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Testing optimal foraging models for air-breathing divers

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Models of diving optimality qualitatively predict diving behaviours of aquatic birds and mammals. However, none of them has been empirically tested. We examined the quantitative predictions of optimal diving models by combining cumulative oxygen uptake curves with estimates of power costs during the dives of six tufted ducks, *Aythya fuligula*. The effects of differing foraging costs on dive duration and rate of oxygen uptake ($\dot{V}_{O_2up}$) at the surface were measured during bouts of voluntary dives to a food tray. The birds were trained to surface into a respirometer after each dive, so that changes in $\dot{V}_{O_2up}$ over time could be measured. The tray held either just food or closely packed stones on top of the food to make foraging energetically more costly. In contrast to predictions from the Houston & Carbone model, foraging time (t_f) increased after dives incorporating higher foraging energy costs but surface time (t_s) remained the same. While optimal diving models have assumed that the cumulative oxygen uptake curve is fixed, $\dot{V}_{O_2up}$ increased when the energy cost of the dive increased. The optimal breathing model quantitatively predicted *ts* in both conditions and oxygen consumption during foraging (m_2t_f) in the control condition, for the mean of all ducks. This offers evidence that the ducks were diving optimally and supports the fundamentals of optimal diving theory. However, the model did not consistently predict t_s or m_2t_f for individual birds. We discuss the limits of optimal foraging models for air-breathing divers caused by individual variation.

An air-breathing animal that is foraging underwater must decide when to leave the site of resource to surface and ventilate its lungs. This requirement to move away from the feeding site to obtain oxygen imposes a considerable limitation during periods of foraging. Air-breathing divers are assumed to have evolved to apportion their time between the surface site and the feeding site to maximize the proportion of time spent foraging (Kramer 1988).

Popular models of diving optimality that have qualitatively predicted the optimal surface duration of a diver (e.g. Kramer 1988; Thompson et al. 1993; Carbone & Houston 1996; Mori 1998) have assumed that the rate of oxygen restocking after a dive exponentially decreases with time, producing a smooth curve of diminishing oxygen gain. Kramer (1988) argued that this is because the partial pressures of the animal's oxygen stores increase with time at the surface, which causes a decrease in the difference in partial pressures between the stores and ambient air, thus decreasing the rate of oxygen diffusion.

Because the lung system of mammals collapses during descent (Kooyman & Ponganis 1998), most of the oxygen stores in these animals are bound to haemoglobin and myoglobin and thus it is likely that this smooth curve would be seen. However, the respiratory tract and air sacs of birds form on average around half of their oxygen storage capacity (e.g. Keijer & Butler 1982; Croll et al. 1992). Therefore, in contrast to mammalian divers, myoglobin and haemoglobin do not dominate the oxygen stores of birds. Walton et al. (1998) suggested that oxygen must enter the caudal air sacs, via the primary bronchi and caudal secondary bronchi, before it becomes available for physiological gaseous exchange in the parabronchi. They predicted that avian divers will produce a biphasic oxygen uptake curve with the first region representing oxygen taken into the air sacs and the second representing recovery of haemoglobin and myoglobin stores. Parkes et al. (2002) have shown that the oxygen uptake curve in tufted ducks is biphasic during longer dives, although this is probably not due to the respiratory anatomy of the bird but rather to changes in respiratory frequency over time.

Both the smooth oxygen uptake curves of earlier models and the biphasic curve of Walton et al. (1998) predict a variety of optimal behaviour patterns. These concern adjustments to surface duration and foraging duration in response to changes in dive depth and energetic costs during the dive. It is likely that the details of the oxygen uptake curve have a critical effect on the gross

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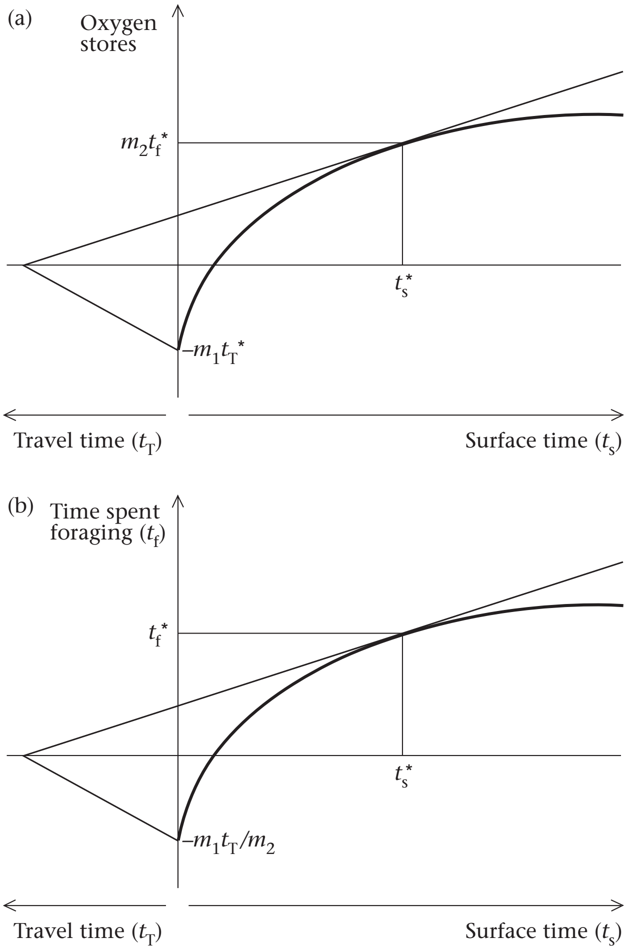

Figure 1. (a) Adaptation of the optimal breathing model (Kramer 1988). The abscissa shows time spent travelling to and from the foraging site to the left of the ordinate, and time at the surface to the right. The ordinate shows the amount of oxygen consumed during travel and gained during surface periods. t_s^* denotes the optimal surface duration for the diver in terms of maximizing the proportion of time at the foraging site. m_1t_T is the amount of oxygen consumed during travel for time t_T. $m_2t_f^*$ represents the amount of oxygen consumed at the foraging site for time t_f, when the duck is diving optimally. (b) Adaptation of the basic model of Houston & Carbone (1992). The ordinate above the abscissa shows time spent at the foraging site, t_f^*. Because some oxygen is consumed during travelling, m_1t_T, foraging duration is decreased (by $-m_1t_T/m_2$).

predictions of diving optimality models (Ruxton et al. 2000). The predictions of present models reveal the importance of empirical studies on oxygen uptake curves so that further progress can be made in understanding observed diving behaviour.

Kramer (1988) developed the optimal breathing model to predict changes in surface duration in response to changes in the depth of foraging (Fig. 1a). The basic model of Houston & Carbone (1992) is a modification of the optimal breathing model (Kramer 1988) that allows prediction of foraging duration as well as surface duration (Fig. 1b). One prediction of the model is that divers will spend less time foraging if the energetic costs of foraging increase, while optimal surface duration will not change. Carbone & Houston (1994) tested some of these predictions by manipulating the costs and benefits of foraging by pochard ducks, *Aythya ferina*. The trends from these experiments qualitatively agree with the model; however, it is erroneous to accept this model as accurate when fundamental aspects, such as the oxygen uptake curves, have not been quantified. Instead, these trends can be considered only as guidelines to empirical research (Pierce & Ollason 1987).

Whereas the models have assumed that the oxygen gain curve is the same after all dives, Parkes et al. (2002) found that increased dive durations are associated with an initial increase in rate of oxygen uptake at the surface in tufted ducks, *Aythya fuligula*. This indicates that the rate of oxygen uptake varies depending upon energetic costs during submergence. This change in the oxygen gain curve in response to varying oxygen consumption is likely to have important implications for the predictions of optimal diving models. Furthermore, assuming animals have to balance the oxygen they consume during a dive with the oxygen they gain at the surface (Kramer 1988), data on the volume of oxygen used to restock the stores would allow a quantitative comparison of the changes in energy expenditure during foraging dives, where the energy cost of foraging has been manipulated.

Our first main objective was to confirm, by quantifying changes in the uptake curve against changes in the energetic costs of foraging, that an increased rate of oxygen uptake is associated with an increase in oxygen consumption. Second, by incorporating power cost estimates for different phases of the dive taken from an earlier study (Lovvorn et al. 1991), we produced a graphical solution of the optimal breathing model (Kramer 1988). This allowed us to determine whether the ducks were diving optimally according to the model and to test the validity of the model. Furthermore, time budget data allowed us to test a specific prediction of the basic Houston & Carbone (1992) model that, as foraging cost increases, foraging duration decreases without a change in surface duration.

METHODS

We used five adult female and one adult male tufted ducks ($\bar{X} \pm$ SE weight$=692 \pm 29$ g). They were reared from eggs obtained (under an English Nature Licence) from Kingsbury Water Park, Sutton Coldfield, U.K., and, when adult, were kept in outdoor holding facilities at the University of Birmingham which included ponds and vegetated areas. For the experiments we used an indoor dive tank (1.0 × 1.6 m and 1.7 m deep) that had access to an adjacent dry area (0.6 × 0.8 m). The ducks were housed on the tank for several weeks before the experiments, allowing them to become used to the noises and activities associated with the experiment and to the concept of diving to a feeding platform for their food. During the experimental period, they were housed on the indoor tank for 6 months under a light:dark regime of 14:10 h. Room temperature ranged between 12 and 22°C and the water temperature between 10 and 18°C. Food consisted

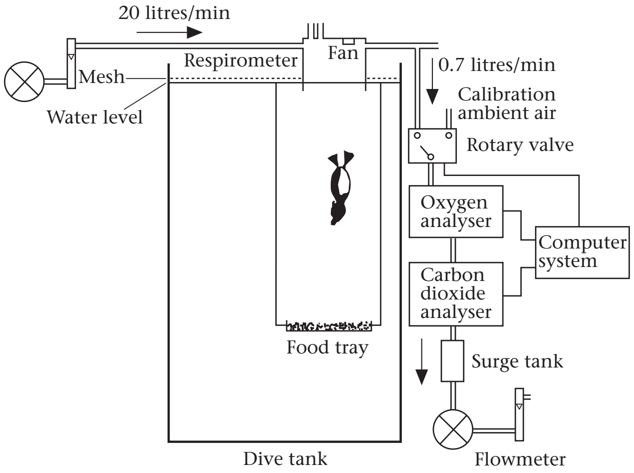

Figure 2. Diagram of experimental apparatus showing a tufted duck diving from the respirometer. For further details see Methods.

of corn, pellets and a variety of live foods including maggots and mealworms. It was not provided on the morning of an experimental day, encouraging the ducks to dive to the feeding tray during the experiment. All ducks maintained their weights during the experiments and received ad libitum food afterwards. The experiment was conducted under a Home Office licence.

For the experiment, we placed the subject bird on the water surface within the confines of a clear acrylic respirometer (35 × 25 × 25 cm) while the other birds were restricted to the dry area, out of view of the subject duck (Fig. 2). The bottom edges of the respirometer were placed 10 cm below the water forming an airtight seal along its sides. This made the effective volume of the respirometer 13 125 ml. The surface of the tank was covered by mesh, apart from the entrance to the respirometer, and so the submerged duck always resurfaced into the respirometer. The duck was encouraged to dive by the availability of maggots on a tray (67 × 82 cm) suspended within the water at a depth of 1.1 m, ensuring the ducks could be easily observed when foraging. We had two experimental conditions. Food was dropped on to the tray either without a substratum present (control condition) or among stones (mean mass 65 g, placed on the tray one stone deep; substratum condition) in an attempt to affect the energetic demands on the duck while it foraged at the tray. Because the maggots remained active underwater for many minutes, they burrowed in between the stones when they were present, forcing the ducks to push the stones about to uncover the food.

Air was continuously pushed through the respirometer at a rate of 333 ml/s by a fixed flow pump such that the concentration of carbon dioxide within the respirometer was always kept below 0.2%. Leak tests (Fedak et al. 1981) were regularly conducted by bleeding a known amount of nitrogen into the respirometer and checking that the calculated decrease in oxygen content, according to the rate of air flow through it, equalled the recorded decrease. A further 11.7 ml/s was drawn as the sample gas, just beyond the outlet hole of the respirometer, with a second air pump (Ametek, model R1 Flow control). A 500-ml flask was placed in front of the sample pump to reduce any flow oscillations. A fan inside the respirometer ensured homogeneity of the gases and thus the measure of oxygen in the sample gas was an accurate measure of oxygen inside the respirometer (Woakes & Butler 1983). Tubing 350 ml in volume was attached to the holes in the respirometer open to ambient air. This ensured that when the duck initially surfaced into the respirometer after the dive, air forced out of the respirometer did not escape the system and was subsequently sucked back in.

Differences between the concentration of oxygen in the gas entering and leaving the respirometer were measured by an oxygen gas analyser (Ametek, model S3A-1/N.22) such that the oxygen uptake of the duck could be calculated (Fedak et al. 1981). Carbon dioxide levels were also measured, with an infrared carbon dioxide analyser (ADC Ltd, model SS-100), to ensure no build up occurred within the respirometer. Temperature and humidity readings were taken (Vaisala, Helsinki, Finland) to check that the variations in water vapour and gas temperature were small enough to have only a negligible effect on the oxygen concentration of the airflow through the respirometer. The connecting tubing was impermeable to oxygen and was as small a bore (3 mm diameter) and as short as possible to limit dead space within the system. The response time of the oxygen sensor was less than 0.2 s and the lag time of the respirometer and tubing was 3.0 s. The residual time constant of the system after deconvolution (the conversion of oxygen concentration in the respirometer to rate of oxygen uptake, see below) was 0.4 s and was determined by nitrogen injections at various points within the respirometer.

The absolute values and gains of the sensors were recalibrated before and after experimental sessions with a precision gas-mixing pump (Wösthoff Pump, type 2M301/a from F, Bochum, Germany) and gain drift was found to be negligible. To allow compensation for the inherent drift in the oxygen analyser, a desktop computer (DLS, P166MMX) controlled a rotary valve, which switched the analyser's gas input from air leaving the respirometer to ambient air each time the duck was diving for food.

Output signals from the oxygen analyser, carbon dioxide analyser and humidity and temperature probes were sent to a terminal block connected to an analogue-to-digital converter unit (AT MIO-16L, National Instruments) in the computer. Every 0.25 s, 180 scans of each sensor device input were made and the mean recorded; these data points were stored on the hard drive, by means of a custom-made program written with a software package for automating data collection and manipulation (LabVIEW, National Instruments, Newbury, U.K.), which also automated control of the rotary valve.

Each experimental session lasted on average 1 h and recordings were collected when a dive bout commenced. As well as total dive duration, we recorded the times of the descent, foraging and ascent phases of each dive when foraging occurred. At the end of longer periods of diving activity, the gas concentrations in the respirometer reached a maximum of 0.18% for carbon dioxide, and

Table 1. Time budget data from six tufted ducks in the control condition and in the substratum condition, where stones were present on the food tray

	Control (N=890)	Substratum (N=1218)	t_5
Dive duration, t_d (s)	11.2±0.72	13.6±0.83	4.19**
Foraging duration, t_f (s)	5.6±0.45	7.6±0.76	3.69*
% time spent foraging, $t_{\%f}$	55.26±1.86†	63.62±3.32†	2.85*
Surface duration, t_s (s)	12.3±1.4	12.5±1.36	

Values given are means±SE. N=number of dives.
†Values are arcsine transformed.
*$P<0.05$; **$P<0.01$; t test comparing control and substratum conditions.

oxygen was reduced by a maximum of 0.35% from its ambient level. The range of humidity levels in the respirometer was 90–93% across the duration of all the experimental sessions (and this range was usually much smaller within an experimental session) and the temperature was constantly 21°C.

Analysis

To convert change in oxygen concentration into rate of oxygen uptake we used a modification of the formula proposed by Woakes & Butler (1983) that allows measurement of fast changes in oxygen uptake from an open circuit respirometer system:

$$V_{O_2} = (Ox_2 - Ox_1)\,V + \frac{(Ox_1 + Ox_2 - 2Ox_{amb})}{2}\,(t_2 - t_1)\,\dot{Q}$$

where V_{O_2}=oxygen uptake between times t_1 and t_2 (ml), Ox_1, Ox_2=fractional concentrations of oxygen at times t_1, t_2 leaving the chamber, V=respirometer volume (ml), Ox_{amb}=fractional concentration of (ambient) oxygen entering the respirometer, t_1, t_2=start and finish of a period where variation in oxygen concentration in the respirometer is recorded and $\dot{Q}$=flow rate out of the respirometer (ml/s). All oxygen volumes are corrected to standard temperature and pressure, dry.

Owing to the small time difference between t_1 and t_2, changes in oxygen concentration were often within the error of the oxygen analyser; however, this low signal to noise ratio was greatly increased by averaging a large number of data points (Parkes et al. 2002).

We analysed a dive whenever the duck visited the foraging tray. Bout criterion interval analysis (Slater & Lester 1982) was used to eliminate all surface durations greater than 28 s. Mean ± SE values are given for N animals, where N is usually, but is sometimes less than, six. To avoid animal bias, we obtained mean values for each bird and used these means to obtain the final mean. A significant difference between means was tested with paired t tests unless stated otherwise. Where we used one-tailed t tests, we state this in the text.

Two values measuring oxygen consumption during activity were generated from direct measurements. The mean rate of oxygen consumption (oxygen metabolised) over the dive cycle ($\dot{V}_{O_2c}$) was calculated by dividing the mean total oxygen uptake during the surface interval, V_{O_2up}, by mean dive duration plus mean surface duration, t_d+t_s. This assumes that the birds are recovering from the previous dive during the surface interval, rather than preparing for the next dive. We calculated the mean total oxygen consumption over a dive cycle of mean duration, V_{O_2d+s}, by combining the mean oxygen consumption rate during submersion of mean dive duration ($\dot{V}_{O_2d}$), multiplied by t_d, with the mean oxygen consumption rate during surface intervals of mean duration ($\dot{V}_{O_2s}$) multiplied by t_s. $\dot{V}_{O_2d}$ and $\dot{V}_{O_2s}$ were estimated with multiple linear regressions (Woakes & Butler 1983) between V_{O_2up}, t_d and t_s.

RESULTS

Diving Time Budgets

Table 1 contains time budget data from six ducks all diving in the two conditions. We recorded 2108 dives. The time budget data were normally distributed about the mean for all but one bird in both conditions (Anderson–Darling normality test; the exception showed mildly bimodal diving behaviour); thus the mean was the most effective measure of the average. The oxygen uptake data for birds in both conditions were also normally distributed about the mean (Anderson–Darling normality test: NS). For all variables, the means of the six ducks were assumed to be a normally distributed, representative sample of the population.

In the control condition, with the foraging tray devoid of substratum, mean foraging duration (t_f) was significantly lower than that when the stones were present (substratum: 5.3–11.0 s; control: 4.4–7.0 s; Table 1). The same trend in terms of mean total dive duration (t_d) was also significant (substratum: 11.3–16.1 s; control: 9.1–14.1 s; Table 1). This is due to the difference in mean foraging duration, since there was no significant difference in total travelling time (t_T; substratum: 4.3–7.6 s; control: 4.6–7.1 s) because the distance to the foraging site was fixed. The percentage of the dive spent foraging ($t_{\%f}$) was also significantly lower in the control condition than in the presence of stones (substratum: 44.7–65.0%; control: 43.2–56.1%; values arcsine transformed for statistical analysis; Table 1). Surface durations (t_s) were not significantly different between the two conditions (substratum: 9.8–18.6 s; control: 8.8–16.7 s; Table 1).

Table 2. Mean values of gas exchange from six tufted ducks in the control condition and in the substratum condition, where stones were present on the food tray

	Control (N=890)	Substratum (N=1218)	t_5
Mean O_2 consumption rates during dives of mean duration, $\dot{V}_{O_2d}$ (ml/s)	0.63±0.04 (0.67±0.06)	0.61±0.06 (0.66±0.02)	0.42
Mean O_2 consumption rates during surface intervals of mean duration, $\dot{V}_{O_2s}$ (ml/s)	0.57±0.05 (0.81±0.03)	0.66±0.05 (0.80±0.02)	1.49
Mean total O_2 consumption over a dive cycle of mean duration, VO_{2d+s}	13.82±1.13	16.48±1.85	2.14
Mean total O_2 uptake during surface interval, VO_{2up} (ml)	14.56±1.72	17.44±2.10	6.28**
Mean rate of O_2 uptake during surface interval, $\dot{V}O_{2up}$ (ml/s)	1.19±0.05	1.39±0.04	4.25**
Mean rate of O_2 consumption over the dive cycle, $\dot{V}_{O_2c}$ (ml/s)	0.61±0.04	0.66±0.03	3.11*

Values given are means±SE. Values in parentheses are partial correlation coefficients. N=number of dives.
*$P<0.05$; **$P<0.01$; t test comparing control and substratum conditions.

Oxygen Consumption during Activity

The multiple regressions between V_{O_2up}, t_d and t_s were significant for each duck. Table 2 shows the mean values for calculated rates of oxygen consumption during mean dives and mean surface intervals, along with the relevant mean partial correlation coefficients. The partial correlation coefficients for the dives were low. Calculated oxygen consumption during the dives was 0.48–0.90 ml/s when stones were present and 0.53–0.79 ml/s in the control condition, with partial correlation coefficients of 0.47–0.76 when stones were present and 0.46–0.83 for the control. The corresponding values of $\dot{V}_{O_2s}$ were 0.49–0.82 ml/s in the presence of stones and 0.39–0.71 ml/s in the control condition, with partial correlation coefficients of 0.66–0.93 in the presence of stones and 0.73–0.89 in the control condition.

The mean total oxygen uptake during the surface interval (V_{O_2up}) and the mean rate of oxygen uptake during the surface interval ($\dot{V}_{O_2up}$) were significantly higher when stones were present. $\dot{V}_{O_2c}$ was significantly higher in the presence of stones. In both conditions, V_{O_2d+s} did not differ significantly from V_{O_2up}.

Calculation of Oxygen Restock Curves

The oxygen uptake of the ducks at the surface includes not only the restocking of the lung, blood and muscle oxygen stores but also the oxygen used for postdive metabolism. The optimal breathing model (Kramer 1988) is based on the curve of the oxygen used to restock only the stores. The rate of uptake in the curves decreases with surface duration to an almost constant value somewhere between 10 and 15 s (Parkes et al. 2002). This constant oxygen uptake can be used as an estimate of the postdive metabolic rate, which is ongoing during the surface period. To remove postdive surface metabolism from the oxygen uptake curves and be left with the oxygen restock curves, we calculated the gradient of the slope between 15 and 20 s. This slope represents the postdive metabolic rate in ml O_2/s, which can be removed from the entire curve (Fig. 3).

Oxygen Uptake at the Surface

The shape of the oxygen uptake curve and oxygen restock curve against surface duration changes with the duration of the dive and the foraging conditions of the dive (Fig. 4). To analyse the changes in the shape of the uptake curve after dives of different periods, we placed dives from the substratum condition into duration bins of 5–9.75 s, 10–14.75 s and 15–19.75 s (Table 3). We used one-tailed tests because the increased foraging costs of the stones were predicted to be associated with an increased rate in oxygen uptake, supporting the conclusions of Parkes et al. (2002). To analyse the changes in the shape of the uptake curve after dives in the two foraging conditions, we controlled for dive duration by comparing means of dives from the same duration bins

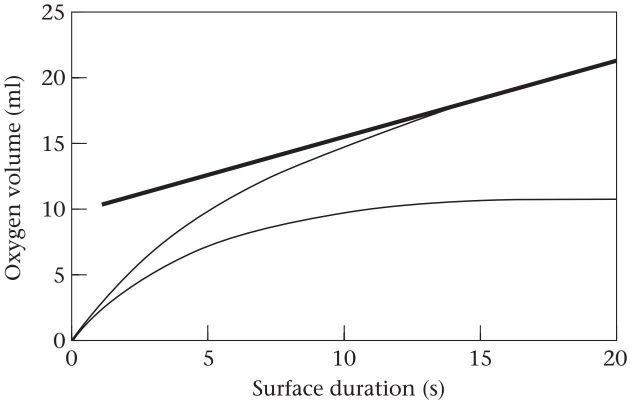

Figure 3. Example of the generation of the oxygen restock curve from the oxygen uptake curve, where the oxygen uptake curve is associated with some dives in the substratum condition, in which stones were present on the food tray (N=1218). The gradient of the thick black line (0.52 ml/s), estimates postdive metabolic rate. This assumes that metabolic rate is constant during the surface interval although in reality it will gradually decrease over time to a point because of a reduction in activity by the bird such as decreases in ventilation frequency and heart rate. This value is removed from the oxygen uptake curve to produce the oxygen restock curve. The oxygen restock curve reaches an approximate plateau from around 13 s onwards.

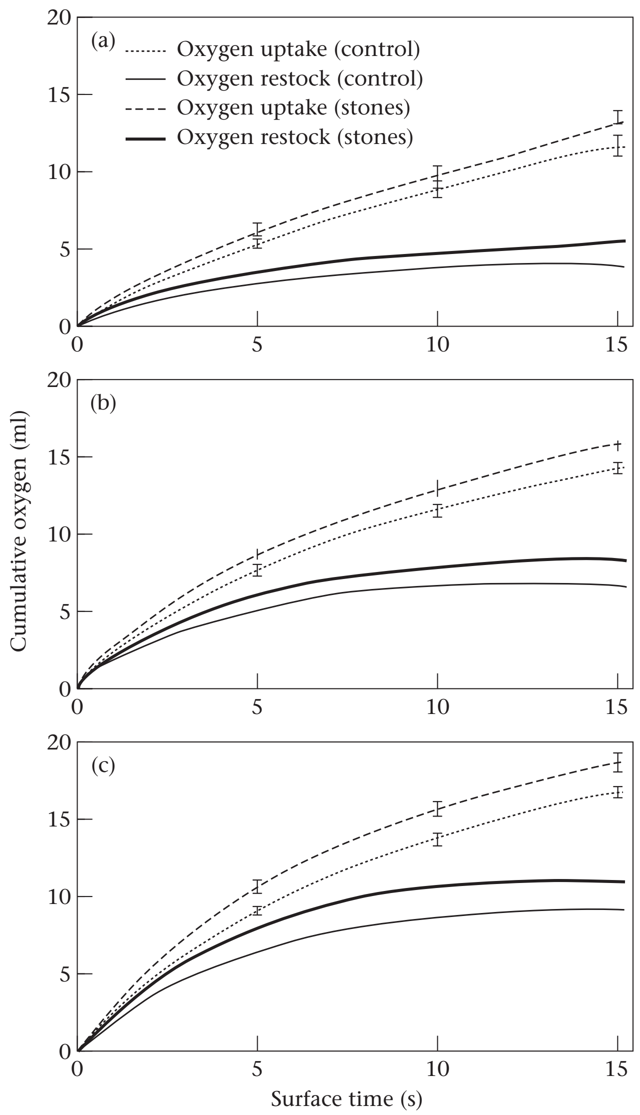

Figure 4. Oxygen uptake and restock curves for the first 15 s postdive of six tufted ducks in the two experimental conditions. Each graph represents a dive duration bin: (a) 5–9.75 s, (b) 10–14.75 s, (c) 15–19.75 s. Dashed lines: total amount of oxygen taken up by the birds; full lines: oxygen added to the stores in the respiratory system, blood and muscles.

(Table 3). Again, one-tailed tests were used because these results were predicted to confirm the trend found by Parkes et al. (2002). In all cases, we compared the uptake curves achieved by testing for a significant difference between the cumulative oxygen values of the curves at 5, 10 and 15 s. When we compared uptake curves between the dive duration bins, all the values at 5, 10 and 15 s were significantly different. When we compared uptake curves between the two foraging conditions, again all the values were significantly different.

The decrease in rate of oxygen uptake into the stores over time may be caused by the decrease in the difference in partial pressure of oxygen between the ambient air and the cardiorespiratory system as the stores become restocked. If this is the case then the shape of the oxygen restock curve in the control condition should be the same as the shape of the curve in the substratum group, accounting for dive duration, after a certain period at the surface. This assumes that the metabolic rate of surface activities during the interval after the dive is the same in both conditions and that this rate is unchanging over the surface period.

To test this, we compared the oxygen restock curve for all control dives, from 0 to 14 s, with the restock curve for all substratum condition dives, from 1 to 15 s (Fig. 5). In a comparison of $\dot{V}_{O_2d}$ and t_d for both conditions, the ducks consumed on average 2 ml of oxygen more per dive when stones were present. If the gradient of the curves is due purely to the difference in partial pressure of oxygen then the shape of the control condition oxygen restock curve should be the same as the shape of the substratum restock curve after 2 ml of oxygen have been added to the oxygen reserves, which takes 1 s. These two curves were fitted to a model determined by nonlinear regression. *F* ratios were run to determine that a third-order polynomial equation was most appropriate for both curves ($r^2>0.99$ in each case). These models were then compared with an ANCOVA with factors of individual duck, condition and the cubic relation with respect to time. There was a significant difference between the two curves ($F_{1,674}=193.1$, $P<0.001$) suggesting that the ducks increase $\dot{V}_{O_2up}$ by their own volition during surface periods in between energetically more costly dives.

The Optimal Breathing Model

Time budget data and oxygen restock curves from the two conditions were combined to construct and test Kramer's optimal breathing model (1988). By using values of power output during different phases of the dive derived from other studies, and converting these values to oxygen consumption (Table 4), we could test whether the experimental ducks were diving optimally according to the model.

Lovvorn et al. (1991) calculated the power requirement per kg of body mass during descent and 'staying at the bottom' of a water column 1.2 m deep, for three *Aythya* species. This is similar to the present study where the foraging tray was suspended at 1.1 m in the water. We used values for the lesser scaup, *A. affinis*, because this species is similar morphologically and behaviourally to *A. fuligula* (Lovvorn et al. 1991; Stephenson 1994). Taking into account an aerobic efficiency (mechanical power output/diving aerobic power input) of 12.6% for *A. affinis* (Stephenson 1994), and then converting power output to rate of oxygen consumption, where 1 W=20.1 ml O_2/s, provides rates of oxygen consumption for the descending and foraging phases of the dive. The ascent phase of the dive is deemed to be passive (Lovvorn et al. 1991), and thus no oxygen consumption for locomotion is attributed to it. Oxygen consumption during this phase is assumed to be equal to resting metabolic rate while the bird is on the water surface (Lovvorn et al. 1991). Using the values in the second part of Table 4 and the oxygen restock curves, we can construct the optimal breathing model (Kramer 1988; Figs 6, 7).

Table 3. Statistical comparison between oxygen uptake curves after dives of six tufted ducks in the control condition and in the substratum condition, where stones were present on the food tray, and between three dive duration bins in the substratum condition

Dive duration bins	5 s	10 s	15 s
5–9.75 s			
Substratum (ml O_2)	6.00±0.42	9.54±0.62	12.90±0.83
Control (ml O_2)	5.21±0.40	8.66±0.52	11.45±0.65
t_4†	2.41*	3.88**	3.87**
10–14.75 s			
Substratum (ml O_2)	8.33±0.20	12.68±0.38	15.87±0.60
Control (ml O_2)	7.37±0.36	11.30±0.40	14.12±0.35
t_5†	3.90**	4.50**	2.96*
t_4‡	9.03***	8.71***	5.81***
15–19.75 s			
Substratum (ml O_2)	10.44±0.41	15.45±0.46	18.40±0.60
Control (ml O_2)	8.89±0.28	13.49±0.45	16.50±0.38
t_4†	2.42*	2.42*	7.45***
t_4‡	5.45**	11.52***	2.99**

Values given are means±SE.
*$P<0.05$; **$P<0.01$; ***$P<0.001$; *t* test comparing conditions and duration bins.
†Significant difference between the two conditions in that duration bin.
‡Significant difference between that duration bin and the duration bin one range smaller (e.g. 10–14.75 s and 5–9.75 s).

We calculated the exact point of intersection of the tangent and oxygen restock curve for each duck and for the mean of all ducks, for both conditions. The oxygen restock curves were fitted to a model (third-order polynomial; equation 1). For the control condition curves, r^2 of the models was 0.99–1.00, with a mean of 1.00 ± 0.001. For the substratum condition curves, r^2 was 0.99–1.00, with a mean of 1.00 ± 0.001. Since the gradient of the tangent and the curve fit were known, their interception could be calculated.

The model used to describe the oxygen restock curve is given by the equation

$$V_{O_2up}=at_s^{*3}+bt_s^{*2}+ct_s^*+d. \qquad (1)$$

Differentiating with respect to V_{O_2up},

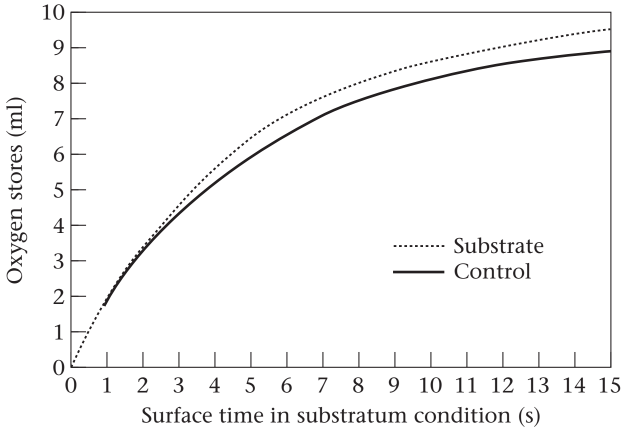

Figure 5. Comparison of the shapes of the oxygen restock curve for six tufted ducks in the control condition (no stones present on the food tray; *N*=890) and in the substratum condition (stones present on the food tray; *N*=1218) from 1 s onwards.

$$dV_{O_2up}/dt_s^*=3at_s^{*2}+2bt_s^*+c. \qquad (2)$$

Since the gradient of the tangent is given by

$$V_{O_2up}/(t_T+t_s^*),$$

from equation (2), it follows that

$$V_{O_2up}/(t_T+t_s^*)=3at_s^{*2}+2bt_s^*+c \qquad (3)$$

$$V_{O_2up}=(t_T+t_s^*)(3at_s^{*2}+2bt_s^*+c). \qquad (4)$$

From equations (1) and (4)

$$at_s^{*3}+bt_s^{*2}+ct_s^*+d=(t_T+t_s^*)(3at_s^{*2}+2bt_s^*+c). \qquad (5)$$

$$2at_s^{*3}+bt_s^{*2}+t_T(3at_s^{*2}+2bt_s^*+c)=d, \qquad (6)$$

and

$$d=-m_1t_T \text{ (Fig. 1a)}. \qquad (7)$$

From equation (6), t_s^* can be found, and $m_2t_f^*=V_{O_2up}$.

For each curve, the model predictions were statistically compared to the observed values for t_s and m_2t_f with a single sample *t* test. Table 5 shows the model predictions and observed values of surface duration and oxygen consumed at the foraging site for the means of all ducks, in both conditions. The model predictions t_s^* and $m_2t_f^*$ for the mean of all the ducks in both conditions were not significantly different from the observed values, t_s and m_2t_f. At the level of the individual ducks, four of the model predictions for t_s^* in the control condition were significantly different from the observed values of t_s ($P<0.01$ and <0.001). All six predictions of $m_2t_f^*$ from the same models were significantly different from the

Table 4. Predicted power costs and oxygen consumption rates during the dives of six tufted ducks in the control condition and the substratum condition where stones were present on the food tray

	Control (N=890)	Substratum (N=1218)
Power requirement to descend to 1.2 m (W/kg)*	5.46	5.46
Power requirement to maintain position at 1.2 m (W/kg)*	1.69	1.69
Mean body mass of experimental ducks (kg)	0.692±0.029	0.692±0.029
Aerobic efficiency (%)†	12.6	12.6
Conversion factor of W to ml O_2/s‡	20.1	20.1
Mean descent time (s; t_{desc})	3.07±0.30	3.17±0.28
Mean ascent time (s; t_{asc})	2.54±0.15	2.83±0.23
Mean total travel time (s; t_T)	5.62±0.43	6.01±0.49
Mean foraging duration (s; t_f)	5.62±0.45	7.80±0.31
Mean resting metabolic rate (ml/s)	0.189±0.022	0.189±0.022
O_2 metabolized during travel phases of dive (m_1t_T)	4.59±0.42	4.78±0.41
O_2 metabolized during mean foraging duration (ml; m_2t_f)	2.32±0.19	3.14±0.31
Mean surface duration (s; t_s)	12.30±1.42	12.50±0.56

Values given are means±SE of mean where available. N=number of dives.
*From Lovvorn et al. (1991).
†From Stephenson (1994).
‡From Stephenson et al. (1989).

observed values of m_2t_f (P<0.001). In the substratum condition, all six of the model predictions of t_s^* for individual ducks were significantly different from the observed values of t_s (P<0.001), and four of the six predictions of $m_2t_f^*$ were significantly different from m_2t_f (P<0.001).

DISCUSSION

This study was designed to investigate the behavioural adjustments of tufted ducks to changes in the energy costs of foraging (m_2), and to test whether these could be predicted by optimal foraging models of air-breathing divers. No other study has attempted to test the quantitative predictions of these models by combining data of cumulative oxygen uptake at the surface with estimates of rates of oxygen consumption during the descent, foraging and ascent phases underwater.

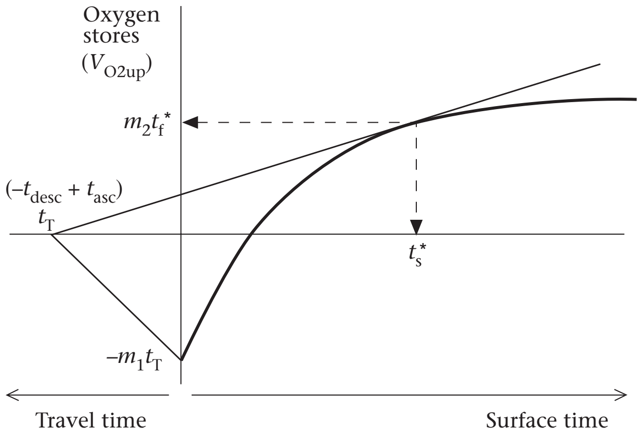

Figure 6. Quantification of the optimal breathing model (Kramer 1988). Values for $-m_1t_T$ and m_2t_f were generated from time budget data combined with estimates of power costs during different phases of the dive (Table 4). To test the validity of the model, for each duck, we compared t_s^* with t_s and m_2t_f with the volume of oxygen consumed during the optimal surface period according to the model ($m_2t_f^*$). t_s^* is represented by the value of X at the point of intersection of the tangent and $m_2t_f^*$ is represented by the value of Y at that point. For definitions of abbreviations, see Fig. 1.

Time Budgets and Foraging Costs

The dive duration and surface duration values for the present study are comparable with time budget data recorded from previous studies on the same genus diving to similar depths (Table 6).

The mean surface duration of the ducks did not differ significantly whether or not stones were present on the foraging tray. This result agrees with the predictions of Houston & Carbone (1992). However, in contradiction to their model, the foraging duration of the ducks was significantly higher when stones were present. The basic Houston & Carbone model (1992) predicts that the diver balances its oxygen gains and losses over a dive cycle, for a given time at the surface. Therefore, if the energy used during travelling does not vary, for instance because the depth of the foraging site is constant, then an increase in the energy costs of foraging forces a decrease in time spent at the foraging site. The model assumes that the curve of oxygen gain with surface duration is fixed. However, our findings show a significant increase in $\dot{V}_{O_2up}$ (mean rate of oxygen uptake during the surface interval) in response to foraging among stones. The presence of the stones was presumed to create more energetically demanding conditions because the ducks had to force their bills between and under the stones to obtain the maggots. This was confirmed by the significantly higher values of $\dot{V}_{O_2s}$ (mean rate of oxygen consumption during surface intervals) in the substratum condition for each dive duration bin (P<0.05). This supports the work of Parkes et al. (2002) who found that V_{O_2up} (total oxygen uptake during the surface interval)

Table 5. t_s^*, t_s, m_2t_f and $m_2t_f^*$ for six tufted ducks in the control condition and the substratum condition where stones were present on the food tray

	Control (N=890)	Substratum (N=1218)
t_s^*, optimal surface duration according to optimal breathing model (s)	12.56	10.26
t_s, mean surface duration of six tufted ducks (s)	12.3±1.42	12.5±1.36
$m_2t_f^*$, O_2 consumed at tray according to optimal breathing model (ml O_2)	2.46	2.98
m_2t_f, mean O_2 consumption at the feeding tray of six tufted ducks according to power cost estimates (ml O_2)†	2.59±0.21	3.51±0.35

Values given are means±SE, where available. N=number of dives.
†t test comparing control and substatum conditions: $t_5=2.71$, $P<0.05$.

increased after longer dives and concluded that $\dot{V}_{O_2up}$ therefore increased after dives where more oxygen had been consumed. In both conditions, V_{O_2up} did not differ significantly from V_{O_2d+s} (mean total oxygen consumption over a dive cycle of mean duration), indicating that the increase in oxygen consumption in the presence of stones, caused by an increase in m_2, is fully compensated for by the increase in oxygen uptake at the surface.

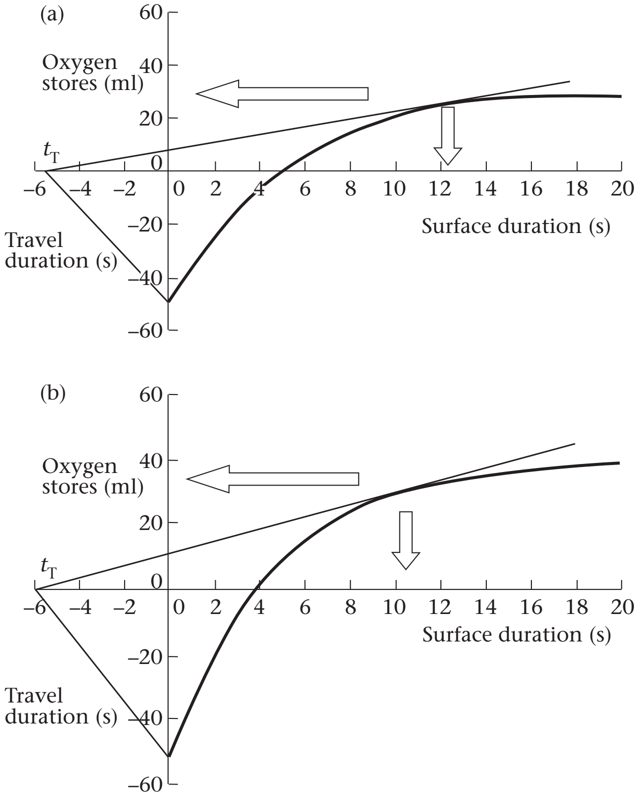

Figure 7. Testing the optimal breathing model (Kramer 1988) using the mean values of six tufted ducks, under the two foraging conditions (a, control; b, substratum; for definitions see Methods). The tangent runs from the total travel time (t_T) and touches the oxygen restock curve at a point determined by fitting the curve to a model and then calculating the intercept (for further details see Results). The arrow pointing to the ordinate indicates $m_2t_f^*$ and the arrow pointing to the abscissa indicates t_s^* calculated from the intercept of the tangent and the curve.

Despite t_s (mean surface duration) not differing between the two conditions, V_{O_2up} was significantly higher in the presence of stones because $\dot{V}_{O_2up}$ was significantly higher. However, $\dot{V}_{O_2d}$ (mean rate of oxygen consumption during dives of mean duration) and $\dot{V}_{O_2s}$ were not significantly different between the two conditions. There are two possible reasons for this. First, the higher rate of oxygen consumption during foraging in the presence of stones was partially offset by the increased time that the ducks spent underwater because of the increased time at the foraging site. This meant that there was more time for air bubbles to escape from the duck's feathers, causing a greater reduction in buoyancy, and therefore a reduction in the energy required to remain submerged. Secondly, and probably more importantly, the descent phase of the dive, which is several times energetically more costly than the foraging phase (e.g. Lovvorn et al. 1991), was a smaller proportion of the dive when the stones were present, because the foraging duration, and hence the total dive duration, was longer. Nevertheless, $\dot{V}_{O_2c}$ was significantly higher when the stones were present, suggesting that these factors did not entirely mask the increased foraging costs imposed by the stones on the average rate of oxygen consumption over the whole dive cycle.

Quantification of the Optimal Breathing Model

Estimates of power costs of each phase of the dive cycle (e.g. Stephenson et al. 1989; Lovvorn et al. 1991; Stephenson 1994) can be used to produce estimates of oxygen consumption during a dive. These values, along with the oxygen restock curves of the present study, are incorporated into the optimal breathing model (Kramer 1988). This model makes two important assumptions: (1) the ducks are diving optimally and (2) on average, oxygen restock at the surface equals oxygen consumption during the dive.

The optimal breathing model (Kramer 1988) successfully predicted both t_s and m_2t_f (oxygen consumption during mean foraging duration) in the control condition for the mean of all ducks (Fig. 7a, Table 5). The model also successfully predicted t_s for all ducks in the substratum condition (Fig. 7b, Table 5). Although the model also successfully predicted m_2t_f, $m_2t_f^*$ was lower than m_2t_f, and

Table 6. Dive duration budget data from previous studies on *Aythya* species of ducks

	Species	Depth (m)	Dive duration (s)	Surface duration (s)	Mean total oxygen uptake during surface interval (ml)
Present study*	*fuligula*	1.1	12.4	12.4	16.0
Woakes & Butler 1983	*fuligula*	1.7	14.4	16.1	16.2
Bevan & Butler 1992a†‡	*fuligula*	0.6	18.9	11.6	12.1
Bevan & Butler 1992a†§	*fuligula*	0.6	16.2	12.8	16.4
Bevan & Butler 1992b	*fuligula*	0.6	14.9	—	—
Stephenson 1994	*affinis*	1.5	13.5	16.3	18.6
Parkes et al. 2002	*fuligula*	1.7	15.6	12.3	17.2
S. Wallace 1998	*fuligula*	1.5	15.9	17.9	—

*Means of data from both conditions.
†Ducks were trained to dive for certain durations using a system of computer-controlled lights.
‡Summer-acclimated birds.
§Winter-acclimated birds.

the power cost estimate for foraging was derived from calculations of the energy required only to equal buoyancy at a certain depth. It does not account for the energy required to manipulate the stones to uncover and gain access to the maggots and therefore m_2t_f is an underestimate of foraging costs in the substratum condition. The difference between $m_2t_f^*$ and the true cost of foraging is thus larger than calculated.

Therefore, according to the model predictions using the mean values of six ducks for each condition, the model is a successful predictor of surface duration. It is also a successful predictor of oxygen consumed during the foraging phase of the dive in the control condition. This provides evidence that the ducks were diving optimally in that they were attempting to maximize the proportion of time spent at the foraging site during each dive. However, quantification of the model using data for individual ducks does not support its validity. The model was not consistent at successfully predicting t_s or m_2t_f in either condition.

Quantification of the optimal breathing model (Kramer 1988) has therefore produced uncertainty concerning its predictive validity. The model appears to be fairly successful at predicting the average diving behaviour of a number of tufted ducks but was unsuccessful at doing so for individual birds. For a single animal, the model may not always incorporate all the parameters that are influential in determining its diving behaviour. This is because an explanation of the differences between the model predictions and observed values is that diving optimally, in terms of the model parameters, would entail costs (Houston et al. 1980; Stephens & Krebs 1986; Johnstone & Norris 2000). For example, some individuals may choose to surface for longer than t_s^* to increase observation time if they are more wary of predators approaching. Other individuals may surface for less time than t_s^* if they perceive that conspecifics may start to compete with them for the available food. The model may sometimes be attempting to predict foraging behaviour at the wrong scale, for example, some divers may attempt to maximize time spent at the foraging site at the unit of a diving bout rather than that of a single dive. Some of the ducks in the present study showed significant negative correlations, albeit weak ones, between the number of preceding dives within a dive bout and the length of time spent at the feeding site. The ducks may have decreased foraging time in response to the decreased density of maggots, which is predicted by the marginal value theorem (Charnov 1976) assuming that the rate of food uptake decreases as the number of maggots decreases. Other factors such as decisions to explore for new food patches and the onset of fatigue could also be influential.

The lack of consistent predictive validity of the model at the individual level for oxygen consumed at the feeding tray suggests that the power output estimates used in the present study may not be accurate. Indeed, there are large variations in power cost values from different studies. For example, Stephenson (1994) estimated considerably higher power costs than did Lovvorn et al. (1991), for instance 0.84 W/kg more to descend and 1.11 W/kg more to maintain a depth (at 1.5 m). These power cost estimates often leave the birds with little or no oxygen for consumption at the foraging tray according to the optimal breathing model (Kramer 1988). Methodologies, duck species and water depth appear to be the main factors influencing these estimations. In the present study we used power requirements estimated by Lovvorn et al. (1991), where power output needed for descent was calculated to a depth of 1.2 m, which was similar to the depth of the feeding tray (1.1 m) in our study. Power output needed to maintain a depth, which is a requirement during foraging at a tray suspended within the water, was also calculated at 1.2 m. The power costs of diving probably varied between ducks because of physiological differences other than just body mass. Unfortunately, we have no indication of variance for the power cost estimates of Lovvorn et al. (1991) and so we used the same values for all ducks in the optimal breathing model (Kramer 1988), which might also explain the lack of predictive validity at the individual level.

At present there is no technique available to record the baseline metabolic rate of a duck during the dive. The

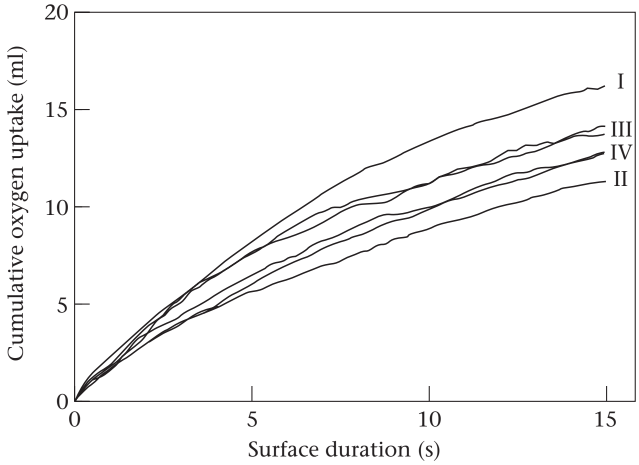

Figure 8. Oxygen uptake curves for the six tufted ducks, categorized into four foraging strategies. Strategy I includes just one duck, lbdg; II includes just one duck, op; III includes two ducks, bdg and pr; IV includes two ducks, pinr and bblu.

only sensible estimate available for our study was metabolic rate while the ducks were at rest on the surface, which we used to represent oxygen consumption during the ascent phase of the dive. This value is unlikely to be entirely accurate. A baseline metabolic cost is difficult to ascertain since it does not remain the same during exercise as during rest (Stainsby et al. 1980). At the risk of adding a poorly known baseline value to the locomotory costs of descent and foraging, it is perhaps preferable to ignore this small energy cost (J. R. Lovvorn, personal communication).

Changes to the Oxygen Restock Curve

There are two possible explanations for the change in shape of the oxygen restock curve after different dives. More rapid oxygen restocking after longer dives or in the presence of the stones could be caused by an increased effort by the bird to load its stores more quickly, for instance by increasing respiratory frequency. An alternative explanation is that the average rate of oxygen reloading is higher (i.e. that the curve is steeper) when the oxygen stores are lower, at the start of the surface period. A greater difference in the partial pressures of oxygen between the cardiorespiratory system and ambient air would allow a more rapid uptake of oxygen at this time. If changes to the shape of the uptake curve are governed by partial pressure differentials alone, then we would expect the restock curve after a less energetic dive, for example a shorter dive or one involving energetically less costly foraging, to be the same shape as the restock curve after a more energetic dive, after a certain portion of the surface period. In other words, once the partial pressure differentials at the surface after a more energetic dive have decreased to the same level as those after a less energetic dive, the rate of oxygen uptake over time should be the same.

The shape of the oxygen restock curve in the control condition from 0 s was statistically different from the shape of the oxygen restock curve in the stones condition after 1 s. This suggests that the rate of oxygen uptake at the surface is not controlled by partial pressure differentials alone. Rather, the ducks are actively increasing $\dot{V}_{O_2up}$ in between energetically more costly dives, perhaps by an increase in respiratory frequency. This agrees with the findings of Butler & Woakes (1979) who reported tachycardia in tufted ducks before dives, serving to load their oxygen stores, and tachycardia after dives related to the duration of the dive. Webb et al. (1998) reported very similar behaviour in northern elephant seals, *Mirounga angustirostris*, which increased $\dot{V}_{O_2up}$ after longer dives without adjusting surface duration. Because increased tachycardia and respiratory frequency increases surface costs while decreasing recovery time and increasing time at the foraging site, optimal foraging in air-breathing divers appears to be more complex than has been previously appreciated.

Variation within a Species

Assessing the qualitative validity of optimal foraging models is entirely viable because trends predicted by the model can be tested. However, it is not possible satisfactorily to test whether empirical data support the model if the model lacks confidence intervals. In the present study, we had to compare observed values for each duck with the model predictions using single sample *t* tests since the model prediction was a fixed value. This statistical analysis accounts for the confidence limits around only one of the two values and so is less thorough than a standard *t* test. It is more likely to indicate a significant difference between observed and predicted values and so the model is more likely to be deemed inaccurate. Models need to include a measure of variability around the solution so that data collected to test the model can be more robustly compared with the predictions.

Houston & McNamara (1985) discussed the problem that optimality models require the behaviour of an animal under a given condition to be regular, whereas it is usually variable. A similar problem is that individual animals can behave quite differently from each other under a given condition (Krebs et al. 1977; Maynard Smith 1978; Kacelnik & Houston 1984; Ball 1994). This variation within a species creates a second difficulty in demonstrating quantitative validity in the present study. Figure 6 represents a graphical solution to the optimal breathing model (Kramer 1988). The solution implies the representation of an entire species through a single data set. However, the process of averaging data to represent a data set can also serve to remove information about that data set. The large variation in diving strategy and rate of oxygen restocking within the group of six ducks cannot be fairly represented by a single restock curve and single values of diving energy costs. In comparing the time budget data and restock curves of the six birds in the present study, there are arguably four foraging strategies present (Fig. 8, Table 7).

From the oxygen uptake curves and time budget data, we placed the six tufted ducks we used into four strategy types (I–IV). Duck lbdg had the highest t_f (mean foraging

Table 7. Data for individual tufted ducks in the control condition, where no substratum was present on the food tray

			Dive duration budget data				
Duck	Strategy type	Oyxgen uptake after 15 s (ml)	Foraging time, t_f (s)	Dive duration, t_d (s)	Surface duration, t_s (s)	No. dives/ bout	$\dot{V}_{O_2c}$ (ml)
lbdg	I	18.1±0.20	7.0±0.29	14.1±0.26	11.4±0.29	23±7	0.54±0.005
op	II	12.7±0.22	4.4±0.16	9.1±0.16	11.7±0.42	12±2	0.56±0.008
bdg	III	15.9±0.52	5.0±0.31	11.7±0.36	8.9±0.62	7±3	0.51±0.010
pr	III	15.4±0.22	4.6±0.13	9.7±0.13	8.8±0.24	11±2	0.65±0.007
pinr	IV	14.3±0.33	6.7±0.26	11.3±0.26	16.7±0.53	4±1	0.67±0.006
bblu	IV	14.3±0.35	6.0±0.36	11.5±0.39	16.3±0.92	3±1	0.75±0.010

Values given are means±SE. For further details on strategy types see Discussion.

duration) and significantly the highest t_d (mean dive duration; $P<0.001$) as well as significantly the steepest oxygen uptake curve (quantified by the highest oxygen uptake after 15 s; $P<0.001$). In contrast, duck op had the shortest t_f and significantly the shortest t_d values ($P<0.01$) as well as significantly the lowest oxygen uptake after 15 s ($P<0.001$). These represent two contrasting strategies of foraging behaviour. Ducks bdg and pr had very similar values for t_f (NS) and t_d (NS), as well as similar oxygen uptake rates (NS) and t_s (NS). They therefore appear to have used similar foraging strategies. Their t_d and t_s values were significantly different from those of lbdg and op ($P<0.001$ and $P<0.01$, respectively), and their oxygen uptake values were significantly different from those of both lbdg and op ($P<0.001$) and so probably represent a third strategy. Ducks pinr and bblu also had similar values to each other in terms of all three time budget values (NS) and oxygen uptake rate (NS). Furthermore, all these values were mostly different from those for the other strategies, with oxygen uptake rate and t_s being significantly different from all other strategies ($P<0.01$ and $P<0.001$, respectively), suggesting a fourth type.

Ducks pinr and bblu dived fewer times in a bout than the other ducks. However, they spent longer than the average time ($\bar{X} \pm \text{SE}=5.6 \pm 0.45$ s) foraging per dive and also appeared to work particularly hard to consume the food while at the foraging tray. Thus, they may have ingested relatively large numbers of maggots per dive. These observations are supported by the two highest $\dot{V}_{O_2c}$ values of all the ducks. In contrast, op foraged for less time than all the other ducks and observations suggest that it also foraged less energetically. This corresponds to the short time it spent at the surface. However, duck op tended to dive more times within a foraging bout than pinr or bblu ($P<0.05$). Duck lbdg spent longest at the tray and also took up oxygen most quickly at the surface to compensate for particularly large amounts of oxygen consumed each dive because of long dive durations. Observations do not suggest that it worked as hard as pinr or bblu when foraging, supported by the low $\dot{V}_{O_2c}$ ($P<0.001$), but lbdg did tend to dive the most times in a diving bout.

Although the categorization of foraging strategies in the present study is somewhat arbitrary, it demonstrates the wide variation in behaviour within a species. Mean values derived from varied individuals, generated to represent the behavioural strategy of a species, are consequently misleading. Tufted ducks may have different optimal diving strategies because of their individual physiologies, or their strategies may be optimal under particular remembered conditions.

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