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Tufted ducks Aythya fuligula do not control buoyancy during diving

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Work against buoyancy during submergence is a large component of the energy costs for shallow diving ducks. For penguins, buoyancy is less of a problem, however they still seem to trade-off levels of oxygen stores against the costs and benefits of buoyant force during descent and ascent. This trade-off is presumably achieved by increasing air sac volume and hence pre-dive buoyancy (B_{nre}) when diving deeper. Tufted ducks, Aythya fuligula, almost always dive with nearly full oxygen stores so these cannot be increased. However, the high natural buoyancy of tufted ducks guarantees a passive ascent, so they might be expected to decrease \mathbf{B}_{nre} before particularly deep, long dives to reduce the energy costs of diving. Body heat lost to the water can also be a cause of substantial energy expenditure during a dive, both through dissipation to the ambient environment and through the heating of ingested food and water. Thus dive depth (d_d), duration and food type can influence how much heat energy is lost during a dive. The present study investigated the relationship between certain physiological and behavioural adjustments by tufted ducks to d_d and food type. Changes in B_{pre} , deep body temperature (T_b) and dive time budgeting of four ducks were measured when diving to two different depths (1.5 and 5.7 m), and for two types of food (mussels and mealworms). The hypothesis was that in tufted ducks, Bpre decreases as dd increases. The ducks did not change B_{nre} in response to different diving depths, and thus the hypothesis was rejected. T_b was largely unaffected by dives to either depth. However, diving behaviour changed at the greater d_d, including an increase in dive duration and vertical descent speed. Behaviour also changed depending on the food type, including an increase in foraging duration and vertical descent speed when mussels were present. Behavioural changes seem to represent the major adjustment made by tufted ducks in response to changes in their diving environment.

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For shallow diving waterfowl such as tufted ducks Aythya fuligula, positive buoyancy affords the largest cost of diving to a depth, and maintaining that depth, during a dive (Stephenson et al. 1989, Lovvorn et al. 1991, Wilson et al. 1992). The most comprehensive study on energy costs of submergence in ducks (Stephenson 1994) calculated that for lesser scaup A. affinis diving to 1.5 m, buoyancy accounted for 62% of the mechanical cost of descent and 87% of the cost of remaining at 1.5 m while foraging. Diving ducks carry large volumes of air with them when they dive, for example the respiratory system of lesser scaup has been calculated to contribute 52% of their initial buoyancy (Stephenson 1995).

For penguins, although buoyancy is less of a problem, they appear to decrease the volume of their final exhalation when anticipating diving to a greater depth. In doing so, they are probably trading off an increase in the energy required to work against buoyant force as they descend against the depth at which they can start to ascend passively (Sato et al. 2002), and also against the oxygen stores available in their respiratory system during the dive (Wilson 2003). Presumably, this adjustment for dive depth (d_d) results in an increase in aerobic dive duration. However, in tufted ducks their oxygen stores are close to full before every dive (Halsey et al. 2005) and thus cannot significantly increase their respiratory air volume in response to a deep dive. However, given that they will always ascend passively when returning from the deepest part of the dive due to their high natural buoyancy, a decrease in buoyancy before deeper (and therefore longer) dives would decrease the overall energy costs of diving.

The volume of air in the plumage layer may also be actively adjusted by the bird (Stephenson 1993) and this time the trade off would be energetic costs due to buoyancy against thermoregulatory costs due to conductive heat loss (Stephenson 1993, de Leeuw 1997, Grémillet et al. 1998). Indeed, body heat dissipated to water is likely to be a substantial source of energy loss in many avian divers (Butler and Jones, 1997) and can be correlated to time spent diving (Green et al. 2003).

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The ingestion of food and water at ambient temperature is also likely to reduce core temperature unless energy is invested to heat the stomach contents. For example, Wilson and Culik (1991) estimated that up to 13% of the daily energy expenditure in Adélie penguins may be used to heat ingested food to body temperature (T_b). Food types differing in mass, specific heat capacity and shape might change T_b to differing degrees. The energy value of a food may also influence its effect on lowering T_b, albeit indirectly, since ducks are likely to ingest a greater quantity of a food with a lower calorific density. Furthermore, to ingest a greater quantity may require an increase in time spent submerged at the foraging site, thus increasing the time for body heat to dissipate to the water.

The aim of the present study was to gain an understanding of the physiological and behavioural adjustments of tufted ducks to changes in the diving environment, specifically d_d and food type, where d_d is increased to the extreme of their natural range (Laughlin 1972/1973, Halsey unpubl. data). To this end, this study is based on a modification of the experimental approach of Stephenson (1994) to measure the buoyancy of freely diving tufted ducks. This is the first study to quantify the effect of d_d on this important determinant of underwater locomotory cost in a species of diving waterfowl, with the hypothesis that pre-dive buoyancy (B_{pre}) decreases as d_d increases. The budgeting of time during the dive cycle, as well as changes in T_b, are also measured since, as discussed above, they are known to be intimately linked with buoyancy control and are also probably correlated with food type.

Methods

Experiments were conducted on a circular diving tank (3.9 m diameter $\times 5.7$ m depth) at the Konrad Lorenz Institute in Vienna, Austria, using four adult tufted ducks (two male and two female; 550–800 g). The experimental set-up was very similar to that used by Stephenson (1994). To clarify this set-up and to explain the modifications as applied to the present study, a brief description of the methodology is given here.

During the experiments, the subject bird was encouraged to dive by the availability of food on a tray suspended in the water and the bird always had to surface into a respirometer chamber (Fig. 1). Buoyant force was measured before, and after (B_{post}), each dive by recording the change in air pressure in the respirometer chamber due to the presence or absence of the duck. This was achieved by means of an automated, closed-circuit system based on the principle of continually measuring differential pressures between the respirometer chamber and a second, reference chamber upon the water surface that could not be entered by the duck. Given that the ducks only breathed out immediately prior to resurfacing, all exhaled respiratory air flowed back into the respirometry box. Thus, from these values of buoyant force, the volume of air lost from the plumage layer during a dive (V_{plum}) could be calculated. Respiratory and plumage air volumes at the beginning and end of dives $(V_{r+p_pre} \text{ and } V_{r+p_post}, \text{ respectively})$, were also calculated (Stephenson 1993 for details). The differential pressure signal was calibrated directly in units of buoyant force (newtons, N), by introducing floats of known buoyancy into the respirometer and measuring the pressure change. This also enabled a determination of the accuracy of the pressure transducer (PS309, Validyne Engineering Corp.) within the respirometer and indicated that a change in air volume in the duck within the respirometer chamber could be measured to about+15ml. Because nearly 200 data points were collected to measure buoyancy at each depth, once averaged, the signal-to-noise ratio was high (Parkes et al. 2002).

Measurements of buoyancy were taken when the ducks were foraging at different depths and for either food type. Thus, the effect of d_d on the buoyant force of the ducks could be compared between 1.5 and 5.7 m, when foraging for either mealworms (1-1.5 cm long), or mussels (0.3 to 2.5 cm). Data for the first dive of each trial were not recorded, to enable the subject duck to discover the depth of the food and the food type for that trial. Prior to the experiments, analyses were performed to determine the nutritional and calorific content of these two food types (Halsey et al. in press). Samples of maggots and mealworms were dried at 80°C for 36 hours. Wet and dry weights were used to calculate water content. All nutritional analyses are reported as both % of wet weight and % of dry weight. The gross energy of each sample was determined by bomb calorimetry (Parr 1356 Calorimeter, Parr Instrument Company). Mineral content was determined using a method similar to AOAC method 4.1.10 (official methods of analysis, 1995). Crude fat content and crude protein content were determined using methods similar to AOAC method 7.056 (official methods of analysis, 1980).

In all conditions, the behaviour of the birds both in the respirometer and at the feeding tray was recorded on videotape by a camera at each location. This provided data on a number of variables of dive time budgeting, all of which are defined, and abbreviations assigned, in Table 1. The T_b of the birds were obtained using purpose built, pulse interval modulated transmitters (Butler and Woakes 1989). The transmitters were implanted two months before the start of the experiments, using the procedure of Stephenson et al. (1986).

The effects on buoyancy, T_b and diving behaviour were tested between four birds using paired t tests. All means are presented as mean \pm SE. To avoid animal bias, mean values were obtained for each bird and these means were used to obtain an overall mean.





Results

Data on diving behaviour and T_b at two different depths and for two different food types were collected for 1139 dives, while buoyancy was measured in 787 dives. For each of the four conditions, the number of dives recorded for each individual duck ranged between 52 and 162, while the number of dives where buoyancy was measured ranged between 23 and 125. All significant differences were at the level of P < 0.05.

Buoyancy and diving behaviour at different depths

Table 1 shows the diving behaviour of tufted ducks diving to 1.5 and 5.7 m and for different food types.

Table 1. Mean $(\pm SE)$) variables of diving b	aviour of four tufted	ducks diving for mealw	forms or mussels, at 1.5 or 5.	7 m depth
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	Mealworms	Mussels	Mealworms	Mussels
	1.5 m		5.7 m	
Duration of dive $(t_{desc} + t_f + t_{asc}; \text{ see below}), t_d$ (s)	15.5+0.8**	$20.3 \pm 0.7^{\dagger}$	23.6 + 1.0	24.1 + 0.9
Duration of surface period (duration in between dives), t_s (s)	$17.1 \pm 2.3^{*}$	20.8 ± 2.1	22.7 ± 2.7	23.3 ± 1.5
Duration of foraging period (duration at the feeding tray), $t_f(s)$	$6.4 \pm 0.9^{*}$	$11.4 \pm 0.9^{\dagger}$	$6.2\pm0.7*$	8.6 ± 0.5
Duration of descent (duration of travel from surface to feeding tray), t_{desc} (s)	$4.1 \pm 0.3^{\dagger}$	$3.5 \pm 0.3^{\dagger}$	$9.8 \pm 0.3^{*}$	8.1 ± 0.5
Duration of ascent (duration of travel from feeding tray to surface, t_{asc} (s)	$5.0\pm0.2^{\dagger}$	$5.5 \pm 0.6^{\dagger}$	7.9 ± 0.4	7.4 ± 0.1
Velocity of (vertical) descent, vel _{desc} (s)	$0.4 \pm 0.0^{*\dagger}$	$0.5 \pm 0.0^{\dagger}$	$0.6 \pm 0.0*$	0.8 ± 0.1
Velocity of (vertical) ascent, vel _{asc} (s)	$0.3 \pm 0.0^{\dagger}$	$0.3 \pm 0.0^{\dagger}$	0.7 ± 0.0	0.8 ± 0.0

[†]Represent a significant difference between 1.5 and 5.7 m for the same food type.

*Represent a significant difference between mealworms and mussels at the same depth. Values are deemed significantly different when P < 0.05.

When foraging for mealworms, t_{desc} and t_{asc} were significantly greater at 5.7 m compared to those at 1.5 m (140 and 58%, respectively), despite vel_{desc} and vel_{asc} also being significantly greater (50 and 133%). The value t_d was also significantly higher (52%). When foraging for mussels, t_{desc} , t_{asc} , vel_{desc} and vel_{asc} were again significantly greater at 5.7 m (131, 35, 60 and 166%), while t_d was significantly higher (19%). Also, t_f was significantly lower (25%). The values B_{pre} and B_{post} , and therefore V_{r+p_pre} and V_{r+p_post} , were similar at both depths. This was the case for both types of food (Table 2).

Diving behaviour with different food types

When feeding on mussels, t_f was significantly longer than when feeding on mealworms, at both 1.5 and 5.7 m (78 and 39%, respectively; Table 1). The value vel_{desc} was also significantly greater at both depths when foraging for mussels (25 and 33%). At 1.5 m, t_d and t_s were significantly greater when foraging for mussels (31 and 22%, respectively). The value t_{desc} was significantly lower when foraging for mussels at 5.7 m (16%).

Deep body temperature

The maximum and minimum T_b of the ducks in the present study were similar at both 1.5 and 5.7 m (minima: 40.69 ± 0.08 and $40.79\pm0.10^{\circ}$ C; maxima: 41.06 ± 0.12 and $41.24\pm0.11^{\circ}$ C, respectively). There were also no differences between maximum T_b or between minimum T_b when mealworms or mussels were consumed, at either of these depths (minima: 40.95 ± 0.12 and $40.65\pm0.21^{\circ}$ C; maxima: 41.26 ± 0.18 and $40.98\pm0.24^{\circ}$ C, respectively).

Nutritional values of mealworms and zebra mussels

There are considerable differences in the proportions of lipid, protein and minerals in each food type, and also a large difference in calorific value per unit mass (Table 3). For example, the energy density of the mealworms is 17 times greater than that of the mussels and therefore 17 times more mass of mussel would need to be ingested to equal the same gross energy gain as when ingesting mealworms.

Discussion

To our knowledge, this is the first study to measure the effects of d_d on buoyancy in a diving species. The physiological and behavioural measurements obtained in the present study are within the ranges of those of previous studies on diving in similar species. The value B_{pre} for dives to 1.5 m in the present study is similar to that measured by Stephenson (1994). The maximum and minimum values of T_b are not significantly different between the present study and that by de Leeuw et al. (1997) at either depth. The variables of diving behaviour are within the range of previous studies on tufted ducks (de Leeuw et al. 1997, Halsey et al. 2003b).

Diving to different depths

As depth to the foraging tray increased, there was no measurable change in B_{pre} and thus the hypothesis of the present study was rejected. Given that tufted ducks normally dive well within their aerobic dive limits (Halsey et al. 2003a) and will always ascend passively because of their high buoyancy regardless of body air volume, they can clearly afford to reduce B_{pre} to reduce the energy costs of diving. The fact that they did not do this, even in the extreme environmental condition of diving to 5.7 m, perhaps underlines that, unlike some bird species diving in the wild (Bevan et al. 2002), they were not close to their physiological limits when foraging in the present study. This would suggest that they do not need to fine-tune their physiology to minimise energy costs during dives. Although energy costs would be reduced by decreasing air volume, perhaps the trade-off in oxygen stores against Bpre would result in a decrease in aerobic dive duration. Although tufted ducks usually dive well within their aerobic dive limit, they seem to prefer to dive with a considerable 'safety margin' with regards to oxygen consumption (Halsey et al. 2005), in which case a decrease in aerobic dive duration would

Table 2. Means (\pm SE) of diving variables of four tufted ducks diving for mealworms or mussels, at 1.5 or 5.7 m depth.

	Food item and foraging depth (m)			
	Mealworms	Mussels	Mealworms	Mussels
	1.5		5.7	
Pre-dive buoyancy (B_{pre} ; N) Post-dive buoyancy (B_{post} ; N) Respiratory and plumage air volume at the start of the dive (V_{r+p_pre} ; ml) Respiratory and plumage air volume at the end of the dive (V_{r+p_post} ; ml) Volume of air lost from plumage during dive (V_{plum} ; ml)	$\begin{array}{r} 3.41 \pm 0.21 \\ 2.29 \pm 0.09 \\ 367 \pm 21 \\ 253 \pm 8 \\ 114 \pm 13 \end{array}$	$\begin{array}{r} 3.17 \pm 0.04 \\ 2.25 \pm 0.05 \\ 345 \pm 4 \\ 252 \pm 5 \\ 93 \pm 4 \end{array}$	$\begin{array}{c} 3.37 \pm 0.20 \\ 2.31 \pm 0.18 \\ 364 \pm 21 \\ 256 \pm 18 \\ 108 \pm 18 \end{array}$	$\begin{array}{r} 3.38 \pm 0.08 \\ 2.25 \pm 0.10 \\ 368 \pm 7 \\ 253 \pm 10 \\ 115 \pm 11 \end{array}$

	Mealworms 7	Cenebrio molitor	Mussels Dreiss	ena polymorpha	Ratios meal	worms: mussels
% Water	60.7		57.3		1.1	
	Wet	Dry	Wet	Dry	Wet	Dry
Gross energy (MJ/kg) % Lipid % Protein % Mineral	15.5 19.7 1.4	27.2 39.3 50.2 3.61	0.7 8.9 30.5	1.6 1.7 3.8 71.3	21.8 2.2 0.0	17.0 23.1 13.2 0.1

Table 3. Differences in water and nutritional content between mealworms and zebra mussels.

provide an alternative explanation for why they do not reduce their $B_{\rm pre}\!.$

With regards to adjusting plumage air volume, the measurements of buoyancy and V_{r+p} variables in the present study support the hypothesis of Stephenson (1995), whose measurements of plumage gas volumes in diving ducks suggest that only slight levels of ptilosuppression occur before the start of a dive and thus there is little scope for an increase in plumage volume when diving to greater depths.

De Leeuw et al. (1997) found no significant difference in minimum and maximum T_b at different feeding depths in tufted ducks and suggested that this could be due to an increase in the volume of the plumage layer prior to diving to greater depths. However, evidence from the present study suggests that this cannot be the explanation for such constant T_b. The large variation in changes in T_b recorded in different avian diving species (Wilson and Grémillet 1996, Bevan et al. 1997, 2002, Grémillet et al. 1998) and between individuals (Green et al. 2003) is probably due to a number of physiological, environmental and behavioural factors. The lack of change of T_b in tufted ducks may most easily be explained either by their relatively short dive durations, or by the heat generated from the high energy costs of diving due to their relatively high positive buoyancy (Wilson et al. 1992).

However, while B_{pre} and T_b do not change in tufted ducks as d_d changes, there are clear changes in diving behaviour. Unlike many avian divers such as the penguins (Peters et al. 1998), tufted ducks always descend close to vertically when foraging (Lovvorn 1994) and thus descent velocity is more or less equal to vertical swimming speed. When the ducks had to dive more deeply for food, their swimming speed was higher. This trend has not previously been satisfactorily tested for in ducks and contrasts to many other diving birds that tend to dive at a consistent swimming speed but change their descent velocity by changing their angle of descent (Wilson et al. 2002, Wilson and Quintana 2004). Cormorants and penguins are predominantly pelagic feeders and thus travelling through the water column at an angle to the vertical may increase their chances of locating prey (Wilson and Wilson 1995). Tufted ducks, in contrast, are mainly benthic feeders, and thus may only be concerned with travelling directly and quickly to the foraging site. The changes in veldesc with dd in the present study can be explained by the fact that, for the same amount of locomotory effort, the ducks would be able to descend at a higher average velocity when diving further into the water column, since mean hydrostatic compression, as well as air lost from the feathers due to the increased transit time, would be greater, and thus buoyancy would be less (Wilson et al. 1992).

When foraging for mealworms, the ducks did not change tf as dd changed, in agreement with the findings of de Leeuw et al. (1997) across the same range of d_d (1.5 to 5.7 m). Thus, t_d was longer when diving to 5.7 m because of the longer travelling times. However, in contrast, the ducks decreased tf when diving to 5.7 m to forage for mussels. According to De Leeuw and van Eerden (1992), this may be because tufted ducks choose smaller mussels when at greater depth to minimise the time spent diving and thus to maximise rate of gross energy intake, since the handling time of mussels increases with shell length. This has also been shown with spectacled eiders feeding on shallowly buried clams (Richman and Lovvorn 2003). Given that t_f at 5.7 m is still greater when foraging for mussels than when foraging for mealworms, there may be a trade-off in this particular condition between increasing t_f in response to foraging for (energy poor) mussels and decreasing t_f in response to diving to 5.7 m by foraging for smaller mussels and thereby increasing the rate of gross energy intake.

Diving for different foods

At 1.5 m, when the birds were foraging for mussels, they had a greater t_f , which in turn increased t_d . Changes in t_f in response to differing food types in diving ducks have been reported previously by Ball (1994). The value t_s was also greater, presumably in response to the consequent increase in oxygen consumption during the dive. The ducks also increased t_f when foraging for mussels at 5.7 m. Assuming that the lower energetic value of mussels (Table 3), plus the costs of crushing the shells in the gizzard (de Leeuw 1997), means that the net rate that energy is gained when foraging for the mussels is lower than when foraging for mealworms, these increases in t_f are predicted by the optimal diving model of Houston and Carbone (1992), albeit very subtly. At 5.7 m, however, t_d (and t_s also) did not increase. The ducks achieved this by increasing vel_{desc} , therefore decreasing t_{desc} to compensate for the increase in t_{f} . Indeed, vel_{desc} also significantly increased at 1.5 m when foraging for mussels, however there was no decrease in t_{desc} . The increase in vel_{desc} at both values of d_d must have been due to an increase in locomotory effort. This behaviour is not predicted by optimal foraging models and was not observed by Ball (1994).

Although de Leeuw et al. (1997) reported a drop in T_b in tufted ducks while consuming mussels, the ducks in the present study showed no greater decrease in T_b when feeding on mussels as opposed to mealworms. The results from the present study might suggest that the amount of water ingested along with the food was of a similar volume whichever food type was consumed. Alternatively, the heat generated by the gizzard crushing the ingested mussel shells may have compensated for the extra water consumed with the mussels.

In summary, tufted ducks, unlike some other bird species, do not respond to changes in depth by adjusting their $B_{\rm pre}$. Arguably, their $T_{\rm b}$ does not change as $d_{\rm d}$ changes either, or indeed as food type changes. Nevertheless, tufted ducks do respond to a changing environment with prominent adjustments in behaviour. These include changes in diving behaviour that have not previously been reported, such as increases in vel_{desc} as $d_{\rm d}$ increases or as the calorific value of the food decreases. Thus the suite of responses of tufted ducks to certain changes in the foraging environment are different from those of many other diving birds in being predominantly behavioural. An overarching explanation for this could be their relatively shallow diving depths and short dive durations.

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