of that air resides in the air sacs, where gas exchange does not take place. This raises the question of whether birds move air from the air sacs across the gas-exchanging surfaces of the lung during dives. The possibility that limb movements might induce air flow through the lungs from the air sacs has been suggested (Eliassen, 1960; Butler, 1991), but no measurements have been made. Our objective in this study was to determine whether there are variations in differential pressure between the anterior and posterior air sacs in tufted ducks during a dive and, if so, whether they are associated with paddle strokes.

Materials and methods

Measurements were made on five young tufted ducks (*Aythya fuligula* L.), (mean mass ± S.D., 592±38 g) taken from a captive colony at the University of Birmingham.

All operative procedures were performed under halothane anaesthesia (2 % in 30 % oxygen, balance N$_2$). Catheters (PE 200 or silastic tubing; i.d. 1.6 mm, o.d. 3.18 mm) were implanted in the interclavicular air sac and the posterior thoracic air sac, and silver bipolar electrodes were implanted into the gastrocnemius and right abdominal muscles to record electromyograms (EMGs). Post-operative analgesia was provided by buprenorphine (Vetergesic 0.06 mg kg^{-1} intramuscularly), and all ducks received oxytetracycline dihydrate (LA, Pitman-Moore, 0.2 ml kg^{-1} intramuscularly).

After a recovery period of 1–4 days, the differential pressure between the posterior thoracic and interclavicular air sacs was measured by connecting the sac catheters to either side of a miniature piezoresistive differential pressure transducer (Endevco, model 8507C-2). Measurements were made, with the transducer either on the bird's back or connected to long (78 cm) tubes, during short (10–20 s) escape dives (see Butler and Jones, 1997) to an average depth of 0.5 m, while the bird was inactive on the water's surface, while it was swimming on the surface and while it was standing or walking on land. When the transducer was under water, the cold temperature of the water (11.8 °C) altered its sensitivity (there was a 6.3 % reduction in sensitivity per °C), but it was enclosed in silicone rubber and was unaffected by the water electrically. The temperature-induced alterations were corrected for by calibrating the transducer under water as well as out of the water. The EMG from the gastrocnemius muscle was used as an indicator of paddling and was recorded by connecting the EMG electrodes to a Grass P511 preamplifier *via* a miniature connector (Microtech, models GM2 and GF2) to a cable (Cooner Wire Co., NMUF-2/30-40462J). Abdominal muscle activity was only successfully measured in one diving duck and in two ducks during walking. The probability of cross talk between electromyographic recordings from the gastrocnemius and abdominal muscles was low. Boggs and Dial (1993) demonstrated within one muscle that electrodes of this type have to be more than 1 cm apart to avoid cross talk within a muscle. Thus, cross talk between electrodes in different muscles, approximately 4 cm apart, as in the current study, is most unlikely. Further reassurance on this point is derived from the asynchronous signals from ipsilateral abdominal and gastrocnemius muscles in the walking ducks.

The accuracy of the differential pressure measurements was tested in several ways. The same tubing used to connect the air sac catheters to the transducer was connected at one end to each port of the transducer and at the other end to an oscillating pressure generator that produced pressure changes of similar magnitude (0.2–0.6 kPa) and at similar frequencies (4–5 Hz) to those observed in the experimental situation. In this configuration, little or no differential pressure was observed in most cases. In the worst case, a small differential pressure of 0.004 kPa was recorded, which constitutes a 0.7–1.3 % error. Therefore, the transducer was well balanced and recorded zero differential pressure when it was at zero. Then 3 mm of fluid was introduced into one tube and the test was repeated. This introduced an apparent differential pressure of 0.06–0.08 kPa with a signal of 0.25–0.35 kPa applied to both tubes. These artefactual differential pressures are small compared with the differential pressures recorded during the experiments (of the order of 0.5 kPa), but nonetheless potentially introduce an error. We attempted to avoid this by either blowing or sucking out any fluid that might have accumulated in the catheters by condensation or capillary action prior to each diving bout. We also tested the effects of movement of the long tubes connected to the

Table 1. *Peak differential pressure between posterior thoracic and interclavicular air sacs in tufted ducks*

Resting breathing	Surface swimming breathing	Paddling in breath-hold dive
0.03±0.005	0.08±0.04	0.49±0.13*

Values are means ± S.D. (N=5 birds).
*Significantly different from the resting value (P<0.05).

differential pressure transducer during the dive by moving them about under water while attached to a common volume. There was either no signal generated by the motion or no signal greater than 0.012 kPa.

χ^2-tests were used to determine (1) whether there was an association between paddle strokes and pressure fluctuations, and (2) whether pressure changes occurred independently of paddling events. In the first case, the null hypothesis was that a correspondence between pressure fluctuations and paddle strokes would occur no more than the randomly predicted 50 % of the time, and in the second case it was that pressure fluctuations were equally likely to occur with and without paddling events. Two-tailed *t*-tests were used to assess the difference between two means. Values are presented as means ± S.D.
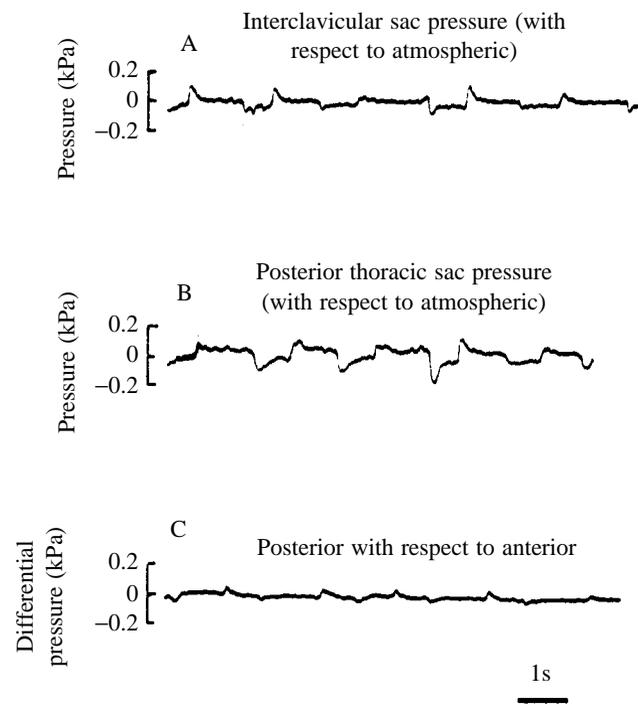

Fig. 1. Air sac pressure measurements from a resting tufted duck *Aythya fuligula*. In A and B, the small pressure changes within single air sacs relative to atmospheric pressure that are responsible for inspiratory and expiratory air flow can be seen. (C) The difference in pressure between posterior thoracic and anterior interclavicular air sacs.
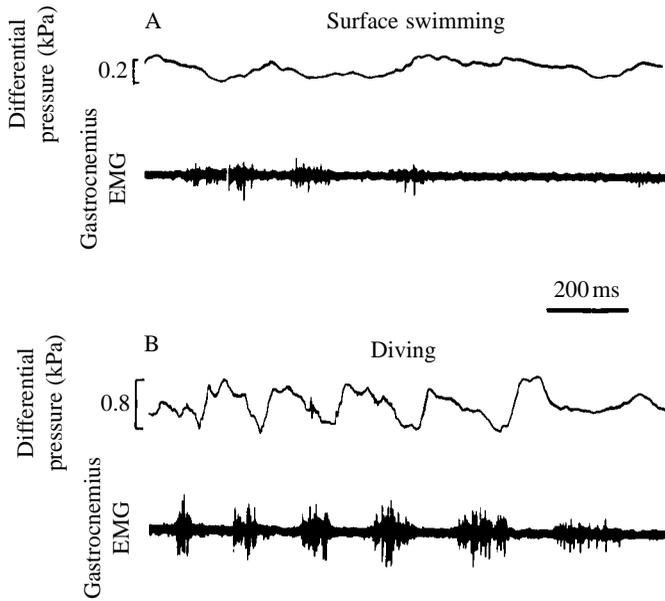
Fig. 2. Fluctuations in differential pressures (upper traces) between posterior thoracic and interclavicular air sacs in a tufted duck *Aythya fuligula* while swimming at the surface (A) and during a breath-hold dive (B). The lower traces are electromyograms (EMG) from the gastrocnemius muscle. Variations in differential pressure correspond with gastrocnemius muscle activity associated with the paddle stroke.

Results

We found a very small differential pressure signal associated with breathing in the resting bird (0.03±0.005 kPa) (Table 1; Fig. 1). During the breath-hold dive, there were fluctuations in differential pressure with a mean value of 0.49±0.13 kPa for the five birds studied, using 34–84 paddle cycles per bird. These pressure fluctuations corresponded to paddle strokes, identified from the activity of the gastrocnemius muscle; examples are shown from two different birds in Figs 2 and 3. Although pressure fluctuations occurred without paddle cycles (<15 %) and paddle cycles occurred without associated changes in pressure (<8 %), overall there were statistically significant associations between paddle cycles and pressure fluctuations in all five ducks ($P<0.005$ in one duck, $P<0.001$ in all others). Both events were sufficiently infrequent that the
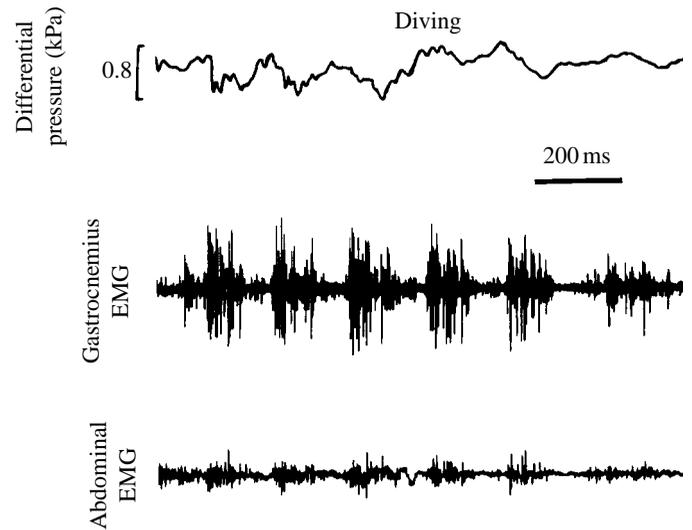

Fig. 3. Electromyographic (EMG) activities in the abdominal and gastrocnemius muscles during underwater paddling, and simultaneous fluctuations in differential air sac pressure between the posterior thoracic and interclavicular air sacs of a tufted duck *Aythya fuligula*.

independence of pressure changes and paddle cycles was statistically rejected. In one duck, abdominal muscle EMGs were also obtained, and the timing of abdominal muscle activity corresponded to that in the gastrocnemius muscle (Fig. 3) and to the differential pressure fluctuations.

We also recorded the impact of walking upon posterior air sac pressures (relative to atmospheric pressure) (Fig. 4) in two instrumented ducks. The mean change in pressure associated with stepping was 0.105±0.05 kPa, which was an average of 99 % of the sac pressure prior to the step.

Discussion

The data presented here indicate that locomotor movements during a dive can induce differential pressures between the posterior and anterior air sacs that might promote movement of air from the air sacs through the parabronchial region of the lung, thereby enhancing the use of the oxygen stored in the
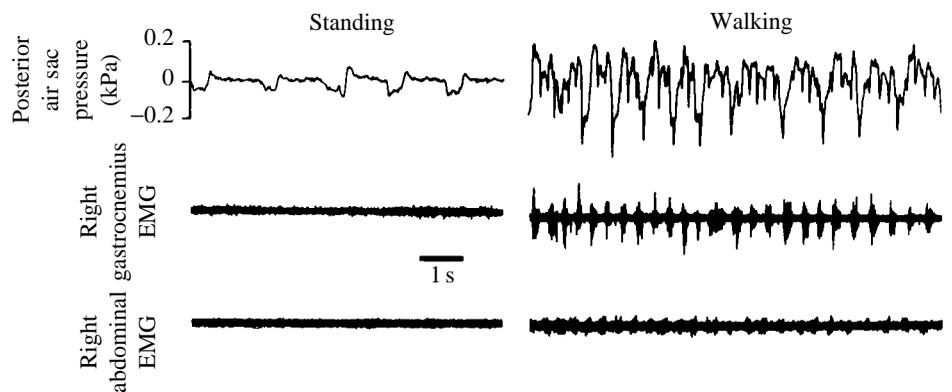
Fig. 4. Fluctuations in air pressure in the posterior thoracic air sac relative to atmospheric pressure and electromyographic (EMG) activity in the right gastrocnemius and abdominal muscles of a tufted duck *Aythya fuligula* while standing and walking.

respiratory system during a dive. It is yet to be determined how these fluctuations in differential pressure translate quantitatively into flows and what the induced patterns may be in the complex arrangement of bronchi in the avian respiratory system under the closed-system conditions that exist during a dive.

That limb movements affect air sac pressures with respect to atmospheric pressure has been demonstrated in the open respiratory systems of running domestic chickens (Brackenbury and Avery, 1980) and flying magpies *Pica pica* (Boggs *et al.* 1997), and the present study indicates a substantial impact of walking on air sac pressures in tufted ducks (Fig. 4). The observation that movement of the limbs affects differential air sac pressures in the closed respiratory system of a diving bird is new and has several implications. First, although all the air sacs are connected and there could not, therefore, be a sustained difference in pressure regionally, there must be sufficient resistance between the anterior and posterior sacs to allow for dynamic or transient regional pressure differences. Second, there must be a greater compressive force applied intermittently to the posterior than to the anterior sacs (or *vice versa*). Data from one duck suggest that the abdominal musculature contracts in phase with the leg stroke (Fig. 3). Furthermore, abdominal muscle activity has been observed in running guinea fowl *Numida meleagris* (P. Nassar, personal communication), and both intercostal and abdominal muscle activities have been observed in domestic dogs (Carrier, 1996; D. R. Carrier, personal communication) in synchrony with the step cycle rather than with the respiratory cycle. These results indicate a locomotory function for the hypaxial musculature in tetrapods, presumably in trunk stabilization.

It will be interesting to investigate the quantitative importance of this mechanism for gas exchange and oxygen consumption in diving birds, especially in wing-propelled divers, and whether it results from abdominal muscle activity influenced by locomotor central pattern generators.

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