VOLUMES OF THE RESPIRATORY AND CIRCULATORY SYSTEMS IN TUFTED AND MALLARD DUCKS

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SUMMARY

Tufted ducks habitually dive for their food and may remain submerged for up to 40 s. Mallards, on the other hand, merely upend themselves for a few seconds when dabbling. It was decided, therefore, to determine the size of the oxygen storage compartments in these two aquatic birds. Haemoglobin concentration, blood volume, and volume of the respiratory system are all significantly larger in the tufted duck than in the mallard. Myoglobin concentration in the pectoral and leg muscles of the tufted duck is similar to that in the locomotory muscles of terrestrial birds and mammals. Amounts of usable oxygen (at STPD) stored in the body were calculated to be 41·5 ml kg^{-1} for tufted ducks and 29·0 ml kg^{-1} for mallards.

INTRODUCTION

Recent studies have shown that there are marked differences in the cardiac response to diving in birds, depending upon whether the animal is forcibly submerged or whether it dives freely. It is possible also that the metabolic adjustments may be different. Ducks can withstand forcible submersion for much longer than would be expected on the basis of their oxygen stores and if they metabolize aerobically at the normal resting rate (Scholander, 1940). This is achieved by blood flow being reduced to all parts of the body except the central nervous system and heart (Johansen, 1964; Butler & Jones, 1971; Jones *et al.* 1979), which are the only organs that metabolize aerobically under these conditions. Thus, oxygen usage is reduced and anaerobiosis, with the production of lactic acid, occurs in the hypoperfused tissues (Scholander, 1940; Andersen, 1959; Pickwell, 1968). Accompanying the selective reduction in blood flow is a progressive reduction in heart rate to 10–15% of the pre-dive level (Butler & Jones, 1968, 1971; Butler & Taylor, 1973). This so-called diving bradycardia is, in fact, the typical element of the cardiovascular, and hence of the metabolic, adjustments to forcible submersion. It was something of a surprise, therefore, to discover that freely diving tufted ducks do not show a maintained bradycardia. There is an increase in heart rate and respiratory frequency a few seconds before the first dive of a series and a dramatic reduction in heart rate immediately upon diving, but

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it soon reaches a level that is similar to that present when the duck is swimming o█ the surface (Butler & Woakes, 1976, 1979, 1982a). This heart rate is maintained until just before the animal surfaces (when tachycardia occurs), even when the dives are relatively long (Butler, 1980).

Even the longest natural dives performed by aquatic birds are nowhere near the durations that have been used during forcible submersion (Butler & Jones, 1982). The domesticated variety of the mallard duck can survive forcible submersions of 5–15 min (Andersen, 1959; Pickwell, 1968). Unfortunately this species does not dive naturally; the mallard normally upends itself and dabbles in shallow water, but the longest natural dive reported for the tufted duck is 40 s (Dewar, 1924). Thus, with no bradycardia (and by implication no other cardiovascular adjustments) during natural diving, it would appear that there is no dramatic conservation of oxygen. Recent studies indicate that oxygen usage actually increases during diving (Woakes & Butler, 1982). This being the case, the amount of oxygen stored in the body of the animal would have a crucial influence on the duration of these natural dives. It was decided, therefore, to measure blood volume, haemoglobin concentration, and volume of the respiratory system of the tufted duck, and to compare the results with those obtained from the dabbling duck, the mallard, which has (or its domesticated variety has) been the subject of many studies on the physiology of diving.

MATERIALS AND METHODS

Tufted ducks (*Aythya fuligula*) and mallards (*Anas platyrhynchos*) of either sex were used in this study. The birds were obtained as young ducklings from the Wildfowl Trust, Slimbridge and were kept on an outside pond, 2·7 m deep. The tufted ducks varied in age from 4 months to over a year and the mallards were all over a year old. In addition to any natural supply of food, the mallards were fed on a mixture of growers' pellets and corn from a bowl, and the tufteds dived for corn that was thrown onto the pond. The birds were able to roam freely within a compound 25 × 18 m.

Approximately 5 ml of blood was obtained by venipuncture from a brachial vein, from 18 tufteds and 11 mallards. Haematocrit (Hct) was measured with a micro-haematocrit centrifuge (Hawksley). No correction was made for trapped plasma. Haemoglobin concentration (Hb) was measured spectrophotometrically after conversion to cyanmethaemoglobin (Wels & Horn, 1965) using Drabkin's reagent (Sigma, London). Methaemoglobin concentration is less than 1% of total haemoglobin in birds (Board *et al.* 1977), so blood oxygen capacity was calculated by using the value of 1·34 ml O_2 (g Hb)$^{-1}$.

Blood volume was calculated from plasma volume, measured by the dilution of iodinated [^{125}I]human serum albumin (Radiochemical Centre, Amersham) and haematocrit (Portman, McConnell & Rigdon, 1952; Burton, Sahara & Smith, 1967). The right jugular vein was exposed and cannulated in 6 tufteds and 6 mallards after local injection of 2% (w/v) lignocaine hydrochloride with adrenaline 1:80000 (Xylocaine, Astra Hewlett Ltd.). The cannula was pushed close to the heart and was used for injecting 1 ml avian saline containing 0·5 μCi of labelled albumin and f█
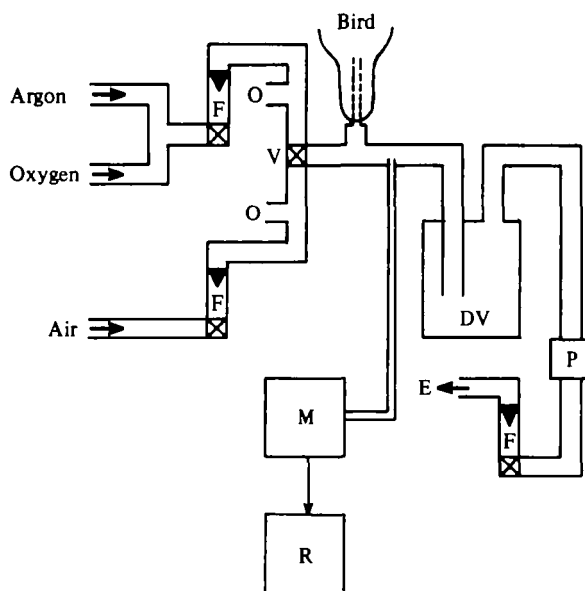
Fig. 1. Schematic diagram of experimental set-up for measurement of volume of respiratory system. (DV = vibration damping vessel; E = exhaust; F = flowmeter; M = mass-spectro-meter; O = overflow; P = air-pump; R = chart-recorder; V = rotary switch valve.)

withdrawing blood samples at 10, 20 and 30 min after complete injection of the albumin. Following injection, the cannula was flushed with blood withdrawn from the duck and finally with a known volume of heparinized saline (10 i.u. ml^{-1}) to ensure that all the albumin entered the duck. The blood samples were centrifuged to obtain clear plasma, 1 ml of which was pipetted into a glass counting vial and the radioactivity was counted 5 times for 1 min in a shielded detector with a scalar ratemeter (Nuclear Enterprises Ltd., Edinburgh). Plasma volume (PV) was obtained as the ratio of total counts injected to the number of counts in the plasma sample and blood volume (BV) was calculated from the equation:

$$BV = \frac{PV \times 100}{100 - Hct}.$$

A modification of the method described by Scheid & Piiper (1969) was used to measure the volume of the respiratory systems in 16 tufteds and 11 mallards (Fig. 1). Each duck was restrained in an upright position in a metal frame; care being taken not to restrict the respiratory movements. After application of a local anaesthetic (Xylo-caine Spray, Astra Hewlett Ltd.) to the glottis, a soft rubber tube of suitable size was advanced approximately 3 cm into the trachea, and this tube was connected to a T-piece. Gas (either air or an argon/oxygen mixture) was supplied at a rate of 15 l min^{-1} for mallards and 10 l min^{-1} for tufted ducks, and was sucked through the cross arm of the T-piece at a rate of 6 l min^{-1} and 4·5 l min^{-1} respectively. Excess supply gas was vented from the overflow. This arrangement prevented room air being sucked into the system by the ducks during inspiration. Initially, the ducks breathed a

mixture of 80% argon and 20% oxygen until the inspired and expired concentrations
of argon were practically identical, as measured by a respiratory mass spectrometer
(20th Century Electronics, Croydon). Then, during expiration, the gas was changed
to air from a cylinder by way of a rotary switch valve (Drallim Controls Ltd., Bexhill).
The concentration of expired argon was monitored by the mass spectrometer and
displayed on a chart recorder (J. J. Lloyd Instruments, Southampton). To ensure
that all the argon was eliminated from the respiratory system, the ducks were manually
massaged at the end until expired argon concentration was less than 0·1%; the
concentration of Ar in the air in the cylinder having been set to zero. The whole
procedure was performed twice more on each duck. The area under the washout
curve was related to a calibration area representing a known volume of argon, thus
giving the volume of argon washed out from the respiratory system. The volume of
the respiratory system (V_r) was then calculated from the equation:

$$V_r = \frac{V_{ar}}{F_o - F_a} \quad \text{(cf. Scheid \& Piiper, 1969)}$$

V_{ar} = volume of argon

F_o = fraction of argon before start of washout

F_a = fraction of argon in air from cylinder.

Evaluation of the data began with the first exhalation of argon mixed with fresh air,
thus giving end-expiratory volume. The ducks stayed quiet and sometimes dormant
during the whole experiment. Volumes are at BTPS.

Myoglobin concentration was measured in the pectoralis major and leg muscles
of 4 tufted ducks, using precisely the technique described by Reynafarje (1963). The
method is based on the assumption that 75% of the wet weight of the muscle consists
of water, so this was checked by drying weighed muscle samples in an oven at 95 °C
until a constant dry weight was obtained. The overall mass of the muscles was also
measured by carefully paring them free of the bones and removing any fat and
connective tissue.

Variance-ratio and t-test for small samples (Bailey, 1959) were used to test for
significant differences between sexes and between species. The fiducial limit of
confidence was taken as 5%.

<center>RESULTS</center>

For all of the measured variables there was no significant difference between
juvenile, male or female tufted ducks, or between male and female mallards. Thus
the data are grouped according to species and the mean values (± S.E.) are given in
Table 1. A direct linear conversion to weight-specific values was made, i.e. no account
was taken of any allometric relationship between any of the variables and body weight.
For a range of birds, Lasiewski & Calder (1971) calculated an exponent of 0·91 for
the volume of the respiratory system, and in mammals, the exponent for blood
volume is 1·02 (Stahl, 1967). Haematocrit is similar for both species. Tufted ducks
have significantly higher Hb and BOC (7·5% greater) than mallards. There was no
consistent variation between the values of blood volume and the time that the blood

Table 1. *Mean values (± S.E.) of the size of the oxygen storage compartments of tufted ducks and mallards*

(Figures in parenthesis indicate number of animals and + indicates a significant difference between both species at the 5 % level.)

	Tufted ducks	Mallards
Haematocrit (%)	48·8 ± 0·9 (18)	47·5 ± 1·0 (12)
Haemoglobin (g. 100 ml⁻¹)	18·4 ± 0·4 (18)	17·1 ± 0·4 (12) +
Calculated blood oxygen capacity (vol. %, STPD)	24·6 ± 0·6 (18)	22·9 ± 0·5 (12) +
Body mass (g)	674 ± 19 (18)	1080 ± 49 (12) +
Blood volume (ml kg⁻¹)	114·2 ± 4·3 (6)	91·2 ± 2·7 (6) +
Body mass (g)	632 ± 49 (6)	1026 ± 27 (6) +
Volume of respiratory system (ml BTPS.kg⁻¹)	180 ± 15 (16)	112 ± 8 (11) +
Body mass (g)	618 ± 18 (16)	1022 ± 41 (11) +
Myoglobin (mg g⁻¹ muscle)	5·5 ± 0·6 (4)	
Mass of leg muscles (% body mass)	8·1 ± 0·4 (4)	
Mass of large pectoral muscles (% body mass)	14·6 ± 0·8 (4)	
Body mass (g)	540 ± 64 (4)	

sample was taken. Therefore, blood volume for each individual bird was calculated as the mean of the values obtained from the 3 samples and the value in Table 1 is the average of these individual means. Weight-specific blood volume is a significant 25% greater in tufteds. For a given body weight, therefore, the oxygen-carrying capacity of the blood is 34% greater in tufteds than in mallards (28·1 ml O_2 kg⁻¹ v. 20·9 ml O_2 kg⁻¹).

The values reported for the volume of the respiratory system are averages of the individual means of the three washout procedures performed on each duck. As with blood volume, the mean weight-specific volume of the respiratory system is significantly (61%) greater in tufted ducks than in mallards.

The water content of the pectoralis major and leg muscles is, on average, 74·6 ± 1·2%($n = 8$) and the myoglobin concentration is similar in each muscle, so the value given in Table 1 is the mean for both muscles. The mass of the leg muscles in the tufteds, as a percentage of body weight, is similar to that reported by Prange & Schmidt-Nielsen (1970) for mallards.

DISCUSSION

The respiratory frequency of the tufted ducks (12·3 ± 0·8 breaths min⁻¹) was slightly greater than the values recorded from inactive free range ducks (Woakes, 1980), but for the mallards, mean respiratory frequency (14·3 ± 0·9 breaths min⁻¹) was less than that recorded during previous experiments on restrained birds (Butler, 1970; Butler & Taylor, 1973). It is assumed, therefore, that the physiological conditions of the intact animals reflected those that would be found in unstressed, air-breathing ducks.

Although Hb is significantly higher in the tufted ducks, it is only by some 7·5%, and the values for both species are within the range reported for other aquatic birds (Bond & Gilbert, 1958; Murrish, 1970; Milsom, Johansen & Millard, 1973). The myoglobin concentration in the muscles of tufted ducks is similar to that found in

Table 2. *Calculated values (in ml O_2 STPD.kg^{-1}) of the usable oxygen stores available to apnoeic tufted and mallard ducks*

(NB, the volume of the respiratory system in Table 1 was converted to STPD for these calculations.)

	Tufted duck		Mallard	
	Vol. of O_2	% of total	Vol of O_2	% of total
Arterial blood	6·3	15·2	4·7	16·2
Venous blood	13·6	32·8	10·2	35·2
Respiratory system	19·8	47·7	12·3	42·4
Muscles (assuming 25 % body wt is muscle)	1·8	4·3	1·8	6·2
Total	41·5		29·0	

locomotor muscles of terrestrial birds and mammals (Lawrie, 1950), but is considerably lower than that found in the pectoral muscles of adult adélie, chinstrap and gentoo penguins (Weber, Hemmingsen & Johansen, 1974).

The weight-specific volumes of the respiratory and circulatory systems in the tufted duck are similar to those reported for the mallard (or its domesticated variety) by Scheid, Slama & Willmer (1974) and Bond & Gilbert (1958) respectively. The present values for the mallard duck are, therefore, substantially below these earlier values in the literature. Hudson & Jones (1982) report a respiratory volume of 109 ml BTPS kg^{-1} in the domestic duck, so the high value of Scheid *et al.* (1974) may result from the fact that they measured end-inspiratory volume and that their ducks were anaesthetized. The present low value for blood volume in the mallard is less easy to explain, particularly as Huang, Sung & Huang (1974) report a value of 126 ml kg^{-1} for domestic ducks. These authors and Bond & Gilbert (1958) used the dye (T-1824) dilution method, but it is not suggested that this could account totally for the differences between the present values and those reported by these two groups of authors. All that can be said is that the present data were obtained at the same time of year, by the same technique and from birds kept under similar conditions. As such, it is felt justifiable to use them at least on a comparative basis.

Thus, from the present study it is clear that the oxygen-carrying capabilities of the tufted duck are greater than those of the mallard. Oxygen uptake is proportional to (body mass)$^{0.73}$ in birds at rest and during exercise (Butler, 1981, 1982), but this would only account for a 12% greater weight-specific oxygen uptake in a 650 g tufted duck compared with a 1 kg mallard, so that the additional oxygen storage is a bonus to the tufted. This could well be related to the fact that this bird dives for its food, in which case it is similar to the situation in diving and non-diving mammals (Packer *et al.* 1969; Lenfant *et al.* 1970a). It might seem strange for the tufted to have such a large respiratory system, compared with the mallard, because this would increase its buoyancy during diving. Certainly in seals the major area for oxygen storage is in the blood (Packer *et al.* 1969; Lenfant, Johansen & Torrance, 1970b), but this may be related to the fact that these animals dive deeply and need to prevent

■r being trapped in the alveoli so as to avoid the bends. The presence of the air sacs in birds means that the respiratory system is an obvious place to store oxygen, and even adélie and gentoo penguins have a respiratory volume as large as 160 ml kg^{-1} during diving (Kooyman *et al.* 1973) and probably dive on inspiration (cf. Kooyman *et al.* 1971). One modification for diving in penguins and the loon is that the bones are not pneumatized (Gier, 1952).

Butler & Woakes (1982*a*) used data from the literature and made several assumptions in order to calculate the usable oxygen stores in the body of an apnoeic tufted duck weighing 0·8 kg. Using the data from the present study, the relative proportions of the anterior and posterior air sacs as reported by Scheid *et al.* (1974), together with the other assumptions made by Butler & Woakes (1982*a*), the usable oxygen stores (at STPD) of a 1 kg mallard and tufted duck have been calculated (Table 2). The value for the tufted is slightly lower than that proposed by Butler & Woakes (1982*a*) since they used a larger value for the volume of the respiratory system (Scheid *et al.* 1974) and did not convert it to STPD. Nonetheless, the calculated usable oxygen stores are 43 % greater in tufted ducks than in mallards and will, therefore, greatly enhance the aerobic diving performance of these birds. The fact that these stores are lower in the mallards is another indication that dabbling ducks are physiologically different from their diving relatives (cf. Butler & Woakes, 1982*b*) and, as such, perhaps they (or their domesticated varieties) should not be used indiscriminately in studies on the physiology of diving in birds.

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