

Oxygen uptake during post dive recovery in a diving bird *Aythya fuligula*: implications for optimal foraging models

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Summary

The rate of oxygen uptake at the surface between dives was measured for four tufted ducks, *Aythya fuligula*, during bouts of foraging dives to a depth of 1.8 m. The ducks surfaced into a respirometer box after each dive so that the rate of oxygen uptake (\dot{V}_{O_2}) could be measured. \dot{V}_{O_2} decreased over time at the surface and there was a particularly rapid phase of oxygen uptake for approximately the first 3 s. The specific shape of the oxygen uptake curve is dependent upon the duration of the preceding dive. The uptake curve after longer dives was significantly steeper during the first 3 s at the surface than after shorter dives, although \dot{V}_{O_2} after the first 3 s was not significantly different between these two dive duration bins. Thus, the mean total oxygen uptake (V_{O_2})

was higher after surface periods following longer dives. Due to the high \dot{V}_{O_2} during the initial part of the surface period, the curve associated with longer dives was statistically biphasic, with the point of inflection at 3.3 s. The curve for shorter dives was not statistically biphasic. The birds may increase their respiratory frequency during the first 3 s after longer dives, producing the increased \dot{V}_{O_2} , which would enable the birds to resaturate their oxygen stores more rapidly in response to the increased oxygen depletion of the longer submergence time.

Key words: tufted duck, *Aythya fuligula*, diving, oxygen uptake, optimal foraging, model.

Introduction

‘Central place forager’ is a term used to describe the behaviour of a foraging animal that repeatedly returns to the same place with food (Orians and Pearson, 1979; Lessells and Stephens, 1983). The close analogy between a bird returning to its nest with food (Kacelnik, 1984) and a diving animal returning to the surface to breathe means that the concept of central place foraging can be applied to surfacing divers (Houston and McNamara, 1985). In this case, the surface of the water is the ‘central place’. Thus, models that examine the behaviour of central place foragers can be transposed to examine the behaviour of a diving animal.

During foraging bouts, assuming that a diver wants to be under the water acquiring food for as much time as possible, repeatedly returning to the surface for oxygen is (generally) in direct competition with food gain (Ydenberg and Clark, 1989). Optimal foraging models, which are based on the marginal value theorem (Charnov, 1976), have been developed to determine the optimal surface time for oxygen loading that maximises the proportion of time spent foraging (Kramer, 1988; Houston and Carbone, 1992; Carbone and Houston, 1996). These models are based on the physiological gains and losses of oxygen over the dive cycle and therefore the post-dive loading curve is an integral, but as yet unquantified, part of many theoretical studies of optimal time allocation

(Thompson et al., 1993; Carbone and Houston, 1994, 1996; Lea et al., 1996; Walton et al., 1998; Mori, 1998, 1999).

Because the mammalian lung system rapidly collapses on immersion (Kooyman and Ponganis, 1998), the majority of the oxygen stores of marine mammals consist of haemoglobin and myoglobin. Thus it is likely that the generic shape for the oxygen loading curve proposed and used by Kramer (1988) in his optimal breathing model (Fig. 1) may be correct for most diving mammals. However, Walton et al. (1998) have argued that this shape is not accurate for diving birds.

The respiratory system of birds differs from that of mammals and consists mainly of large distended air sacs and a lung, which is comparatively small and rigid (Scheid, 1979). However, the estimated contribution of the air sacs to the total body oxygen stores of diving birds ranges from 23% to 64%, e.g. tufted duck (Keijer and Butler, 1982), thick-billed murre (Croll et al., 1992), lesser scaup (Stephenson, 1995), Adélie penguin (Kooyman and Ponganis, 1998), king penguin (Ponganis et al., 1999). Therefore, it has been suggested that the respiratory system will have a profound influence on the dynamics of post-dive oxygen loading. The oxygen stored within the air sacs of tufted ducks during a dive is made available for consumption through locomotion, and associated abdominal activity. This produces pressure differentials

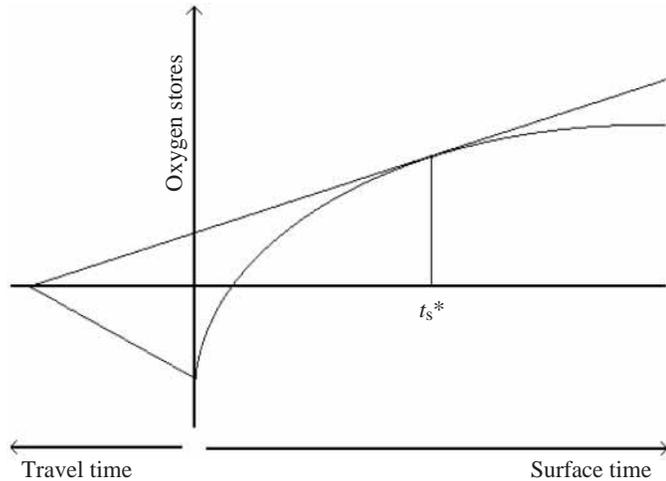


Fig. 1. The optimal breathing model (Kramer, 1988). The abscissa shows time spent travelling to and from the foraging site to the left of the ordinate, and time at the surface to the right. The ordinate shows the amount of oxygen consumed during travel and gained during surface periods. The value t_s^* denotes the optimal surface time for the diver, according to the model, in terms of maximising the proportion of time at the foraging site.

between the posterior and anterior air sacs, which could reciprocally force the gas stored in the air sacs through the lungs (Boggs et al., 1998). Walton et al. (1998) suggest that the gas in the air sacs at the end of a dive is therefore depleted of oxygen. They argued that, at the start of a surface interval, fresh air must be taken up into the respiratory tract before oxygen uptake by haemoglobin and myoglobin can occur, since fresh air must enter the caudal air sacs before any oxygen becomes available to the lungs.

Consequently, Walton et al. (1998) predict that avian divers will produce a 'kinked' oxygen uptake curve, with the first phase representing oxygen taken more rapidly into the air sacs and the second representing the relatively slower replacement of haemoglobin and myoglobin stores. In contrast to the smooth curve, this biphasic modification of the oxygen resaturation curve results in the prediction that all dives shorter than a certain duration will have identical optimal surface times (Walton et al., 1998) (Fig. 2). In addition, these dives will also achieve identical levels of oxygen resaturation during the subsequent surface period (Walton et al., 1998).

Both the smooth oxygen uptake curves of earlier models as well as the biphasic curve of Walton et al. (1998) predict a number of optimal behavioural patterns. These concern adjustments to surface time and foraging time in response to changes in dive depth and energetic costs during the dive. Some qualitative behavioural trends recorded in diving birds are predicted by optimal time allocation models incorporating the smooth oxygen replacement curve (Carbone and Houston, 1994; Carbone et al., 1996; Lea et al., 1996), while trends reported by Walton et al. (1998) are predicted by their model, which incorporates the biphasic curve. However, it is premature to affirm the success of any of these models when

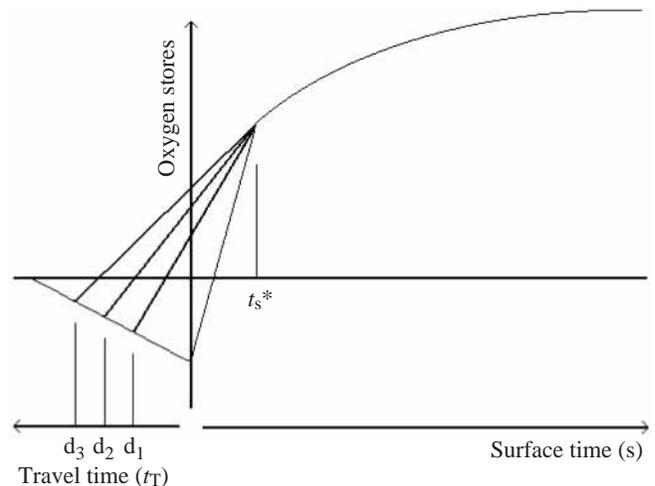


Fig. 2. Model, as in Fig. 1, incorporating a biphasic oxygen uptake curve (Walton et al., 1998). Due to the initial rapid resaturation of oxygen into the respiratory oxygen stores upon surfacing, a biphasic oxygen resaturation curve means that a range of dive depths (d_1 – d_3), associated with travel time (t_T), have identical optimal surface times (t_s^*).

key assumptions have not been verified. It is likely that the details of oxygen uptake curves have a critical effect on the gross predictions of optimal foraging models for divers (Ruxton et al., 2000). The differing predictions of present models reveal the importance of empirical study on oxygen uptake curves so that further progress can be made in understanding observed diving behaviour.

The purpose of the present study was to test the hypothesis that the post-dive oxygen gain curve for tufted ducks *Aythya fuligula* is biphasic. The delineation of the loading curve for voluntarily diving birds was achieved using a fast-response respirometry system, which is able to measure small changes in oxygen concentration over a fairly fine time resolution given a repetitive measurement signal. This enabled the quantification of a critical aspect of optimal foraging models for diving vertebrates and the determination of the extent to which the biphasic adaptation for diving birds is apparent.

Materials and methods

Four tufted ducks, *Aythya fuligula* L., were used for the experiment, two males and two females, of mean body mass 643 ± 26 g. The birds were raised from eggs and housed together in a large indoor tank [1.6×1.7 m (maximum depth)] at Birmingham University. The ducks were fed corn and growers' pellets (Dodson and Hornell Ltd, Kettering, UK) from a dry area (1.0×0.5 m) mounted on the side of the tank. White grit and small amounts of corn were thrown onto the water daily to encourage natural diving behaviour.

The experimental dive tank was located in a large outdoor aviary close to where the animals were housed. Two large metal fencing panels (1.75×3.45 m) were bolted together perpendicularly and placed in one corner of the dive tank,

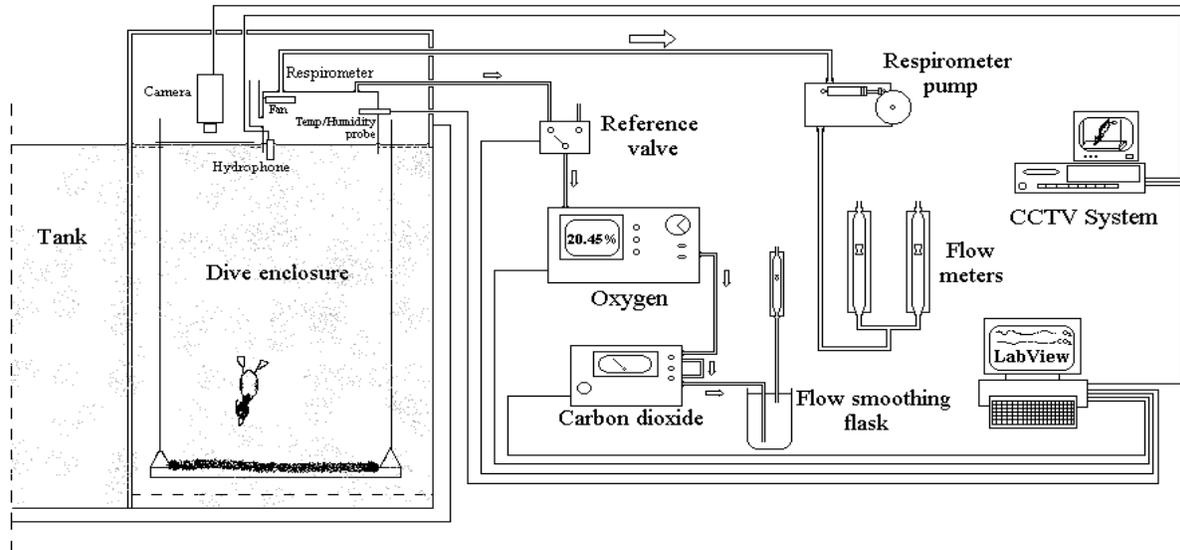


Fig. 3. Diagram of the experimental apparatus showing a tufted duck in an enclosed section of a large dive tank. For further details, see Materials and methods.

creating a 1.75×1.75 m cross-section area with a maximum depth of 2.7 m, in which the experiments were conducted. The metal panels stood 0.75 m above the water and, by using smaller fencing panels as a roof and additional side netting, a corral was formed above the water to prevent the birds from escaping.

The birds were trained to dive to a feeding platform (67×82 cm) positioned at a depth of 1.8 m. During the experiments the birds were fed corn and live mealworms. The latter was found to encourage diving behaviour. A false mesh floor was fitted to the bottom of the tank to prevent birds from diving for food that had spilt from the feeding platform. A submersible pool cleaner (Dolphin, Maytronics Ltd) was periodically used to clean fallen food from the floor of the tank. The water temperature varied between 10 and 15°C during the experimental period.

Respirometry experiments

The surface of the tank was covered in netting except for a small area over which the open base of the small, clear acrylic respirometer chamber (35×25×25 cm) was positioned and from which the individual birds dived. The open base of the respirometer was placed 4 cm below the surface of the water to form an airtight seal along its sides. This made the effective volume of the respirometer 18 375 ml. The respirometer contained a fan that ensured thorough mixing of the air within the chamber. A flow of 500 ml s⁻¹ was drawn through the respirometer by a fixed flow pump, keeping CO₂ below 0.2% at all times. Metabolic gas concentrations were determined using a zirconia oxygen sensor (Ametek, Thermox Instruments, model S3A-1/N.22) and an infrared carbon dioxide sensor (ADC Ltd, model SS-100) connected in series. The sample pump in the CO₂ sensor was used to draw an air sample from an outlet in the respirometer and through the gas sensors at a constant flow rate of 17 ml s⁻¹. A 500 ml flask was

used just prior to the sample pump to reduce any flow oscillations (see Fig. 3 for a diagram of the experimental apparatus). Total flow through the respirometer was 517 ml s⁻¹. Tubing of 300 ml 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 a dive, the small volume of air forced out of the holes did not escape from the system and was subsequently sucked back into the respirometer.

All connecting tubing was impermeable to oxygen and was as short and as small bore as possible to reduce dead space. The response time of the oxygen analyser was less than 0.2 s and the lag time of the respirometer box and tubing was 2.5 s. The residual time constant of the system after deconvolution (see later) was 0.4 s and was determined by N₂ injections at various points within the respirometer to simulate instantaneous changes in oxygen uptake. The effect of the residual time constant is a slight filtering of the V_{O₂} data, which results in a slight blurring of the cumulative oxygen uptake curves.

The O₂ and CO₂ analysers were calibrated each day with known gas concentrations produced by a precision gas-mixing pump (Wösthoff Pumps, Bochum). Atmospheric pressure was recorded every hour (Digital Weather Barometer, Prosser Scientific Instruments Ltd, UK) and a relative humidity and temperature probe (Vaisala, Finland) was fixed inside the respirometer to allow airflow through the respirometer to be corrected for water vapour.

A LabVIEW program (National Instruments Corporation, USA) was written to record data on respirometer oxygen concentration during the experimental sessions. A subroutine of the program controlled a reference valve, which sampled ambient oxygen concentration for 10 s every 20 min. This allowed the detection and correction of baseline drift in the

measuring system. 300 scans were averaged every 250 ms for humidity, temperature, %O₂, %CO₂ and reference valve position, and the data were then recorded onto the internal hard drive of the computer running the program (Dell Computers Dimensions XPS P60).

During the experimental sessions, the bird's behaviour was recorded onto video tape to determine time budget data by using a black and white video camera (JVC, model TK-S240) and video recorder (Mitsubishi, model Time Lapse HS-5424E[B]A). An additional small hole in the surface net was replaced with a clear perspex sheet, through which activity at the feeding platform could also be filmed. Two 500 W lamps were attached to the roof of the corral and used to illuminate the feeding platform. A light-emitting diode placed in the field of view of the video camera was turned on at the start of each data recording session. This allowed accurate synchrony between the video footage of behaviour and the respirometer oxygen composition data so that rates of oxygen uptake against time for each surface period could be determined. Preliminary data showed that the ducks first inspired when they were fully surfaced on the water.

Analysis of respirometry data

Percentage oxygen concentration data were converted into rate of oxygen uptake using a modification of the formula given by Woakes and Butler (1983), which allows accurate determination of fast changes in gas concentrations (see Equation 1 below). By treating the respirometer as both an open and a closed system, oxygen uptake could be determined for 0.25 s intervals, despite the system having a much longer response time (36 s). The changes in oxygen concentration in the respirometer between t_1 and t_2 were very small and often within the error of the oxygen analyser, creating a low ratio of measurement signal against signal noise. However, the noise component of each measurement was random and therefore equally likely to be negative or positive. Thus, recording multiple data points for each value of t allowed signal averaging to recover the measurement signal at each 0.25 s by reducing the magnitude of the mean noise value (Bentley, 1983), i.e. averaging maintained the root-mean-square (rms) value of the measurement signal while reducing the rms value of the noise. Because a very large number of data points ($N=870$ and 878) were collected and averaged, the signal-to-noise ratio was greatly increased. A change of 1 ml O₂ in the respirometer could then be measured with an error of approximately ± 0.03 ml:

$$\dot{V}_{O_2} = (Ox_2 - Ox_1)V + \left(\frac{Ox_1 + Ox_2 - 2Ox_{amb}}{2} \right) (t_2 - t_1)\dot{Q}, \quad (1)$$

where V_{O_2} = total oxygen consumption between times t_1 and t_2 (ml), Ox_1 and 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 and t_2 = start and finish, respectively, of a period of time where variation of oxygen concentration in the respirometer is recorded, and \dot{Q} = flow rate out of the respirometer (ml s⁻¹). All gas concentrations and volumes were corrected to STPD.

Oxygen data for the last 1 s surface interval were removed so that any elevated pre-dive \dot{V}_{O_2} was not included in the analysis (Butler and Woakes, 1979; Woakes and Butler, 1983). For analysis of oxygen uptake data, values are means \pm s.e.m. for four animals. To avoid animal bias, mean values were obtained for each bird and these means were used to obtain the final mean. A significant difference between means was tested with paired t -tests.

Statistics for biphasic determination

Bout criterion interval analysis (Slater and Lester, 1982) was used to eliminate all (inter-bout) dives with a surface time greater than 35 s. Preliminary data suggested that longer dives had a more pronounced effect on the oxygen loading dynamics, possibly due to the amount of oxygen used while submerged, and so the dive data were split into two groups for analysis. Dives were split at 16.0 s, which gave two dive duration bins, 'short' and 'long', with N -values as equal as possible (short, dive duration <16.0 s, $N=870$; long, dive duration ≥ 16.0 s, $N=878$). The mean V_{O_2} data were smoothed by taking a running three-point average and then log-transformed to linearise the exponentially decreasing oxygen uptake data. 'Broken stick' analysis was then performed to see if the biphasic regression line was statistically a better fit than a linear one (Seber, 1977). To construct a biphasic regression line, the logged mean oxygen uptake data were split at a selected data point. A linear regression line was then fitted to the data, which corresponded from the start of the surface time up to and including the chosen break point. Similarly, another linear regression line was fitted just after the chosen break point to the remainder of the data. The uptake data during the surface recovery had therefore been split into two phases around a chosen data point. The linear equations for each of these phases allowed the intersecting point of inflection, C , to be calculated (see Equation 5) and an overall biphasic regression equation to be determined (see Equations 6, 7).

An illustration of this technique can be seen in Fig. 4. For this worked example the break point in the data was arbitrarily chosen at 6 s. Regression analysis was conducted on the data up to and including this break point (Linear phase 1) and again on all remaining data points (Linear phase 2). The point of intersection for these two regression lines also represents the point of inflection, C , of the biphasic regression line. Equation 5 can therefore be used with parameters determined by the linear regression analysis to calculate this point of inflection. A generalised regression equation for a biphasic line can then be produced using Equations 6 and 7. It is at this point that the 'broken stick' analysis is conducted to see if the biphasic regression line is statistically a better description of the data than a linear regression line (Fig. 4B).

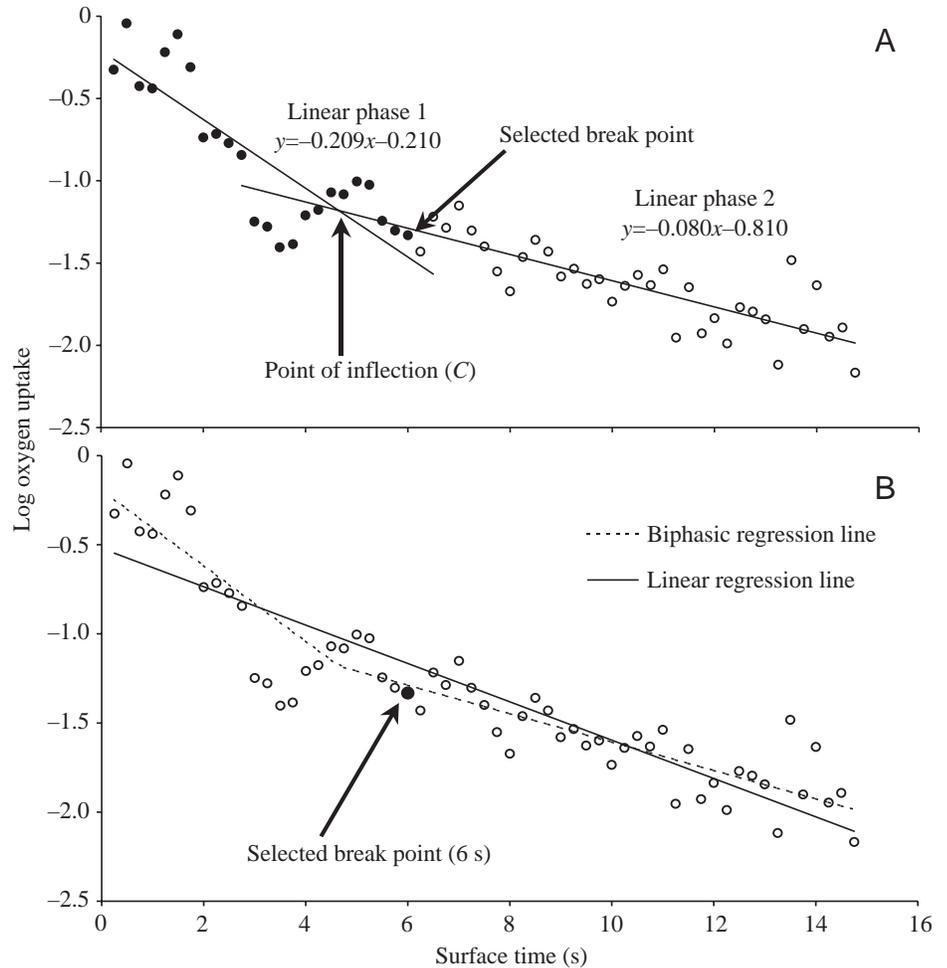


Fig. 4. Charts to show the methodology of biphasic modelling using broken stick analysis. (A) V_{O_2} data for four tufted ducks were smoothed and plotted on a logarithmic axis. The break point was arbitrarily chosen at 6 s. Linear regression was performed up to and including the break point (Linear phase 1) and also on all remaining data points (Linear phase 2). Regression parameters were then used to determine the point of inflection (C) where the two lines intersect. (B) V_{O_2} data for four tufted ducks were regressed onto the two regression lines shown (biphasic and linear). The biphasic regression line was calculated as shown in Fig. 4A. Commonly in this type of analysis the biphasic point of inflection (C) was not identical to the selected break point.

Locating inflection points for biphasic regression

Least-squares regression was performed on the uptake data with the break point at 6 s post dive, as given in the example (Fig. 4). An iterative sequence of least-squares regression with the chosen break point decreasing by 0.25 s every execution was then completed. The biphasic regression line that had a break point with the lowest residual variance, and so represented the best description of the data, was used as the biphasic regression solution to the uptake data.

For the biphasic regression, both phases of the broken stick model were calculated by linear regression and so can be defined as follows:

Linear phase 1 (before the break):

$$y_1 = a_1x + b_1, \quad (2)$$

and Linear phase 2 (after the break):

$$y_2 = a_2x + b_2. \quad (3)$$

The point of intersection for Equations 2 and 3 can be determined with respect to x by solving Equations 1 and 2:

$$a_1x + b_1 = a_2x + b_2, \quad (4)$$

$$x = -(b_1 - b_2) / (a_1 - a_2) = C. \quad (5)$$

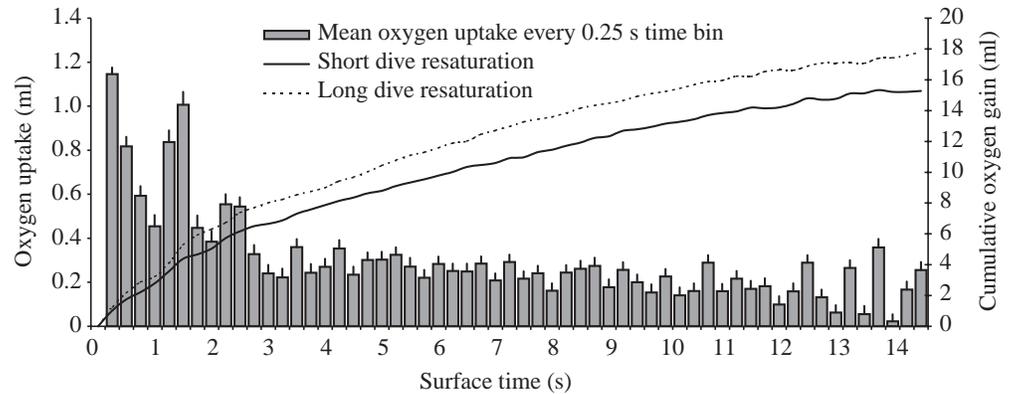
Since this point of intersection also represents the point of inflection for biphasic oxygen uptake, C , the generalised regression equations for a biphasic line, where a_1 , a_2 and b_1 are parameters for the linear components of the broken stick model are:

$$\text{if } x \leq C, \quad y = a_1x + b_1; \quad (6)$$

$$\text{if } x > C, \quad y = b_1 + a_1x - (a_1 - a_2)(x - C). \quad (7)$$

To test the significance of the biphasic regression equation, least-squares regression was performed using both the biphasic construct and simple linear regression. An F -test was then performed on the residual mean sum of squares for both equations to determine statistically whether the biphasic regression was a significant improvement. Degrees of freedom (d.f.) for linear regression is $N-1$ whereas d.f. for biphasic uptake is $N-4$ as a_1 , a_2 , b_1 and C have been calculated to define the biphasic equation. Other methodologies are available to determine whether biphasic relationships exist within the data. These are more complex as they allow for a smoother transition between the two phases of the biphasic construct (Koops and Grossman, 1993).

Fig. 5. Bar chart showing mean oxygen uptake for four tufted ducks during the first 14.5 s post surface (values are means + s.e.m.). The line graphs show the cumulative oxygen gain curve for short (<16.0 s; solid line) and long dives (≥ 16.0 s; broken line) for the first 14.5 s post dive.



Results

Diving time budgets

The data for four tufted ducks were split into bins of short duration dives (<16.0 s; $N=870$) and long duration dives (>16.0 s; $N=878$). The time budget data were therefore not normally distributed within the groups. Table 1 contains a summary of these data. The oxygen uptake data for individual birds in both groups were normally distributed about the mean (Kolmogorov–Smirnov test; not significant).

Oxygen uptake

The mean rate of oxygen uptake (\dot{V}_{O_2}) for all dives, over the first 15 s, was $1.14 \pm 0.33 \text{ ml s}^{-1}$. However, the rate of oxygen uptake was not constant (Fig. 5). The \dot{V}_{O_2} data for all dives show that upon surfacing there was a more rapid phase of oxygen uptake for approximately the first 3 s, during which \dot{V}_{O_2} was $2.45 \pm 0.09 \text{ ml s}^{-1}$.

\dot{V}_{O_2} was significantly higher for the first 3 s of surface time after both short and long dives (short dives, $2.22 \pm 0.13 \text{ ml s}^{-1}$; long dives, $2.67 \pm 0.12 \text{ ml s}^{-1}$) than for the rest of the surface period, up to 15 s (short dives, $0.72 \pm 0.28 \text{ ml s}^{-1}$, $P < 0.001$; long dives, $0.82 \pm 0.37 \text{ ml s}^{-1}$, $P < 0.001$). \dot{V}_{O_2} significantly differed between short and long dives during the first 3 s ($P < 0.01$) but did not significantly differ between short and long dives for the rest of the surface period up to 15 s.

After long dives, the mean total oxygen uptake during the first 15 s of the surface interval (17.9 ml) was significantly higher than that after short dives (15.3 ml, $P < 0.001$; Fig. 6). Statistical comparison of the mean uptake curves for the two dive duration bins was achieved by testing for a significant difference between the cumulative oxygen values of the curves at 5 s, 10 s and 15 s. The values at 5 s, 10 s and 15 s were

Table 1. Summary of time budget data

	All dives	Short dives	Long dives
Dive duration (s)	16.00	13.27 (5.3–16.0)	17.50 (16.0–26.8)
Surface duration (s)	12.25	11.00 (4.0–34.3)	14.00 (6.0–34.7)

Values given are medians.

Values in parentheses are ranges.

$N=870$ for short dives, $N=878$ for long dives.

significantly higher in the oxygen uptake curve associated with longer duration dives than in the shorter ones (Table 2).

Biphasic analysis

The break points with the lowest residual variance used to calculate the biphasic regression lines were 5.00 s for short dives and 3.00 s for long dives (Fig. 7). Using these values in Equations 1, 2 and 5 gave the point of inflection for biphasic oxygen uptake, C , as 3.3 s for short dives and 3.3 s for long dives. Least-squares regression analysis was performed using both linear and biphasic equations on log transformed smoothed mean \dot{V}_{O_2} data for both long (Fig. 7) and short dives.

All linear and biphasic regression lines used were highly significant (Table 3). F -tests were then used on the residual mean sum of squares for the linear and the biphasic regression lines to see whether the biphasic constructs were a significantly better description of the data. Biphasic regression was not significantly better for short dives ($C=3.34$, $F_{56,53}=1.45$, not significant). For long dives, the biphasic regression was a significantly better fit for the data than linear regression ($C=3.28$, $F_{56,53}=1.96$, $P < 0.01$). Thus, oxygen uptake is only biphasic for long duration dives, with the point of inflection at 3.3 s (Fig. 8). Due to the effect of the residual time constant on the cumulative oxygen uptake curves, the points of inflection may be slightly inaccurate. Nevertheless, the true point of inflection for both these curves is very close to 3.3 s.

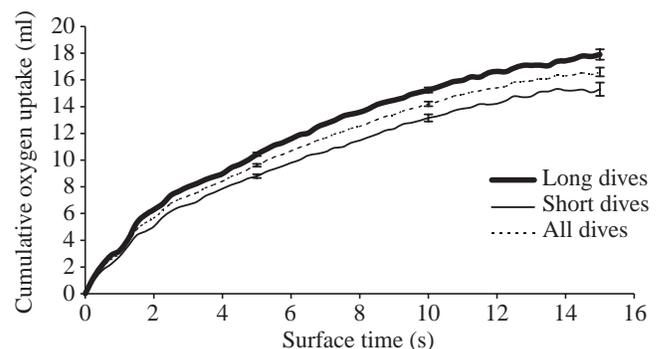


Fig. 6. Comparison of the mean oxygen uptake curve of four tufted ducks at 5 s, 10 s and 15 s surface duration \pm s.e.m. after short dives and long dives.

Fig. 7. Histogram showing the calculated residual variances with the break point every 0.25 s for the first 6 s post dive for long dives of four tufted ducks. The break point with the lowest residual variance occurred 3.00 s post dive and was used to define the biphasic regression line. See statistics in Materials and methods for details of the biphasic determination.

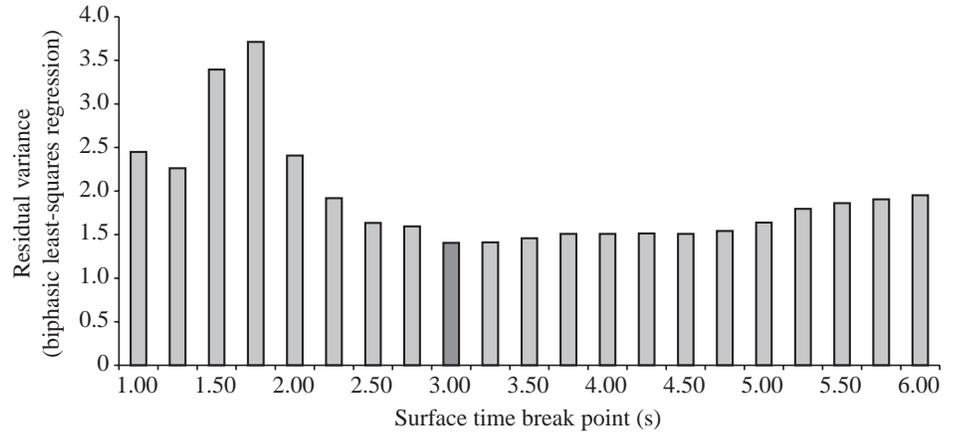


Table 2. Statistical comparison between oxygen uptake curves after dives of short and long duration, and for all dives combined

Time at surface (s)	Cumulative O ₂ uptake after short dives (ml)	Cumulative O ₂ uptake after long dives (ml)	Cumulative O ₂ uptake after all dives (ml)
5	8.80±0.14	10.44±0.13***	9.62±0.11
10	13.16±0.26	15.24±0.20***	14.20±0.17
15	15.30±0.51	17.90±0.39***	16.60±0.33

Values are means ± S.E.M. (N=4).

***Values for short and long dives are significantly different ($P<0.001$).

Table 3. Results of biphasic determination

Dive duration	Regression line	Point of inflection	Regression P value	Biphasic improvement	
				d.f.	P value
Short	Linear		<0.001	56	
	Biphasic	3.34	<0.001	53	0.086
Long	Linear		<0.001	56	
	Biphasic	3.28	<0.001	53	0.007**

Calculations were performed on the log-transformed smoothed data for both dive duration bins to linearise the exponential data.

All regression lines, both linear and biphasic, were highly significant. ** $P<0.01$.

Discussion

The dive durations, surface durations and oxygen uptake volumes at the surface in the present study are comparable to time budget data recorded from previous studies on the same genus diving to similar depths (Table 4).

The rate of oxygen uptake \dot{V}_{O_2} changes over time at the surface after both long and short dives. In both cases, \dot{V}_{O_2} is higher at the start of the surface period and decreases against time. This relationship is not linear, as shown by the oxygen uptake curves for long and short dives in Fig. 5. Rather, both curves can be seen to consist of far higher \dot{V}_{O_2} for approximately the first 3 s of surface time.

The shape of the oxygen uptake curve changes with the duration of the dive (Figs 5, 6) and oxygen was taken up significantly faster during surface periods associated with longer

dive durations. This suggests that, as dive duration increases, and presumably total oxygen consumed during the dive (V_{O_2d}) increases, initial surface \dot{V}_{O_2} increases. While \dot{V}_{O_2} from 3 s to 15 s was not significantly different between the two conditions, it was significantly higher after longer dives during the first 3 s. Whether this is due partly to an increase in effort by the birds to take up oxygen more quickly, or is purely a passive phenomenon dependent upon the difference in partial pressure of oxygen inside and outside the cardio-respiratory system, is not clear. Higher \dot{V}_{O_2} for the first 3 s after longer dives, coupled with a \dot{V}_{O_2} beyond 3 s that does not vary with dive duration, creates a sharper 'kink' in the oxygen uptake curve after longer dives.

Implications for optimal foraging models

The kink in the oxygen uptake curve produced by the ducks

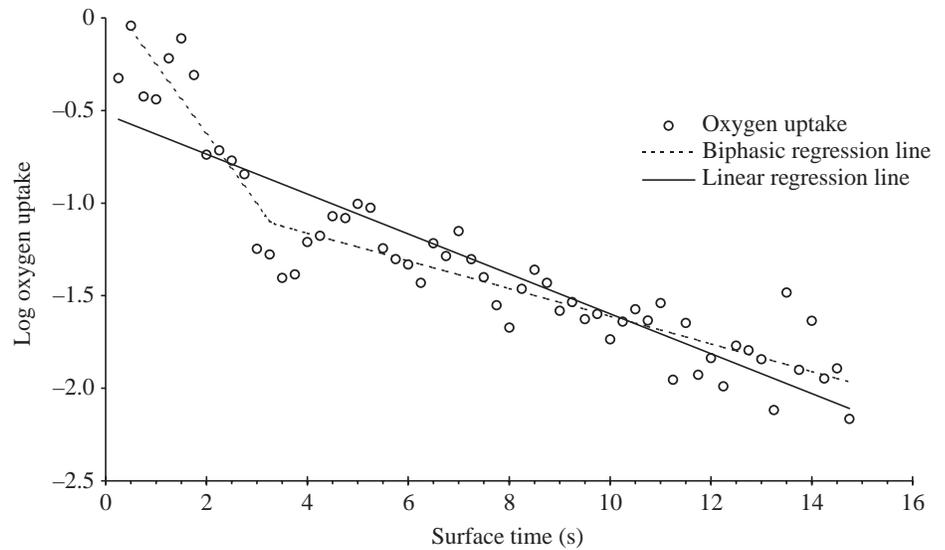


Fig. 8. Chart to show biphasic modelling for long duration dives during the first 15 s post surface for four tufted ducks. The smoothed V_{O_2} data (open circles) have been log-transformed. Least-squares regression is then performed using the linear and the biphasic regression lines. Phases 1 and 2 of the biphasic regression line can be seen with the point of inflection at 3.28 s post surface.

Table 4. Mean values of time budget data for similar respirometer studies with *Aythya* species diving to similar depths

<i>Aythya</i> species	Depth (m)	Dive time (s)	Surface time (s)	Mean total oxygen uptake during surface interval (ml)	Study
<i>A. fuligula</i>	1.8	15.6	14.0	16.63	Present study
<i>A. fuligula</i>	1.7	14.4	16.1	16.2	Woakes and Butler (1983)
<i>A. fuligula</i>	0.6	18.9	11.6	12.1	Bevan and Butler (1992)*, ^a
<i>A. fuligula</i>	0.6	16.2	12.8	16.4	Bevan and Butler (1992)*, ^b
<i>A. affinis</i>	1.5	13.5	16.3	18.6	Stephenson (1994)
<i>A. fuligula</i>	1.5	15.9	17.9	–	S. Wallace (unpublished)

*Ducks were trained to dive for set durations using a system of computer-controlled lights.

^aSummer acclimated birds.

^bWinter acclimated birds.

for long dive durations was sufficiently pronounced to make the measured curve statistically biphasic, while the uptake curve for short dive durations was not. This indicates that the break in the curve becomes more prominent during surface periods when the dive duration was longer and V_{O_2} was higher. So, for tufted ducks, dives of a relatively short duration are followed by surface periods where rates of oxygen uptake produce a curve similar to that predicted by Kramer (1988). Longer dive durations produce oxygen uptake curves with a clearer biphasic element and so become more like the curve predicted by Walton et al. (1998).

According to the predictions of Walton et al. (1998), a range of dives up to a certain duration will be associated with very similar surface durations because the tangent from travel time t_T will be 'locked' to the kink of the curve. However, the mean surface duration for long duration dives is more than fourfold greater than the surface duration at which the kink often occurs (15.4 s versus approx. 3.3 s). For tufted ducks, therefore, the volume of oxygen consumed during the dive may be high enough that the tangent routinely touches the curve beyond the kink (Houston, 2000). Shorter dives, where less oxygen is consumed, produce smoother oxygen uptake curves and so

there is not such a pronounced kink to intercept the tangent. Extended dives by tufted ducks, although utilising very high volumes of oxygen, might possibly produce oxygen uptake curves with such an acute kink that the tangent still touches it. However, although occasional dives of over 40 s have been reported in tufted ducks (Stephenson et al., 1986), Table 4 indicates that the vast majority of dives by this species are unlikely to be long enough to cause such a large change to the post-dive oxygen reloading dynamics. Furthermore, field studies suggest that dives are normally fairly short, for example Magnúsdóttir and Einarsson (1990) recorded a mean dive time for tufted ducks diving on Lake Mývatn of 18.3 s.

Respiratory frequency during periods of oxygen uptake

Walton et al. (1998) may have made an incorrect assumption that oxygen must be taken up into the caudal air sacs before it is then made available for gaseous exchange. In fact, on inspiration, a significant proportion of air directly enters the paleopulmonic parabronchi via the main bronchus (Bretz and Schmidt-Nielsen, 1971; Butler et al., 1988; Powell, 2000). Indeed, Powell (2000) suggests that when the tidal volume is large, some inspired gases reach as far as the cranial air sacs,

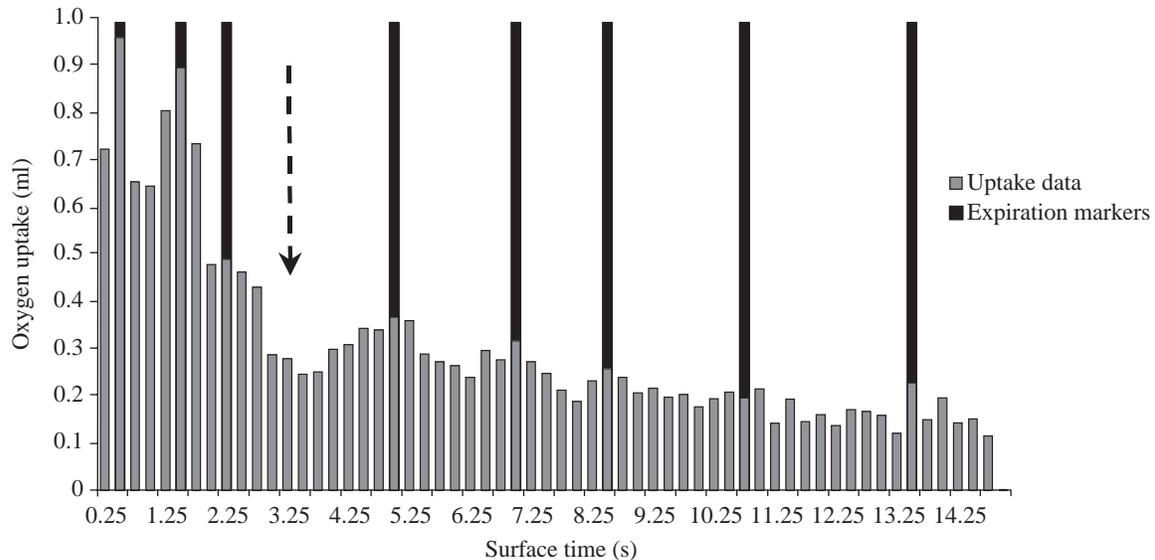


Fig. 9. Mean \dot{V}_{O_2} observed after long dives of four tufted ducks. Data were smoothed by taking a three-point moving average. As well as the general exponential decrease in \dot{V}_{O_2} over the first 15 s post surface, there is a cyclical aspect to the data. This is highlighted subjectively on the graph (black bars), and is believed to correspond to expiration (peak) and inspiration (trough), occurring at frequencies similar to those recorded by Butler and Woakes (1979) in a diving pochard (*Aythya ferina*). The arrow indicates the point of inflection for biphasic uptake.

via the paleopulmonic parabronchi, during the same breath. In this case, birds would not exhibit a biphasic oxygen uptake curve for the reasons stated by Walton et al. (1998), since fresh air would reach the lungs on the first inspiration. Nevertheless, tufted ducks do demonstrate biphasic oxygen uptake after relatively long dives and so there must be an alternative explanation for this kinked curve.

\dot{V}_{O_2} not only decreases against surface duration but shows a cyclical aspect that is not attenuated when the data are smoothed after long duration dives (Fig. 9). This cyclical aspect is not as clear after short duration dives. After long duration dives, the peaks in \dot{V}_{O_2} data reflect a drop in respirometer oxygen concentration and presumably correspond to exhalation by the bird. Similarly, the drop in \dot{V}_{O_2} would therefore correspond to inspiration. If this is so, then the first post-dive exhalation occurs about 0.5 s after surfacing.

Butler and Woakes (1979) studied the respiratory patterns of diving pochards (*Aythya ferina*) before and after feeding dives using implanted tracheal thermistors. They reported that the respiratory frequency decreased from 54.5 breaths min^{-1} , 1 s after surfacing to 42.7 breaths min^{-1} after 5 s and longer. If the respirometry system used in the present study was able to detect individual breaths, the rates of post-dive ventilation for the pochard are comparable to those from the present study. There is clearly a change in respiratory frequency after the third exhalation, according to Fig. 9. The first three expiration markers cover approx. 2.5 respiratory cycles in 2.25 s, implying a respiratory frequency of 66.7 breaths min^{-1} . The next five markers cover approx. 4.75 cycles in 8.75 s, a respiratory frequency of 32.5 breaths min^{-1} . The biphasic inflection point, at 3.3 s, occurs in between the third and fourth expirations. Thus, the biphasic nature of oxygen uptake

following longer dives may be explained by a fairly sudden slowing of ventilation rate after the first three exhalations. This agrees with reports of other diving vertebrate species reloading their oxygen stores and removing carbon dioxide after dives (Butler and Jones, 1997). However, not all air-breathing divers exhibit the same respiratory patterns as avian species. Weddell seals show a steady decline in minute volume (volume of air inhaled per minute) during the first 5 min post-dive, and beyond this point the decline decays to a constant (Kooyman et al., 1971).

A hypothesis borne from the assumptions on avian anatomy by Walton et al. (1998) is that the break point of the oxygen uptake curve would occur just after the second post-surface expiration, since this would be the first opportunity for the inspired gases to diffuse into the blood and tissues through the paleopulmonic parabronchi. The biphasic point of inflection is at 3.3 s for long duration dives, whereas the second exhalation occurs at 1.5 s (Fig. 9). This is further evidence that the biphasic uptake that occurs during longer dives in the tufted duck is probably associated with a change in respiratory frequency, rather than as a consequence of the anatomy of its respiratory system.

List of symbols

a_1, a_2, b_1	linear components of the broken stick model
C	intersecting point of inflection
Ox_1, Ox_2	fractional concentrations of oxygen at times t_1, t_2 after leaving the chamber
Ox_{amb}	fractional concentration of (ambient) oxygen entering the respirometer
\dot{Q}	flow rate out of the respirometer (ml s^{-1})

t	time
t_1 and t_2	start and finish, respectively, of the measured period of time
t_s	optimal surface time
t_T	travel time
V	respirometer volume
\dot{V}_{O_2}	rate of oxygen uptake
\dot{V}_{O_2}	total oxygen consumption between times t_1 and t_2
$V_{O_{2d}}$	total oxygen consumed during the dive

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