

THE RELATIONSHIP BETWEEN DIVING ACTIVITY AND OXYGEN STORAGE CAPACITY IN THE TUFTED DUCK (*AYTHYA FULIGULA*)

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Summary

For a period of 6 months, a group of eight tufted ducks ('control' ducks) were kept on a shallow outdoor pond and performed short dives to obtain food (maximum depth, 0.65 m; observed mean duration, 10.9 ± 0.54 s). At the same time, a group of seven tufted ducks ('dive-trained' ducks) were kept on an adjacent deeper and partly covered pond, and performed 'extended' dives under the surface mesh in order to feed (maximum distance to food, 10 m; observed mean dive distance, 6.0 ± 0.25 m; observed mean duration, 24.8 ± 0.58 s). At the end of this time, the calculated total usable oxygen store was approximately the same in control and dive-trained ducks (44 and 42 ml O₂ STPD kg⁻¹, respectively), although the relative quantities of usable oxygen in each of the three main storage sites (respiratory system, blood and skeletal muscle) differed between groups.

The end-expiratory lung/air sac volume was found to be significantly smaller ($P < 0.01$) in the dive-trained ducks (165 ml BTPS kg⁻¹) than in the control ducks (232 ml BTPS kg⁻¹). The dive-trained ducks, however, had a significantly greater ($P < 0.01$) blood volume (141 ml kg⁻¹) than the control ducks (107 ml kg⁻¹), although the blood oxygen capacity and several haematological indices (measured haemoglobin content, red blood cell count and haematocrit, and calculated mean corpuscular haemoglobin and mean corpuscular haemoglobin concentration) were statistically the same in both groups. Mean corpuscular volume was significantly greater ($P < 0.05$) in the dive-trained ducks. The myoglobin content of the myocardium was the same in both groups. The pectoralis muscle and the locomotory leg muscles, however, contained significantly higher concentrations of myoglobin in the dive-trained ducks than in the control ducks (pectoralis, $P < 0.05$; lateral gastrocnemius and semitendinosus, $P < 0.01$).

It is suggested that the anatomical adaptations which occur in response to chronic increases in diving activity may increase the aerobic diving capacity of the

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tufted duck by effecting a decrease in buoyancy (reduced end-expiratory lung/air sac volume) and an increase in blood oxygen storage capacity (hypervolaemia). Locomotory muscle function may be maintained in the face of decreasing oxygen delivery during extended dives by means of increased myoglobin content after dive-training.

Introduction

In aquatic birds, two important determinants of dive duration are the oxygen storage capacity and the rate of consumption of those oxygen stores (\dot{V}_{O_2}) (West, 1981; Woakes & Butler, 1983; Hudson & Jones, 1986). Comparative studies indicate that habitual divers are adapted, both anatomically and physiologically, in ways that enable them to perform longer and/or more frequent dives than non-divers.

High oxygen storage capacity tends to be associated with good diving ability in different species of aquatic birds. The lung/air sac system contains a greater volume of oxygen in the tufted duck (*Aythya fuligula*), a diving duck, than in the mallard (*Anas platyrhynchos*), a dabbling duck (Keijer & Butler, 1982). Furthermore, good divers are often, although not always, found to have higher blood volumes and higher haemoglobin and myoglobin concentrations than their terrestrial or non-diving aquatic counterparts (Bond & Gilbert, 1958; Lenfant *et al.* 1969; Milsom *et al.* 1973; Balasch *et al.* 1974; Weber *et al.* 1974; West, 1981; Keijer & Butler, 1982; Baldwin *et al.* 1984; Hudson & Jones, 1986). Interesting as they are, these comparative studies unfortunately give no indication as to the degree to which differences are inherited and how much is due to the 'training' effects, if any, of different levels of diving activity.

Kodama *et al.* (1977) reported small differences in some haematological parameters between diving and non-diving immature harbour seals, *Phoca vitulina*, but concluded that 'the characteristically large oxygen storage capacity is phylogenetically determined, and not the result of acclimatization to an increasing frequency of apneic dives'. However, their study was complicated by the concurrent effects of growth on blood parameters and by the fact that diving activity was unlikely to have been particularly intense in the diving seals. Their results show that a total lack of diving experience has little effect on the normal development of high blood oxygen capacity in young harbour seals, but they do not indicate whether relatively high levels of diving activity could result in a further enhancement of oxygen stores.

To our knowledge, no studies of the effects of altered diving activity on oxygen storage capacity have been made on birds. The present experiment was therefore designed to test the hypothesis that adaptations in oxygen storage capacity will occur in response to chronic increases in voluntary diving activity in the tufted duck, *Aythya fuligula*.

Materials and methods

Fifteen 1-year-old tufted ducks of both sexes were used. They were randomly

assigned to two groups: (a) a group of eight ducks (the control ducks) which were kept on a shallow outdoor pool (0.65 m deep), and (b) a group of seven ducks (the dive-trained ducks) which were kept on an adjacent deeper outdoor pool (1.9–2.8 m deep) which was covered by plastic mesh at a depth of 4 cm over all the surface except for an area 4.5 m × 1 m at the shallower end. All birds were fed the same diet of mixed grain and poultry growers pellets (Heygates Ltd), which was thrown onto the water once per day. The quantity provided was sufficient to ensure that the ducks had free access to food throughout the day. In addition, on one day per week the ducks were provided with dry food in bowls at the side of each pond. The dive-trained birds were required to dive under the mesh to obtain food, most of which settled to the bottom of the pond at a distance of 4–10 m from the uncovered surface. The ducks were exposed to these conditions from May to November 1986, and then they were recaptured and kept on indoor tanks (0.4 m deep for control ducks and 1.7 m deep for dive-trained ducks) for a further 3 weeks when the measurements were made. At all times the dive-trained ducks were required to perform deeper dives for food (minimum depth 1.7 m) than the control group (maximum depth 0.65 m).

End-expiratory lung/air sac volumes were measured using an argon gas washout technique (Scheid & Piiper, 1969; Keijer & Butler, 1982). Five minutes after the application of local anaesthetic to the glottis (Xylocaine spray, Astra Hewlett Ltd) a soft rubber tube, connected to a T-piece, was inserted approximately 3 cm into the trachea. Gases (either air or a 20% oxygen/80% argon mixture) were passed through the cross arm of the T-piece at a rate of 4.5 l min⁻¹, held constant using gas flow regulators (Flo Stat, Platon Ltd). Concentrations of O₂, N₂ and Ar in the gas downstream of the tracheal tube were monitored continuously using a mass spectrometer (MGA 2000, Airspec Ltd) and the concentration of Ar was recorded and simultaneously integrated to give volume. The duck was allowed to breathe the 20% O₂/80% Ar mixture until the exhaled N₂ concentration was less than 0.2%, even after gentle manual massage. The gas was changed to air during a normal expiration and the Ar concentration in subsequent breaths was measured, again employing manual massage to remove all Ar from the respiratory system.

Haemoglobin concentration, red blood cell count and haematocrit were measured using blood samples (2–4 ml) withdrawn from the brachial vein into heparinized syringes. Haematocrit was measured by spinning whole blood in a microhaematocrit centrifuge (Hawkesley) for 4 min and no correction was made for plasma trapping. Haemoglobin concentration was measured spectrophotometrically using a standard diagnostic kit (Sigma). Red blood cell number was measured using a Coulter Industrial D particle counter (Coulter Electronics Ltd); red blood cells were separated from plasma and resuspended to the original haematocrit in Isoton II, an azide-free balanced electrolyte solution, and several 50 µl samples of a 1 in 20 000 dilution were counted against suitable blanks. The haematological indices, mean corpuscular volume (MCV), mean corpuscular haemoglobin content (MCH) and mean corpuscular haemoglobin concentration (MCHC), were obtained by calculation.

Three weeks after the venous blood samples had been taken, plasma volume was measured using the Evans blue dye (EO133, Sigma) dilution technique as described by West (1981). Serial plasma samples, diluted in a suitable volume of heparinized saline, were analysed colorimetrically at 620 nm using a PU8610 kinetics spectrophotometer (Pye Unicam Ltd). At the end of the dye dilution experiment, the ducks were killed and dissected for muscle samples. The heart, whole pectoralis and supracoracoideus muscles, and the lateral gastrocnemius and semitendinosus muscles of the left leg were removed, weighed, and small samples of each were frozen in liquid nitrogen and then stored in a deep freeze at -80°C . Myoglobin contents of the pectoralis, lateral gastrocnemius, semitendinosus and heart muscles were measured by the method of Reynafarje (1963), as modified for the tufted duck (Turner & Butler, 1988), assuming that 75 % of the wet mass of muscle consists of water (Keijer & Butler, 1982).

Mean values for each animal were used in the calculation of the statistics presented in Tables 1 and 2. Since the sample sizes were small, the non-parametric Mann-Whitney U-test was used (Eason *et al.* 1980) to quantify the significance of differences between mean values. The fiducial limit of statistical significance was taken as $P < 0.05$.

Estimation of oxygen storage capacity

The amount of oxygen which is available for use during dives in control and dive-trained tufted ducks is estimated using the above data and by making the following assumptions. (1) Tufted ducks hyperventilate before voluntary dives (Butler & Woakes, 1979) and the fractional concentrations of oxygen in the anterior and posterior air sacs are assumed to be 16 % and 19.5 %, respectively – similar to those in the hyperventilating starling, *Sturnus vulgaris* (Torre-Bueno, 1978). (2) The posterior air sacs are assumed to constitute 45 % of the total respiratory volume (Scheid *et al.* 1974). (3) Mean fractional concentration of oxygen in the respiratory system immediately before submergence is, therefore, assumed to be 17.6 %. (4) Assuming that the physiological properties of tufted duck blood are the same as those of the Pekin duck, *Anas platyrhynchos*, a maximum of 75 % of the oxygen in the respiratory system is usable during dives (Hudson & Jones, 1986). (5) The oxygen-binding capacity of tufted duck haemoglobin is assumed to be the same as that measured in the black-headed gull, *Larus ridibundus*, and the pigeon, *Columba livia*; $1.2 \text{ ml O}_2 \text{ g}^{-1}$ pigment (Viscor *et al.* 1984). (6) Assuming a relative molecular mass of 18 000 (Weber *et al.* 1974), the theoretical oxygen-binding capacity of avian myoglobin is $1.24 \text{ ml O}_2 \text{ g}^{-1}$ pigment. (7) It is assumed that arterial blood is 100 % saturated and venous blood is 70 % saturated following pre-dive hyperventilation. (8) Venous blood is assumed to constitute 70 % of the blood volume (Rothe, 1983). (9) A maximum of 96 % of the oxygen in the blood is assumed to be usable (Hudson & Jones, 1986). (10) The concentration of myoglobin in pectoralis muscle (which constitutes approximately 70 % of the total muscle mass) is assumed to represent the average for all muscles

Table 1. Mean values (\pm S.E.) of the volumes of the respiratory and circulatory systems, and blood haematological indices in control and dive-trained tufted ducks

	Control	Dive-trained
Body mass (g) (November 1986)	638 \pm 26 (8)	740 \pm 24 (7)**
End-expiratory lung/air sac volume (ml STPS kg ⁻¹)	232 \pm 14 (5)	165 \pm 19 (4)**
Plasma volume (ml kg ⁻¹)	56.2 \pm 8.4 (2)	75.4 \pm 2.3 (6)**
Venous haematocrit (%)	43.1 \pm 1.4 (8)	45.3 \pm 1.8 (7)
Calculated blood volume (ml kg ⁻¹)	107 \pm 10 (2)	141 \pm 6 (6)**
Haemoglobin content (g 100 ml ⁻¹ blood)	15.6 \pm 0.4 (8)	15.5 \pm 0.7 (7)
Calculated blood oxygen capacity (ml O ₂ 100 ml ⁻¹ blood)	20.9 \pm 0.51 (8)	20.8 \pm 0.96 (7)
RBC count ($\times 10^6 \mu\text{l}^{-1}$ blood)	2.38 \pm 0.08 (8)	2.17 \pm 0.08 (7)
Calculated MCV (μm^3)	182.8 \pm 8.7 (8)	209.7 \pm 9.7 (7)*
Calculated MCH (pg)	66.3 \pm 2.9 (8)	71.8 \pm 2.9 (7)
Calculated MCHC (g 100 ml ⁻¹)	36.4 \pm 1.0 (8)	34.5 \pm 1.8 (7)

MCV, mean corpuscular volume; MCH, mean corpuscular haemoglobin content; MCHC, mean corpuscular haemoglobin concentration.

The sample size (N) is given in parentheses.

Statistically significant differences between mean values are indicated by the symbols * ($P < 0.05$) or ** ($P < 0.01$).

(Keijer & Butler, 1982). (11) Skeletal muscle is assumed to constitute 25 % of the total body mass (Keijer & Butler, 1982).

Results

Mean dive duration for control ducks diving to a depth of 0.65 m was 10.9 ± 0.54 s ($N = 52$) and the longest recorded dive lasted 22 s. For dive-trained ducks, mean dive duration was 24.8 ± 0.58 s ($N = 157$) and mean distance travelled to food was 6.0 ± 0.25 m ($N = 157$). The longest dive recorded under these conditions lasted 44.5 s. For dive-trained ducks, 49.4 % of the observed dives were 25 s or longer, and 7 % were 35 s or longer.

Table 1 gives the mean values (\pm S.E.) of end-expiratory lung/air sac volume and blood variables. The end-expiratory lung/air sac volume was a statistically significant 29 % smaller ($P < 0.01$) in dive-trained ducks than in control ducks. In contrast, plasma volume was a significant 34 % greater ($P < 0.01$) in dive-trained ducks. Since the venous haematocrit was the same in both groups of birds, the calculated blood volume was also significantly greater ($P < 0.01$) in dive-trained ducks. Haemoglobin content of the blood was no different between groups, however, and the calculated blood oxygen capacities were, therefore, also the same. Measured red blood cell count and calculated MCH and MCHC were also

Table 2. Mean values (\pm s.e.) of the mass and myoglobin content of the heart, the flight muscles (pectoralis), and two of the locomotory leg muscles (lateral gastrocnemius and semitendinosus) in control and dive-trained tufted ducks

	Control	Dive-trained
Total mass of pectoralis and supracoracoideus muscles (g)	118.7 \pm 6.9 (6)	124.1 \pm 6.7 (6)
(Proportion of body mass)	(17.8%)	(16.9%)
(Proportion of total muscle mass)	(71.1%)	(67.4%)
Left lateral gastrocnemius mass (g)	1.71 \pm 0.07 (6)	1.84 \pm 0.07 (6)
Left semitendinosus mass (g)	2.41 \pm 0.07 (6)	2.64 \pm 0.11 (6)
Heart mass (g)	6.23 \pm 0.53 (6)	7.14 \pm 0.18 (6)
Myoglobin content (mg g ⁻¹ wet mass):		
Pectoralis	4.7 \pm 0.6 (5)	7.4 \pm 0.8 (6)*
Lateral gastrocnemius	7.1 \pm 0.4 (5)	9.8 \pm 0.3 (6)**
Semitendinosus	4.8 \pm 0.5 (5)	7.4 \pm 0.3 (6)**
Myocardium	7.0 \pm 0.7 (5)	6.8 \pm 0.5 (6)

Sample size (N) is given in parentheses and statistically significant differences between mean values are indicated by the symbols * ($P < 0.05$) or ** ($P < 0.01$).

statistically the same in both groups of ducks. Calculated MCV, however, was found to be significantly greater ($P < 0.05$) in the dive-trained ducks.

Mean values (\pm s.e.) of the masses and myoglobin contents of selected muscle tissues are given in Table 2. Masses of the heart, flight muscles (pectoralis and supracoracoideus muscles) and two locomotory leg muscles (lateral gastrocnemius and semitendinosus) were the same in both groups of ducks. The myoglobin content of the myocardium was the same in both groups of ducks, but that of the skeletal muscles was found to be higher in dive-trained ducks than in control ducks.

The effect of chronically elevated levels of diving activity on calculated oxygen storage capacity is summarized in Table 3. The estimated total usable oxygen storage capacity was similar in dive-trained (42.0 ml O₂ STPD kg⁻¹) and control ducks (44.0 ml O₂ STPD kg⁻¹), and also similar to the value reported by Keijer & Butler (1982) for this species (41.5 ml O₂ STPD kg⁻¹). However, it appears that the relative sizes of the three main storage sites – lung/air sac system, blood and muscle – differ between the two groups in this study. The estimated amount of usable oxygen stored within the blood and muscles was greater whereas that in the respiratory system was smaller in dive-trained than in control ducks.

Discussion

The tufted duck is a benthic feeder, living on freshwater rivers, lakes and ponds in the upper middle latitudes of Europe and western Asia (Cramp & Simmons,

Table 3. Estimated usable oxygen storage capacities (in ml O_2 STPD kg^{-1}) and the proportions (%) in the lung/air sac systems, blood and skeletal muscles of control and dive-trained tufted ducks

	Control		Dive-trained	
	O_2	%	O_2	%
End-expiratory lung/air sac system	26.7	60.7	18.9	45.0
Blood	15.8	35.9	20.8	49.5
(arterial)	(6.0)		(7.9)	
(venous)	(9.8)		(12.9)	
Muscle	1.5	3.4	2.3	5.5
Total	44.0		42.0	

1977). The 'preferred' diving depth for this species is approximately 1–3 m, and dive durations are typically 10–25 s at these depths (Dewar, 1924; Laughlin, 1972/73). However, it is possible that in the winter, when the water surface freezes over, dive distances and durations may need to be increased for the birds to obtain food at increasing distances from ice holes. When this situation was simulated it was found that during 'extended' dives (long distance, long duration dives) tufted ducks displayed a gradually developing bradycardia which is likely to be part of a coordinated oxygen-conserving response (Stephenson *et al.* 1986). Butler & Woakes (1982) found that the carotid body chemoreceptors have a significant cardioinhibitory influence after approximately 15–20 s of submerged swimming in the tufted duck, and Butler & Stephenson (1988) found that the bradycardia observed during extended dives is also due partly to stimulation of the carotid body chemoreceptors. Since approximately half of all dives performed by the dive-trained ducks (but none of the dives performed by the control ducks) on the outdoor pond were 25 s or longer in duration, the oxygen stores in diving dive-trained ducks may have been depleted regularly to an extent sufficient to cause oxygen-conserving cardiovascular reflexes. The results of the present study suggest that chronic increases in diving activity stimulate anatomical adaptations which may facilitate the prolongation of aerobic dives in the adult tufted duck.

The observed reduction in end-expiratory lung/air sac volume in dive-trained ducks probably has opposing effects in terms of diving energetics. It may represent an adaptation which effects a reduction in the power output required to dive, a mechanism that has been suggested on the basis of comparative studies to be important in other diving birds (Dehner, 1946; Schorger, 1947; Owre, 1967; Casler, 1973). Approximately 94% of the work done by the hindlimbs of diving lesser scaup, *Aythya affinis*, is required to overcome a buoyant force of 1.79 N kg^{-1} (M. R. A. Heieis, D. R. Jones, R. W. Blake & R. Stephenson, in preparation). Reduction of the end-expiratory lung/air sac volume by $67 \text{ ml BTPS kg}^{-1}$ may reduce the buoyant force by as much as 0.66 N kg^{-1} or 63%. In this case, the overall power output would be reduced by approximately 59%. Thus, oxygen

uptake (\dot{V}_{O_2}) during voluntary dives may be reduced from the 'control' value of $0.95 \text{ ml O}_2 \text{ s}^{-1} \text{ kg}^{-1}$ (Woakes & Butler, 1983) to approximately $0.59 \text{ ml O}_2 \text{ s}^{-1} \text{ kg}^{-1}$ in dive-trained ducks, assuming that the efficiency of locomotion remains approximately 6.9% (M. R. A. Heieis, D. R. Jones, R. W. Blake & R. Stephenson, in preparation) during extended dives. However, the reduction in lung/air sac volume also effectively reduces the oxygen storage capacity of the respiratory system from $26.7 \text{ ml O}_2 \text{ STPD kg}^{-1}$ in control ducks to $18.9 \text{ ml O}_2 \text{ STPD kg}^{-1}$ in dive-trained ducks (Table 3). Nevertheless, from the above calculations, the energetic disadvantage incurred by a 29.3% reduction in lung/air sac O_2 store is more than cancelled by a 37.9% reduction in \dot{V}_{O_2} . Furthermore, the blood oxygen store was elevated in dive-trained ducks (Table 3), so that the estimated total usable oxygen stores were similar in both groups of ducks. Thus, the reduced end-expiratory lung/air sac volume may represent a significant energetic advantage to dive-trained ducks performing extended dives.

It is possible that rather than there being a reduction in lung/air sac volume *per se*, the low end-expiratory lung/air sac volumes in the dive-trained ducks may indicate an increase in the compliance of the respiratory system. It is likely that lung/air sac volumes are the same in the two groups of ducks when the animals are at the water surface so that buoyancy and body position are maintained. The dive-trained ducks may therefore be capable of exhaling to a lower residual volume immediately before diving. The ducks in this study were tied down to prevent struggling and were manually massaged to ensure complete exhalation of nitrogen from the respiratory system during Ar/O_2 breathing. It is possible that this procedure may have caused the dive-trained ducks to attain, and maintain, a lower residual volume as a result of the suggested greater compliance of the respiratory system in these birds. That diving ducks can reduce residual respiratory gas volume when restrained has been demonstrated by subjection of lesser scaup, *Aythya affinis*, to head-out body immersion. This procedure caused a reduction in buoyancy (by an average of 23% over a 5-min period) as a result of a reduction in residual lung/air sac volume, while tidal volume remained constant (M. R. A. Heieis, D. R. Jones, R. W. Blake & R. Stephenson, in preparation).

The increase in blood oxygen storage capacity in dive-trained ducks resulted entirely from an increase in blood volume, with no changes in the oxygen capacity or haematological indices of the blood. The hypervolaemia (consisting of a 34% higher plasma volume in dive-trained ducks) was of a similar proportional increase to that observed in horses, dogs and humans after physical training (Oscari *et al.* 1968; Convertino *et al.* 1980; McKeever *et al.* 1985, 1987). However, unlike the situation in trained mammals, the hypervolaemia must have been accompanied by an increased rate of erythropoiesis to avoid haemodilution in ducks. Furthermore, the blood oxygen store of dive-trained ducks increased without haemoconcentration, thereby avoiding a reduced oxygen transport efficiency due to increased blood viscosity, as may be the case in the northern elephant seal, *Mirounga angustirostris* (Hedrick *et al.* 1986). The calculated MCV in both groups of ducks was slightly greater than most previously published values (e.g. Bond & Gilbert,

1958; Balasch *et al.* 1974; Viscor *et al.* 1984). The functional significance of the higher value in dive-trained ducks is unknown, although one can speculate that any consequent increase in blood viscosity may have been counteracted by a reduced plasma protein concentration in these ducks (Viscor *et al.* 1984).

The skeletal muscle oxygen store, although almost twice that of the control ducks (see Keijer & Butler, 1982) represents only 5.5% of the estimated total usable store in the dive-trained tufted ducks (Table 3). If it is assumed that the 3.5-fold increase in \dot{V}_{O_2} during voluntary dives compared with rest (Woakes & Butler, 1983) is the result mainly of increased metabolism in the working leg muscles, then even in dive-trained ducks the myoglobin-bound oxygen in these muscles would last only approximately 2 s after cessation of blood flow. Based on the changes in heart rate during extended dives, it has been suggested that the blood supply to the leg muscles is probably maintained throughout all dives shorter than approximately 35 s duration (Butler, 1982; Stephenson *et al.* 1986), and this was recently confirmed in a preliminary study using a radioactive tracer technique in a freely diving lesser scaup, *Aythya affinis* (Jones, 1987). Thus, the elevated myoglobin concentrations in the lateral gastrocnemius and semitendinosus muscles of dive-trained tufted ducks probably serve primarily to facilitate the diffusion of oxygen (which may fall to a relatively low partial pressure in the blood during extended dives) from the blood to the muscle mitochondria, rather than as a store. If the inactive tissues (which include the pectoralis muscles in these foot-propelled divers) receive a reduced blood supply during extended dives (Butler, 1982; Stephenson *et al.* 1986), then an increased myoglobin content may constitute a significant oxygen store serving to delay the onset of lactic acid accumulation in these tissues.

The precise stimuli which caused the observed anatomical adaptations in dive-trained ducks remain to be determined. Specifically, it is not possible to separate the contributions of increased breath-hold times from altered exercise levels. Butler & Turner (1988) observed that dive-training has a greater effect than swim-training in increasing the oxidative capacity of the locomotory muscles in tufted ducks, but this may simply reflect differences in duration and intensity of the training rather than an actual difference in the stimulus presented to the muscles during apnoeic exercise (diving) and surface swimming. However, it is clear that increased diving activity is a sufficient overall stimulus for anatomical adaptation, exclusive of any additional effects resulting from maturation (Kodama *et al.* 1977) or seasonal changes in microclimate (MacArthur, 1984). The use of several assumptions renders the calculation of usable oxygen storage capacity very speculative. Nevertheless, by applying these assumptions equally to both groups of ducks, it is clear that chronic increases in diving activity result in anatomical adaptations which effectively improve the 'aerobic diving capacity' of tufted ducks.

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References

- BALASCH, J., PALOMEQUE, J., PALACIOS, L., MUSQUERA, S. & JIMENEZ, M. (1974). Haematological values of some great flying and aquatic-diving birds. *Comp. Biochem. Physiol.* **49A**, 137–145.
- BALDWIN, J., JARDEL, J.-P., MONTAGUE, T. & TOMKIN, R. (1984). Energy metabolism in penguin swimming muscles. *Molec. Physiol.* **6**, 33–42.
- BOND, C. F. & GILBERT, P. W. (1958). Comparative study of blood volume in representative aquatic and nonaquatic birds. *Am. J. Physiol.* **194**, 519–521.
- BUTLER, P. J. (1982). Respiratory and cardiovascular control during diving in birds and mammals. *J. exp. Biol.* **100**, 195–221.
- BUTLER, P. J. & STEPHENSON, R. (1988). Chemoreceptor control of heart rate and behaviour during diving in the tufted duck (*Aythya fuligula*). *J. Physiol., Lond.* **397**, 63–80.
- BUTLER, P. J. & TURNER, D. L. (1988). The effect of training on maximal oxygen uptake and aerobic capacity of locomotory muscles in tufted ducks, *Aythya fuligula*. *J. Physiol., Lond.* (in press).
- BUTLER, P. J. & 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.
- BUTLER, P. J. & WOAKES, A. J. (1982). Control of heart rate by carotid body chemoreceptors during diving in tufted ducks. *J. appl. Physiol.* **53**, 1405–1410.
- CASLER, C. L. (1973). The air-sac systems and buoyancy of the anhinga and double-crested cormorant. *Auk* **90**, 324–340.
- CONVERTINO, V. A., GREENLEAF, J. E. & BERNAUER, E. M. (1980). Role of thermal and exercise factors in the mechanism of hypervolaemia. *J. appl. Physiol.* **48**, 657–664.
- CRAMP, S. & SIMMONS, K. E. L. (ed.) (1977). *The Birds of the Western Palearctic*, vol. 1, pp. 577–586. Oxford: Oxford University Press.
- DEHNER, E. W. (1946). An analysis of buoyancy in surface-feeding and diving ducks. Ph.D. thesis, Cornell University.
- DEWAR, J. M. (1924). *The Bird as a Diver*. London: H. F. & J. Witherby.
- EASON, G., COLES, C. W. & GETTINBY, G. (1980). *Mathematics and Statistics for the Biosciences*. Chichester: J. Wiley & Sons Ltd.
- HEDRICK, M. S., DUFFIELD, D. A. & CORNELL, L. H. (1986). Blood viscosity and optimal haematocrit in a deep-diving animal, the northern elephant seal (*Mirounga angustirostris*). *Can. J. Zool.* **64**, 2081–2085.
- HUDSON, D. M. & JONES, D. R. (1986). The influence of body mass on the endurance to restrained submergence in the Pekin duck. *J. exp. Biol.* **120**, 351–367.
- JONES, D. R. (1987). The duck as a diver. In *Advances in Physiological Research* (ed. H. McLennan, J. R. Ledsome, C. H. S. McIntosh & D. R. Jones), pp. 397–409. New York: Plenum Press.
- KEJER, E. & BUTLER, P. J. (1982). Volumes of the respiratory and circulatory systems in tufted and mallard ducks. *J. exp. Biol.* **101**, 213–220.
- KODAMA, A. M., ELSNER, R. & PACE, N. (1977). Effects of growth, diving history, and high altitude on blood oxygen capacity in harbor seals. *J. appl. Physiol.* **42**, 852–858.
- LAUGHLIN, K. F. (1972/73). The bioenergetics of the tufted duck (*Aythya fuligula*) at Loch Leven, Kinross. *Proc. R. Soc. Edinb. B* **74**, 333–345.
- LENFANT, C., KOOYMAN, G. L., ELSNER, R. & DRABEK, C. M. (1969). Respiratory function of the blood of the Adelie penguin, *Pygoscelis adeliae*. *Am. J. Physiol.* **216**, 1598–1600.
- MACARTHUR, R. A. (1984). Seasonal changes in hematological and respiratory properties of muskrat (*Ondatra zibethicus*) blood. *Can. J. Zool.* **62**, 537–545.
- McKEEVER, K. H., SCHURG, W. A. & CONVERTINO, V. A. (1985). Exercise training-induced hypervolaemia in greyhounds: role of water intake and renal mechanisms. *Am. J. Physiol.* **248**, R422–R425.
- McKEEVER, K. H., SCHURG, W. A., JARRETT, S. H. & CONVERTINO, V. A. (1987). Exercise training-induced hypervolaemia in the horse. *Med. Sci. Sports Exerc.* **19**, 21–27.
- MILSON, W. K., JOHANSEN, K. & MILLARD, R. W. (1973). Blood respiratory properties in some Antarctic birds. *Condor* **75**, 472–474.

- OSCAI, L. B., WILLIAMS, B. T. & HERTIG, B. A. (1969). Effect of exercise on blood volume. *J. appl. Physiol.* **24**, 622–624.
- OWRE, O. T. (1967). Adaptations for locomotion and feeding in the anhinga and the double-crested cormorant. *Orn. Monogr.* **6**, 1–138.
- REYNAFARJE, B. (1963). Simplified method for the determination of myoglobin. *J. Lab. clin. Med.* **61**, 138–145.
- ROTHER, C. F. (1983). Venous system: physiology of the capacitance vessels. In *Handbook of Physiology. The Cardiovascular System*, vol. 3 (ed. J. T. Shepherd & F. M. Abboud), pp. 397–452. Bethesda: American Physiological Society.
- SCHEID, P. & PIIPER, J. (1969). Volume, ventilation and compliance of the respiratory system in the domestic fowl. *Respir. Physiol.* **6**, 298–308.
- SCHEID, P., SLAMA, H. & WILLMER, H. (1974). Volume and ventilation of air sacs in ducks studied by inert gas wash-out. *Respir. Physiol.* **21**, 19–36.
- SCHORGER, A. W. (1947). The deep diving of the loon and old-squaw and its mechanism. *Wilson Bull.* **59**, 151–159.
- STEPHENSON, R., BUTLER, P. J. & WOAKES, A. J. (1986). Diving behaviour and heart rate in tufted ducks (*Aythya fuligula*). *J. exp. Biol.* **126**, 341–359.
- TORRE-BUENO, J. R. (1978). Respiration during flight in birds. In *Respiratory Function in Birds, Adult and Embryonic* (ed. J. Piiper), pp. 89–94. Berlin: Springer-Verlag.
- TURNER, D. L. & BUTLER, P. J. (1988). The aerobic capacity of locomotory muscles in the tufted duck, *Aythya fuligula*. *J. exp. Biol.* **135**, 445–460.
- VISCOR, G., FUENTES, J. & PALOMEQUE, J. (1984). Blood rheology in the pigeon (*Columba livia*), hen (*Gallus gallus domesticus*), and black-headed gull (*Larus ridibundus*). *Can. J. Zool.* **62**, 2150–2156.
- WEBER, R. E., HEMMINGSEN, E. A. & JOHANSEN, K. (1974). Functional and biochemical studies of penguin myoglobin. *Comp. Biochem. Physiol.* **49B**, 197–214.
- WEST, N. H. (1981). The effect of age and the influence of the relative size of the heart, brain and blood oxygen store on the responses to submersion in mallard ducklings. *Can. J. Zool.* **59**, 986–993.
- WOAKES, A. J. & BUTLER, P. J. (1983). Swimming and diving in tufted ducks, *Aythya fuligula*, with particular reference to heart rate and gas exchange. *J. exp. Biol.* **107**, 311–329.