

A METHOD FOR CONTROLLING THE FEEDING BEHAVIOUR OF AQUATIC BIRDS: HEART RATE AND OXYGEN CONSUMPTION DURING DIVES OF DIFFERENT DURATION

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Summary

Tufted ducks, *Aythya fuligula*, were trained to dive for different durations in shallow tanks using a computer-controlled system of lights. The birds were rewarded with food for a correct response, i.e. performing a dive of the required duration. When dive durations (t_d) elicited by the system were longer than the durations required, the extra time was spent feeding. As the required duration was increased, so the time spent feeding decreased, and the required and actual dive durations approached equality. This occurred at approximately 40 s, although some birds did perform dives of up to 45 s.

Heart rate (f_H) and oxygen consumption (\dot{V}_{O_2}) were measured from the birds during voluntary diving using an implanted radiotransmitter and respirometry, respectively. The oxygen consumption during submersion decreased with increasing mean t_d , and may reflect a reduction in aerobic metabolism as a dive progressed, possibly as a result of reduced buoyancy or through a gradual switch to anaerobic metabolism.

Over a total dive cycle (the time spent submerged plus that spent on the surface between dives), f_H proved to be a very good predictor of \dot{V}_{O_2} , with an error of only +7.9%. This compares favourably with other methods used to determine the energy expenditures of animals, e.g. the doubly labelled water and the time energy budget methods, and shows that the electronic acquisition of f_H could be a useful tool for estimating the energy usage of free-living, aquatic birds.

Introduction

When the tufted duck (*Aythya fuligula*) dives for a mean dive duration (t_d) of 14.4 s, the overall aerobic energy expenditure is similar to that whilst swimming on the surface at maximum sustainable speed (Woakes and Butler, 1983). The oxygen stored within the body (in the lungs, blood and tissues) is sufficient to maintain this elevated metabolic rate for a calculated maximum t_d of approximately 51 s

Key words: diving, heart rate, oxygen consumption, ducks, training system, *Aythya fuligula*.

(Woakes and Butler, 1983). So, for dives of normal duration (10–20 s; Dewar, 1924; Draulans, 1982), there should be no need for the ducks to resort to anaerobic metabolism. However, t_d increases with depth of water or distance travelled under water (Dewar, 1924; Stephenson *et al.* 1986). During winter, when the ducks may have to dive under ice to obtain food, t_d may increase, thus increasing the demands made on the oxygen stores.

Stephenson *et al.* (1986) monitored heart rates (f_H) in ducks under conditions that simulated those encountered by birds diving under ice. They found that f_H started to decrease towards the end of long dives (>35 s), possibly indicating that there is a gradual shift from an exercise response (tachycardia and peripheral vasodilatation) to the 'classical' dive response (bradycardia, peripheral vasoconstriction and an increasing dependence on anaerobic metabolism; Irving, 1939). Alternatively, the depressed f_H during the long dives may indicate that there is a reduction in the amount of energy that the duck needs to expend in order to remain submerged. Whether the reduction in heart rate is caused by a progressive shift to the 'classical' dive response or by a decrease in work load, it will, presumably, be accompanied by a reduction in the oxygen consumed during the dive. Indeed, Woakes and Butler (1983) reported that, for six tufted ducks, the oxygen consumption during submersion tended to decrease with increasing mean t_d . Although the overall trend was not statistically significant, the \dot{V}_{O_2} during submersion of the animal performing the longest dives was significantly lower than that of the animal performing the shortest dives.

Woakes and Butler (1983) also monitored f_H during diving and found that, although it was significantly higher than that at rest, it was significantly lower than that when the birds were swimming and consuming oxygen at the same rate. Stephenson (1987) re-analysed the data of Woakes and Butler (1983) and calculated the mean \dot{V}_{O_2} and mean f_H over the total dive cycle (i.e. the time spent diving plus the time spent at the surface before the next dive, t_c). He found that the data fell on the oxygen uptake/heart rate line obtained from birds swimming at the surface (Woakes and Butler, 1983). This suggests that heart rate can be used as an indicator of the oxygen consumption of aquatic birds in the field during different activities, not perhaps on a time scale of a few seconds, where heart rate can fluctuate rapidly (Stephenson, 1987), but certainly over complete dive cycles (cf. Fedak *et al.* 1988).

As the dive durations of tufted ducks are proportional to the depth of water (Dewar, 1924), spontaneous dives of relatively long duration can only be obtained in tanks that would be too deep for the attachment of monitoring equipment such as catheters. Previous attempts in this laboratory to train ducks to remain submerged for specific durations (diving to depress a lever and waiting for the delivery of food) have been unsuccessful. Above certain required dive durations (approx. 20 s) the animals dived, depressed the lever, surfaced, then dived again to obtain the food. The aims of the present study were, therefore, threefold: (1) to devise a system whereby tufted ducks could be trained to dive in shallow indoor tanks for durations close to the recorded maximum for the species; (2) to measure

\dot{V}_{O_2} and f_H of these tufted ducks over dives of long duration; (3) to investigate the relationship between \dot{V}_{O_2} and f_H over the total dive cycle.

Materials and methods

Seven tufted ducks of either sex (mean mass \pm s.e. of mean = 571 g \pm 14) were held in an outside aviary where they had free access to a pool (10 m \times 4.5 m \times 1.9–2.8 m deep).

When required, birds were transferred indoors, where they were kept on individual tanks (0.6 m \times 0.6 m \times 1.0 m; water depth 0.6 m). Water temperature was not controlled and varied throughout the year (mean water temperature = 14.4 °C). A thin film of one-way plastic (Scotch tint solar control film) was fixed onto the front of the glass of the tanks to avoid any disturbance to the ducks caused by movements in the room. To elicit dives of long duration in these shallow tanks, a system of computer-controlled lights was used to train ducks to dive on command and to remain submerged for food.

The diving tanks and training procedure

The requirements of the training system were that the bird should dive in relatively shallow water for extended durations and not be able to obtain food unless it remains submerged for the required duration. This was achieved by using a computer and interface coupled with a set of eight infrared light emitters on one side of the tank 2.5 cm above the water surface and a complementary set of eight sensors on the other side. When the duck was on the surface, at least one of the infrared light beams was interrupted. A computer program set the required duration of each dive and the duration of the interval between dives, achieved by controlling lights situated at the bottom of the tank and a food-dispensing system (Fig. 1). At the start of a training session, which lasted for 2–3 h, data for dive duration, duration of the interval at the surface and time allowed for the duck to respond to the stimulus were entered into the program and could be adjusted to suit each individual.

A session was started by the illumination of a yellow light at the bottom of the tank (Fig. 2A). As soon as the duck responded to this by diving within the allowed time, a red light was illuminated (together with the yellow light) to act as a bridging stimulus between the initial stimulus and the delivery of food (Fig. 2B). If the duck did not respond within the allowed time, the yellow light was turned off and that cycle terminated. The duration of a dive was recorded by the computer. As soon as it equalled the required dive duration, a green light was switched on, the yellow and red lights were extinguished, and the feeder was operated (Fig. 2C). The food delivered fell through the grid of a false bottom in the tank, so the duck had to be present at the time of delivery to obtain food. If the duration of the dive was shorter than required, the yellow and red lights were switched off and the cycle was aborted. Using this system it was possible to train, simultaneously, four ducks on separate tanks. The food delivered by the system was in the form of

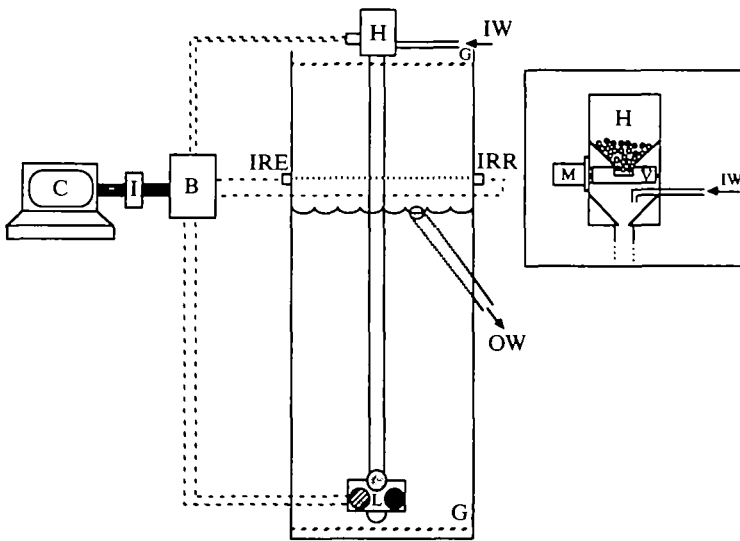


Fig. 1. A diagrammatic representation of the tank and accessories used to train tufted ducks to dive for different durations. The inset represents a more detailed view of the food delivery system. B, control box; C, computer; G, grids; H, hopper containing corn; I, interface; IRE, infrared emitter; IRR, infrared receiver; IW, inflowing water; L, light box comprising three different coloured lights; M, motor; OW, outflowing water; V, rotating valve, used to deposit a set amount of corn. The dashed lines emanating from the control box represent electrical connections.

corn (Heygates Ltd) and was supplemented by growers pellets (Heygates Ltd) given at least once a week. By regulating the pellet supplement, the body mass of the birds was maintained at a steady level.

With a naive duck, the time allowed to react to the stimulus was set very long to allow the animal to get used to the illumination of the lights. This also ensured that there was a large chance that any dives made by the duck would fall within one of these periods, thus triggering the illumination of the red light. By setting the required dive duration to a few seconds only, operation of the feeding system would also occur frequently. For each stimulus, the time it took for the duck to respond and the duration of the dive were stored on disc for later analysis.

Fig. 3 illustrates the effectiveness of the system for the first five ducks (three males and two females) that were trained. It took these animals 1–5 days to learn what was expected of them, and dives of 10–15 s duration were achieved within 2 weeks. It can be seen from Fig. 3 that, as the required dive duration increased, the difference between actual and expected dive durations decreased, i.e. the time spent feeding decreased. These data predict that actual dive duration should equal required duration at 39 s. The maximum dive duration achieved with this system was 43.6 s.

When a duck was fully accustomed to the tanks and the feeding system, it was trained to dive for durations of approximately 20 s. All ducks were then implanted,

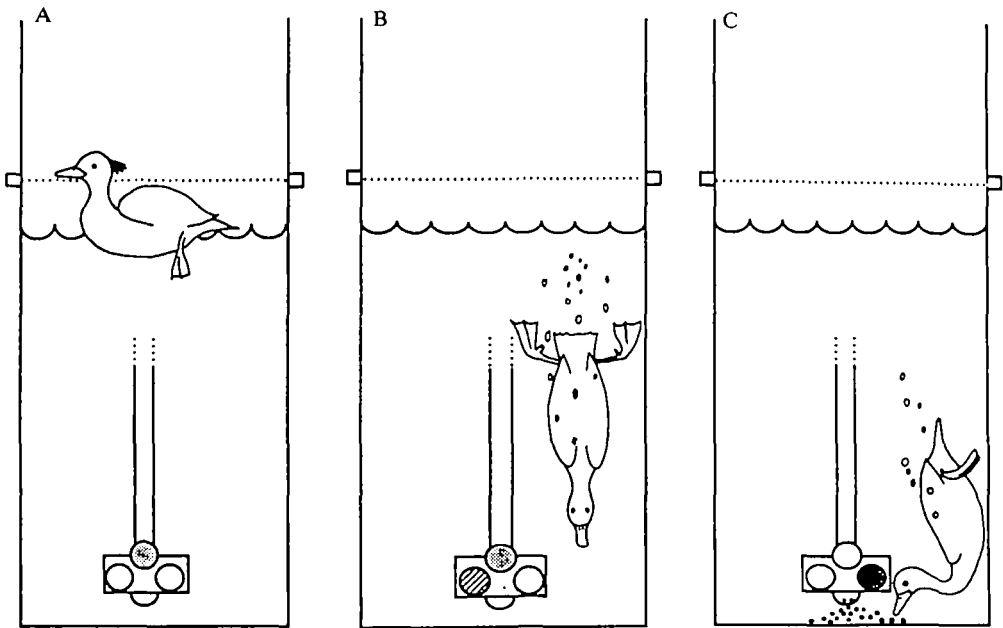


Fig. 2. Sequence of lights used to train the ducks. (A) Yellow light illuminated to elicit diving. (B) Red light also switched on when duck dives. (C) Green light lit and food dispenser activated. For further details see text.

under halothane anaesthesia, with a pulse interval modulated radiotransmitter (Butler and Woakes, 1989) to monitor heart rate. Details of the implantation procedure are given by Stephenson *et al.* (1986). After recovering from the implantation of the radiotransmitter, the ducks were further trained until they were able to dive for durations close to the observed maximum of 45 s (Dewar, 1924; Stephenson *et al.* 1986).

Oxygen consumption was measured by respirometry as described previously (Woakes and Butler, 1983; Butler and Woakes, 1984). The birds were trained to dive from within a respirometer (internal volume=22.82 l), which housed two fans to ensure that the gases within it were well mixed. Air was drawn through the box at a rate of 15–20 l min⁻¹. The concentrations of the gases leaving the respirometer were continuously monitored by a rapidly responding mass spectrometer (MGA 200, Airspec) that had been calibrated with gas mixtures prepared by a precision gas-mixing pump (Wöstoff Pumps, Bochum). A rotary valve automatically switched the gas being sampled from the outflowing to the inflowing air every 60 s for 2 s. The signal from the implanted radiotransmitter was picked up by a receiver (Sony 5090), and was converted into an electrocardiogram (ECG) by a purpose-built decoder (Woakes, 1980).

Experimental protocol

The birds were placed in the respirometer at least 1 h before any measurements

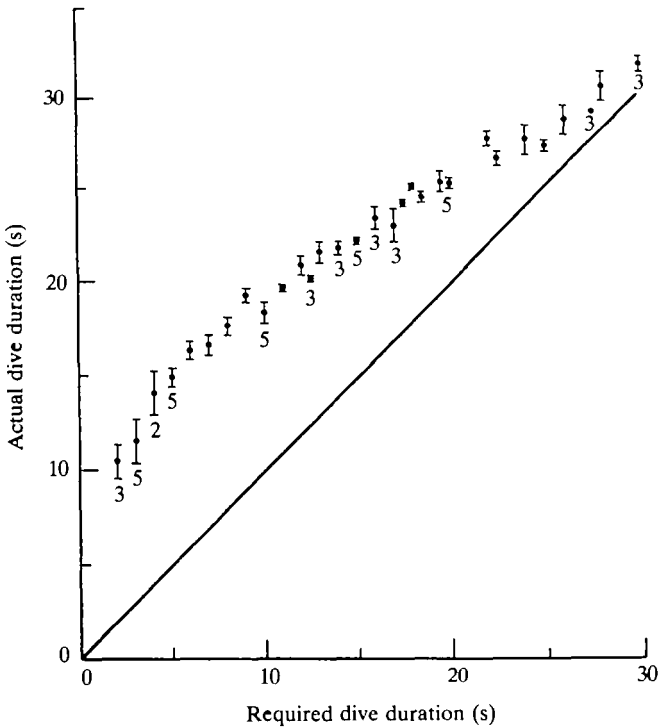


Fig. 3. Response of five tufted ducks (3 ♂, 2 ♀) to training on the system illustrated in Figs 1 and 2, showing mean values (\pm s.e.) of actual durations of dives performed at different required durations. The number of ducks contributing to each point is four, except where indicated otherwise. The line from the origin indicates actual dive durations equal to required durations.

were taken. They were well accustomed to the respirometer and settled down within a few minutes, as indicated by a low resting heart rate. The training program was then started and was set to elicit dives of between 25 and 40 s. As not all dives were of sufficient duration to be rewarded with food, shorter dives were also recorded. Each feeding session lasted 3 h. The mass spectrometer was calibrated before and after each experiment. Air temperature and relative humidity were measured within the respirometer box and in the inlet air; water temperature was also measured. f_H was determined by passing the ECG through an instantaneous rate meter (Devices Ltd). f_H , ECG and the output from the mass spectrometer were displayed on a four-channel pen recorder (Lectromed Ltd).

The traces from the pen recorder were digitized using a digitizer (GTCO Digipad 5, S.S.I. Ltd) connected to a computer (BBC model B). A BASIC program converted the traces into the oxygen uptake during the interval spent at the surface between dives (O_{2up}), and measured the duration of this interval (t_i), the duration of the dive (t_d) and the duration of the total dive cycle (t_c). O_{2up} divided by t_c gives the rate of oxygen consumption over the dive cycle ($\dot{V}_{O_{2c}}$).

The oxygen consumption during diving activity was calculated by the mathematical technique described by Woakes and Butler (1983). The same technique was also applied to the resting measurements. Briefly, the air in the respirometer is mixed in a very short time ($\tau < 1$ s) by two fans and, because of this very good mixing, the measurements of oxygen and carbon dioxide in the outlet gas are effectively a measure of the mean concentrations of these gases inside the respirometer. By treating the box as both an open- and a closed-circuit system, and by measuring differences in gas concentration to within 0.001 %, gas exchange over periods as short as 2 s could be calculated, though this was usually done for the complete interdive interval. If the O_{2up} of the duck is equivalent to the amount consumed whilst at the surface plus the amount consumed during the preceding dive, then a linear multiple regression analysis can be performed between t_d , t_i and O_{2up} (see Woakes and Butler, 1983, for the assumptions made). The format of the regression equation is:

$$y = a + b_{y1}x_1 + b_{y2}x_2,$$

where, in the present study, y is O_{2up} in ml, x_1 is t_d in s, x_2 is t_i in s, a is the y intercept, b_{y1} is the partial regression coefficient of y on x_1 , representing the average rate of oxygen consumption during submersions of mean duration t_d in $ml\ s^{-1}$ ($\dot{V}_{O_{2d}}$), and b_{y2} is the partial regression coefficient of y on x_2 , representing the average rate of oxygen consumption during the surface intervals of mean duration t_i in $ml\ s^{-1}$ ($\dot{V}_{O_{2i}}$).

Analysis of a dive was only carried out if the dive itself lasted longer than 10 s and if the next dive occurred within 60 s.

The volumes of all gases were converted to STPD. Mean values are given \pm s.e. for N animals. To avoid animal bias, mean values were obtained for each duck and these means were used to obtain the final mean. A significant difference between means was tested with Student's t -test (assuming unequal variance) or the paired t -test, as appropriate, using the MINITAB statistical package. Significance was tested at the 95 % confidence level.

Summary of symbols used

t_d	dive duration (s).
t_i	duration of the interval spent at the surface between dives (s).
t_c	duration of the dive cycle, $t_d + t_i$ (s).
O_{2up}	oxygen uptake during t_i (ml).
\dot{V}_{O_2}	rate of oxygen consumption ($ml\ s^{-1}$).
$\dot{V}_{O_{2c}}$	rate of oxygen consumption over t_c ($ml\ s^{-1}$).
$\dot{V}_{O_{2d}}$	average rate of oxygen consumption during submersions of mean duration t_d ($ml\ s^{-1}$).
$\dot{V}_{O_{2i}}$	average rate of oxygen consumption for surface intervals of mean duration t_i ($ml\ s^{-1}$).
f_H	heart rate ($beats\ min^{-1}$).
f_{H5}	heart rate over the last 5 s of a dive (excluding the 1 s prior to surfacing).

Results

Heart rates were obtained from five ducks and resting values ranged from 95 to 129 beats min^{-1} , with a mean of 119 ± 6 beats min^{-1} . Resting \dot{V}_{O_2} ($N=7$) of the individual ducks ranged from 0.162 to 0.294 ml s^{-1} , with a mean of 0.218 ± 0.029 ml s^{-1} .

It was possible to train ducks to dive from within a respirometer box for a maximum t_d of 43.6 s. The total number of dives recorded (n) was 1012. The dive durations for individual birds were normally distributed about the mean. Mean $\text{O}_{2\text{up}}$ was 23.49 ± 2.18 ml, at a mean t_d of 24.3 ± 1.7 s and a mean t_i of 30.0 ± 1.9 s ($N=7$). Mean $\dot{V}_{\text{O}_{2c}}$ was 0.441 ± 0.035 ml s^{-1} . Mean diving f_{H_5} , measured over the last 5 s of each dive (but excluding the final second, which contains the pre-surface increase), had values for each animal of between 111 and 186 beats min^{-1} , with a mean of 145 ± 17 beats min^{-1} ($N=5$).

From the linear multiple regression analysis, the mean $\dot{V}_{\text{O}_{2d}}$ and $\dot{V}_{\text{O}_{2i}}$ of the seven ducks were 0.374 ± 0.044 ml s^{-1} (range 0.182–0.545 ml s^{-1}) and 0.442 ± 0.044 ml s^{-1} (range 0.255–0.567 ml s^{-1}), respectively (see Table 1). For each duck, the multiple regression between $\text{O}_{2\text{up}}$, t_d and t_i was highly significant. The partial correlation coefficients (r), however, were low, ranging from 0.35 to 0.59 for the dives and from 0.50 to 0.73 for the surface intervals. There was a tendency for $\dot{V}_{\text{O}_{2d}}$ to decrease as mean dive duration increased (dashed line, Fig. 4), although for the present data the relationship was not significant. If, however, the data from the present study are pooled with those from Woakes and Butler (1983), the relationship is significant, and 87% of the variation in $\dot{V}_{\text{O}_{2d}}$ can be predicted from the mean dive duration (solid line, Fig. 4). The relationship between the two variables is described by the equation:

$$\dot{V}_{\text{O}_{2d}} = 0.838 - 0.019 (\pm 3.34 \times 10^{-3}) t_d, \quad r^2 = 0.87.$$

The data for f_{H} and $\text{O}_{2\text{up}}$ from all the dives were subdivided, on the basis of dive duration, into classes at 5 s intervals (10–14.9 s etc.). The results of the analysis subsequently performed are shown in Table 2 and Fig. 5. f_{H} , both throughout the dive cycle and over the final 5 s of a dive, was significantly correlated with the mean

Table 1. Mean (\pm S.E.) of measured variables in seven tufted ducks at rest and during diving

	Duration (s)	Oxygen consumption (ml s^{-1})	Heart rate (beats min^{-1})
Rest	—	0.218 ± 0.029	119 ± 6
Dives	24.3 ± 1.7	$0.374 \pm 0.044^*$	$174 \pm 21^\dagger$
Surface, between dives	30.0 ± 1.9	$0.442 \pm 0.044^*$	—
Total dive cycle	54.4 ± 3.4	0.441 ± 0.035	202 ± 17
<i>N</i>	7	7	5

* Estimated oxygen consumption for events of the stated mean duration.

† Heart rate during the whole period spent under water.

Table 2. Means of measured variables at different dive durations from the pooled data for seven tufted ducks

Range of dive durations (s)	t_d (s)	t_i (s)	t_c (s)	O_{2up} (ml)	$\dot{V}_{O_{2c}}$ (ml s ⁻¹)	f_{H_5} (beats min ⁻¹)	n
10–14.9	12.0	25.0	37.0	17.49	0.489	181	56
15–19.9	17.8	29.4	47.3	22.54	0.479	174	159
20–24.9	22.5	29.4	52.0	24.04	0.464	169	309
25–29.9	27.2	31.0	58.2	26.09	0.448	146	292
30–34.9	32.2	32.6	64.9	27.65	0.425	136	121
35+	37.2	36.3	73.4	30.01	0.408	115	46

t_d , mean dive duration; t_i , mean time at the surface between dives; t_c , mean total dive cycle duration; O_{2up} , mean total oxygen uptake during surface interval; $\dot{V}_{O_{2c}}$, mean rate of oxygen consumption over total dive cycle; f_{H_5} , heart rate over last 5 s of dive (excluding the 1 s prior to surfacing); n , number of dives recorded at that duration range.

Figures given are the mean values.

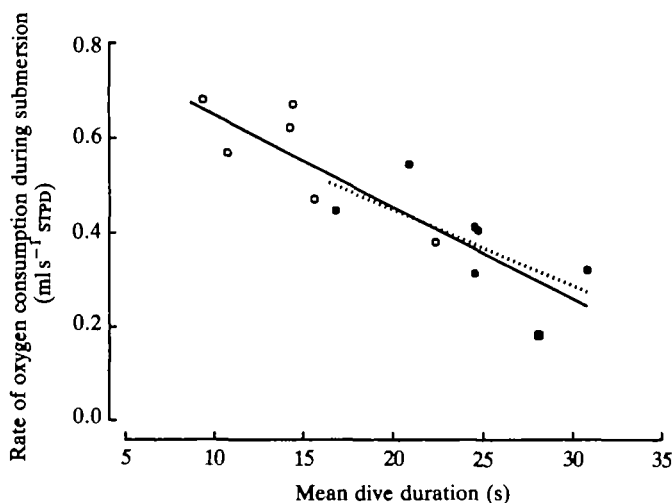


Fig. 4. Relationship between the average rate of oxygen consumption during submersion ($\dot{V}_{O_{2d}}$) and mean dive duration (t_d). The filled circles are the values obtained from the seven ducks used in the present study. The regression line of these data (dashed line) is described by the equation $y=0.80-0.017x$, $r^2=0.47$, where y is $\dot{V}_{O_{2d}}$ and x is t_d . The open circles are the values from the six ducks used by Woakes and Butler (1983). The regression line through the pooled data (solid line) is described by the equation $y=0.838-0.019x$, $r^2=0.87$.

t_d of each class, with f_H decreasing as t_d increased. Similarly, as class t_d increases there is a decrease in $\dot{V}_{O_{2c}}$. Mean f_H over the total dive cycle and $\dot{V}_{O_{2c}}$ are well correlated with the different class t_d , and the derived regression line is not significantly different ($P>0.10$) from that obtained by Woakes and Butler (1983) for swimming ducks (Fig. 6).

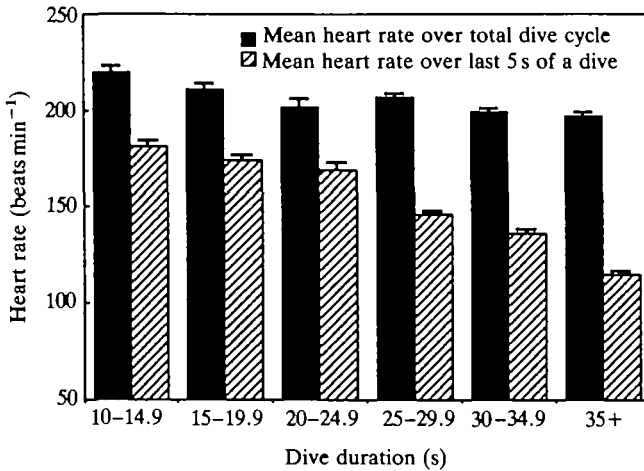


Fig. 5. Heart rate over the total dive cycle and over the last 5 s of a dive (excluding the final second prior to surfacing), at different mean dive durations. The values are the means \pm s.e. The means were obtained from the pooled data for all the ducks, the data having been split into dives of different durations.

If the regression equation of \dot{V}_{O_2} against f_H , derived from the swimming data of Woakes and Butler (1983), is used to predict the \dot{V}_{O_2} of the ducks in the present study from their measured heart rates, the error involved in applying it to individual birds can be considerable (Table 3). If, however, the equation is applied to the mean heart rate data (i.e. that from all the birds), there is remarkably good agreement between the predicted and the measured oxygen consumptions, with a

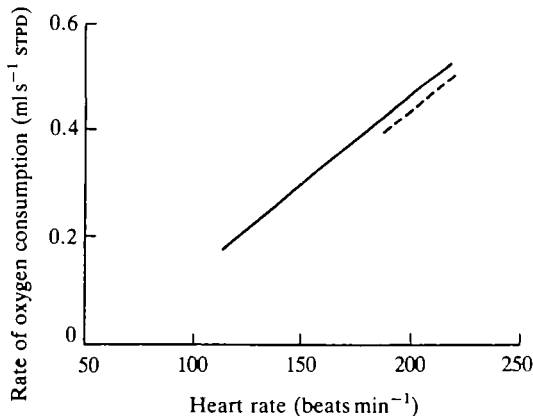


Fig. 6. Relationship between rate of oxygen consumption and heart rate. The solid line is the relationship between the two variables for swimming ducks (Woakes and Butler, 1983): $y=0.00327x-0.193$. The dashed line is derived from data over the total dive cycle obtained at different dive durations (see Fig. 5 and Table 2): $y=0.00322x-0.212$, $r^2=0.72$. In both cases y is the rate of oxygen consumption (ml s^{-1}) and x is heart rate (beats min^{-1}).

Table 3. Errors involved in predicting mean oxygen consumption (\dot{V}_{O_2} , $ml s^{-1}$) from mean heart rate (f_H , $beats\ min^{-1}$) in resting and diving tufted ducks

Source	Measured		Predicted \dot{V}_{O_2}	Percentage error*	
	f_H	\dot{V}_{O_2}		Range	Mean
Data from individual birds					
Resting	119	0.218	0.196	-60 to +42	-10.0
Over total dive duration	174	0.374†	0.375	-51 to +56	1.1
Over total dive cycle	202	0.441	0.477	-3 to +80	7.9
Pooled data from all birds‡				From dives of different duration	
Total dive cycle	206	0.452	0.481	+1 to +11	6.5

The equation used to predict oxygen consumption from heart rate was $y=0.003271x-0.193$, where y is oxygen consumption ($ml s^{-1}$) and x is heart rate ($beats\ min^{-1}$) (Woakes and Butler, 1983).

* The percentage error between the measured oxygen consumption and that predicted from the heart rate.

† Estimated from multiple regression analysis.

‡ From data in Fig. 5 and Table 2.

mean algebraic error of only -10% in resting birds and of +7.9% over a complete dive cycle (Table 3). Interestingly, if the pooled data are used (Table 2 and Fig. 5), the mean error between predicted and measured oxygen consumption is +6.49% (Table 3).

Discussion

One of the main objectives of this study was to devise a system whereby tufted ducks could be trained to dive for relatively long durations in shallow tanks of water. The ease with which some (although it has to be said not all) of the ducks were trained makes this method a very potent one for the study of the physiology of diving in these birds. Dives of over 35s duration can be obtained in a water depth of only 0.6 m whereas such durations in nature normally occur in water of over 4 m depth (Dewar, 1924). This means that it is now possible to study the metabolism of these, and similar-sized, aquatic birds and to record physiological variables, such as blood pressure, blood flows etc., during dives of relatively long duration. This should allow far more detailed studies of diving in these birds to be performed than has previously been possible. As with any apparatus, the present system has some drawbacks, probably the biggest of which is that the ducks, when diving, will not be subjected to the same hydrostatic pressures that they would be in deeper water. The beneficial effects of an increase in hydrostatic pressure, e.g. an increase in the partial pressure of the gases in the respiratory system and a decrease in the buoyancy resulting in lower energy costs during diving, will not, therefore, apply.

The mean resting oxygen consumptions of the tufted ducks in the present study were higher than those found in previous studies (Woakes and Butler, 1983, 1986; Butler *et al.* 1988). The temperature of the water was, however, approximately 5°C lower in this study than in the others, which would cause an increase in the metabolic rate in order to enhance heat production to maintain body temperature (Stahel and Nicol, 1988; Bevan and Butler, 1989).

The partial correlation coefficients obtained from the linear multiple regression analyses were not as high as those obtained by Woakes and Butler (1983), and this may have been due to the duration of the interval between dives being controlled by the training apparatus. t_i in the present study was approximately twice that found in other studies on spontaneously diving tufted ducks (Butler and Woakes, 1979; Woakes and Butler, 1983), allowing the ducks to perform other activities between the dives (cf. Stephenson *et al.* 1988). The $t_d:t_i$ ratio increased as t_d increased, reflecting the fairly constant t_i imposed by the training system. A minimum t_i of 25 s was allowed in the present study before the ducks were prompted to dive again, on the assumption that this would allow them to recover fully from the previous dive. This would be especially relevant for the longer dives, during which anaerobic metabolism may have been brought into play. When using the training system in the future, it may be advisable to activate the training cycle immediately after the ducks have surfaced, thus allowing the animal to determine the time it spends at the surface.

The mean $\dot{V}_{O_{2d}}$ from all the ducks was significantly lower than that found by Woakes and Butler (1983). This is not surprising as the dives were 70% longer and one of the findings of this study is that birds diving for longer durations have a lower $\dot{V}_{O_{2d}}$ than those that dive for shorter durations. At first sight, this might suggest that some birds are more efficient than others and can, therefore, remain submerged for longer periods. It might also be indicative of what happens to oxygen consumption during a single dive. Consequently, Fig. 4 may be illustrating the actual change in oxygen consumption that occurs in each duck during a dive, i.e. aerobic metabolism decreases throughout a dive. It is interesting to note that, for dives longer than 35 s duration, f_H over the last 5 s was nearly at the resting level, even though the ducks were still beating their legs to remain submerged. This may reflect a lower oxygen demand during the later portion of a dive.

To elicit dives of up to 45 s duration, the ducks had to be trained over several weeks. Stephenson *et al.* (1989) found that ducks trained to dive for long distances and long durations had a reduced end-expiratory lung/air sac volume compared with that of control birds. Consequently these birds should have had a lower metabolic requirement during diving as their buoyancy, and hence the work required to remain submerged, would have been reduced. It may be that the training of the ducks in the present study contributed to their ability to withstand submergence with low energy costs (cf. Woakes and Butler, 1983).

During exercise, many animals preferentially perfuse the active muscles as a result of peripheral vasoconstriction of the inactive muscles and visceral organs (Armstrong *et al.* 1987; Musch *et al.* 1987). This is also true of tufted ducks. When

swimming at maximum sustainable speed, they redistribute blood away from the inactive pectoral muscles and parts of the gastrointestinal tract (Butler *et al.* 1988). During long dives there may be a more severe vasoconstriction occurring in these areas coupled with an adequate supply to the active leg muscles, central nervous system and heart. There is, of course, a possibility that during the later portion of the long dives the ducks gradually increase the amount of energy obtained through anaerobic metabolism, leading to an accumulation of lactate, and conserving the dwindling oxygen stores for the oxygen-dependent tissues. However, until the levels of blood lactate are measured during a dive, this can only be surmised. Before the animal resorts to net anaerobic metabolism, there could well be an increase in lactate production in some parts of the body, matched by an increase in lactate oxidation in the active skeletal muscle, i.e. there might be an increase in the turnover of lactic acid but not a net accumulation (Brooks, 1985). The ability of diving mammals to oxidise lactate has been demonstrated for Weddell seals. A high level of lactate in the blood after a long dive did not deter the seals from making shorter dives immediately afterwards, during which the levels of lactate actually fell, indicating that the seals were utilizing the lactate as a substrate for ATP production (Castellini *et al.* 1988).

In measuring the energetics of free-living animals, two main techniques have been used – time energy budgets (TEB) and the doubly labelled water (DLW) method (Weathers and Nagy, 1980; Walsberg, 1983; Weathers *et al.* 1984; Bryant and Tatner, 1986; Costa and Prince, 1986; Obst *et al.* 1987; Westerterp *et al.* 1988; Schulz *et al.* 1989). The former is very laborious and time-consuming, whereas the latter only gives an average energy expenditure over the sampling period. With the advent of radiotelemetry and data storage techniques, it is possible to monitor heart rate in freely behaving animals, so it would be useful if heart rate could be used to estimate the energy expenditure of the animals. This is especially true with the arrival of data-logging devices which could store heart rates over long periods before being recovered and the data retrieved (Hill, 1986).

From the Fick equation, $\dot{V}_{O_2} = \text{heart rate} \times \text{cardiac stroke volume} \times \text{the difference in oxygen content in arterial and mixed venous blood (overall tissue oxygen extraction)}$. Thus, it can be seen that heart rate is proportional to oxygen consumption as long as the tissue oxygen extraction and cardiac stroke volume remain fairly constant or change in proportion to the change in heart rate. In birds, heart rate is the major contributor to increasing cardiac output (Bech and Nomoto, 1982; Grubb, 1982; Grubb *et al.* 1983; Kiley *et al.* 1985). However, the oxygen extraction by the tissues can rise with intensifying work loads (Grubb, 1982; Woakes and Butler, 1986; Faraci, 1986), though not to the same extent as heart rate (Butler *et al.* 1977). Nonetheless, for exercising birds under steady-state conditions (excluding flight), heart rate is linearly related to oxygen consumption (Bamford and Maloij, 1980; Woakes and Butler, 1983; Barnas *et al.* 1985). However, during diving, steady-state conditions are rarely achieved, especially with respect to heart rate, which is highly variable. Fedak *et al.* (1988) found that, although heart rate during diving and breathing was unrelated to oxygen

consumption, mean heart rate over a complete dive cycle increased linearly with mean oxygen consumption, a result similar to that found in the present study.

Under all the conditions in which mean heart rate and mean oxygen consumption were determined in the present study, the values of the two variables produced a regression line that was not significantly different from that obtained from swimming ducks (Woakes and Butler, 1983). It would, therefore, appear that heart rate can be used in the field to determine the energetics of free-living aquatic birds with the same level of accuracy as the DLW and TEB techniques (Nagy, 1989). It should be noted that the variability found in the individual birds was fairly large (cf. Gessaman, 1980) so, when looking at animals in the field, recordings of heart rate must not be restricted to a few individuals, but extended to as many as possible.

In almost all other studies that have investigated the use of heart rate for predicting oxygen consumption, the investigators have used conversion factors derived from the individual subjects or from the group of which the individual was a member (Gessaman, 1980; Schulz *et al.* 1989). The present study may be the only one where the relationship between heart rate and oxygen consumption has been derived from one group of animals and then applied to a totally different group. This probably explains the very high variability when trying to predict the oxygen consumption of individual birds. However, since almost all studies in the field will be carried out on different groups of animals, the accuracy of applying the equation to group data could make this an extremely useful tool for environmental biologists.

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References

- ARMSTRONG, R. B., DELP, M. D., GOLJAN, E. F. AND LAUGHLIN, M. H. (1987). Distribution of blood flow in miniaturized swine during exercise. *J. appl. Physiol.* **62**, 1285–1298.
- BAMFORD, O. S. AND MALOIJ, G. M. O. (1980). Energy metabolism and heart rate during treadmill exercise in the marabou stork. *J. appl. Physiol.* **49**, 491–496.
- BARNAS, G. M., GLEESON, M. AND RAUTENBURG, W. (1985). Cardiovascular and respiratory responses of exercising domestic fowl to spinal cord cooling at different ambient temperatures. I. Cardiovascular responses and blood gases. *J. exp. Biol.* **114**, 415–426.
- BECH, C. AND NOMOTO, S. (1982). Cardiovascular changes associated with treadmill running in the Pekin duck. *J. exp. Biol.* **97**, 345–358.
- BEVAN, R. M. AND BUTLER, P. J. (1989). Oxygen consumption during voluntary diving in the tufted duck, *Aythya fuligula*, acclimated to summer and winter temperatures. *J. Physiol., Lond.* **418**, 132P.
- BROOKS, G. A. (1985). Glycolytic end product and oxidative substrate during sustained exercise in mammals: The 'lactate shuttle'. In *Circulation, Respiration and Metabolism* (ed. R. Gilles), pp. 208–218. Berlin: Springer-Verlag.
- BRYANT, D. M. AND TATNER, P. (1986). Energetics of the annual cycle of dippers *Cinclus cinclus*. *Ibis* **130**, 17–38.
- BUTLER, P. J., TURNER, D. L., AL-WASSIA, A. AND BEVAN, R. M. (1988). Regional distribution of blood flow during swimming in the tufted duck (*Aythya fuligula*). *J. exp. Biol.* **135**, 461–472.

- BUTLER, P. J., WEST, N. H. AND JONES, D. R. (1977). Respiratory and cardiovascular responses of the pigeon to sustained level flight in a wind tunnel. *J. exp. Biol.* **71**, 7–26.
- 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.
- BUTLER, P. J. AND WOAKES, A. J. (1984). Heart rate and aerobic metabolism in Humboldt penguins, *Spheniscus humboldti*, during voluntary dives. *J. exp. Biol.* **108**, 419–428.
- BUTLER, P. J. AND WOAKES, A. J. (1989). Telemetry. In *Techniques in Comparative Respiratory Physiology: an Experimental Approach* (ed. C. R. Bridges and P. J. Butler), pp. 139–170. Cambridge, New York: Cambridge University Press.
- CASTELLINI, M. A., DAVIS, R. W. AND KOOYMAN, G. L. (1988). Blood chemistry regulation during repetitive diving in Weddell seals. *Physiol. Zool.* **61**, 379–386.
- COSTA, D. P. AND PRINCE, P. A. (1986). Foraging energetics of grey-headed albatrosses *Diomedea chrysostoma* at Bird Island, South Georgia. *Ibis* **129**, 149–158.
- DEWAR, J. M. (1924). *The Bird as a Diver*. London: H.F. and G. Witherby.
- DRAULANS, D. (1982). Foraging and size selection of mussels by the tufted duck, *Aythya fuligula*. *J. Anim. Ecol.* **51**, 943–956.
- FARACI, F. M. (1986). Circulation during hypoxia in birds. *Comp. Biochem. Physiol.* **85A**, 613–620.
- FEDAK, M. A., PULLEN, M. R. AND KANWISHER, J. (1988). Circulatory response of seals to periodic breathing during exercise and diving in the laboratory and open sea. *Can. J. Zool.* **66**, 53–60.
- GESSAMAN, J. A. (1980). An evaluation of heart rate as an indirect measure of daily energy metabolism of the American kestrel. *Comp. Biochem. Physiol.* **65A**, 273–289.
- GRUBB, B. R. (1982). Cardiac output and stroke volume in exercising ducks and pigeons. *J. appl. Physiol.* **53**, 207–211.
- GRUBB, B. R., JORGENSEN, D. D. AND CONNER, M. (1983). Cardiovascular changes in the exercising emu. *J. exp. Biol.* **104**, 193–201.
- HILL, R. D. (1986). Microcomputer monitor and blood sampler for free-diving Weddell seals. *J. appl. Physiol.* **61**, 1570–1576.
- IRVING, L. (1939). Respiration in diving mammals. *Physiol. Rev.* **19**, 112–134.
- KILEY, J. P., FARACI, F. M. AND FEDDE, M. R. (1985). Gas exchange during exercise in hypoxic ducks. *Respir. Physiol.* **59**, 105–115.
- MUSCH, T. I., FREIDMAN, D. B., PITELLI, K. H., HAIDET, G. C., STRAY-GUNDERSEN, J., MITCHELL, J. H. AND ORDWAY, G. A. S. (1987). Regional distribution of blood flow of dogs during graded dynamic exercise. *J. appl. Physiol.* **63**, 2269–2277.
- NAGY, K. A. (1989). Field bioenergetics: accuracy of models and methods. *Physiol. Zool.* **62**, 237–252.
- OBST, B. S., NAGY, K. A. AND RICKLEFS, R. E. (1987). Energy utilization by Wilson's storm-petrel (*Oceanites oceanites*). *Physiol. Zool.* **60**, 200–210.
- SCHULZ, S., WESTERTERP, K. R. AND BRUCK, K. (1989). Comparison of energy expenditure by the doubly labeled water technique with energy intake, heart rate, and activity recording in man. *Am. J. clin. Nutr.* **49**, 1146–1154.
- STAHEL, C. D. AND NICOL, S. C. (1988). Temperature regulation in the Little penguin *Eudyptula minor*, in air and water. *J. comp. Physiol.* **148**, 93–100.
- STEPHENSON, R. (1987). The physiology of voluntary diving behaviour in the tufted duck (*Aythya fuligula*) and the American mink (*Mustela vison*). PhD thesis, University of Birmingham.
- STEPHENSON, R., BUTLER, P. J., DUNSTONE, N. AND WOAKES, A. J. (1988). Heart rate and gas exchange in freely diving American mink (*Mustela vison*). *J. exp. Biol.* **134**, 435–442.
- STEPHENSON, R., BUTLER, P. J. AND WOAKES, A. J. (1986). Diving behaviour and heart rate in tufted ducks (*Aythya fuligula*). *J. exp. Biol.* **126**, 341–359.
- STEPHENSON, R., TURNER, D. L. AND BUTLER, P. J. (1989). The relationship between diving activity and oxygen storage capacity in the tufted duck (*Aythya fuligula*). *J. exp. Biol.* **141**, 265–275.
- WALSBERG, G. E. (1983). Avian ecological energetics. In *Avian Biology* (ed. D. S. Farner and J. R. King), pp. 161–220. New York: Academic Press.

- WEATHERS, W. W., BUTTEMER, W. A., HAYWORTH, A. M. AND NAGY, K. A. (1984). An evaluation of time-budget estimates of daily energy expenditure in birds. *Auk* **101**, 459–472.
- WEATHERS, W. W. AND NAGY, K. A. (1980). Simultaneous doubly labeled water ($^3\text{HH}^{18}\text{O}$) and time-budget estimates of daily energy expenditure in *Phainopepla nitens*. *Auk* **97**, 861–867.
- WESTERTERP, K. R., BROUNS, F., SARIS, W. H. M. AND HOOR, F. T. (1988). Comparison of doubly labelled water with respirometry at low- and high-activity levels. *J. appl. Physiol.* **65**, 53–56.
- WOAKES, A. J. (1980). Biotelemetry and its application to the study of avian physiology. PhD. thesis, University of Birmingham.
- WOAKES, A. J. AND 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.
- WOAKES, A. J. AND BUTLER, P. J. (1986). Respiratory, circulatory and metabolic adjustments during swimming in the tufted duck, *Aythya fuligula*. *J. exp. Biol.* **120**, 215–231.