

DIVING ENERGETICS IN LESSER SCAUP (*AYTHYA AFFINIS*, EYTON)

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Summary

Mechanical and aerobic energy costs of diving were measured simultaneously by closed-circuit respirometry in six lesser scaup *Aythya affinis* Eyton (body mass=591±30 g) during bouts of voluntary feeding dives. Durations of dives ($t_d=13.5\pm 1.4$ s) and surface intervals ($t_i=16.3\pm 2.2$ s) were within the normal range for ducks diving to 1.5 m depth. Mechanical power output (3.69 ± 0.24 W kg⁻¹) and aerobic power input (29.32 ± 2.47 W kg⁻¹) were both higher than previous estimates. Buoyancy was found to be the dominant factor determining dive costs, contributing 62% of the mechanical cost of descent and 87% of the cost of staying at the bottom while feeding. Drag forces, including the contribution from the forward-moving hindlimbs during the recovery stroke of the leg-beat cycle, contributed 27% and 13% of the mechanical costs of descent and feeding, respectively. Inertial forces created by net acceleration during descent contributed approximately 11% during descent but not at all during the feeding phase. Buoyant force at the start of voluntary dives (6.2 ± 0.35 N kg⁻¹) was significantly greater than that measured in restrained ducks (4.9 ± 0.2 N kg⁻¹). Loss of air from the plumage layer and compression due to hydrostatic pressure decreased buoyancy by 32%. Mechanical work and power output were 1.9 and 2.4 times greater during descent than during the feeding phase. Therefore, energetic costs are strongly affected by dive-phase durations. Estimates by unsteady and steady biomechanical models differ significantly during descent but not during the feeding phase.

Introduction

It was suggested many years ago that freely diving birds are unlikely to exhibit the pronounced reduction in oxygen consumption that occurs in forcibly submerged animals (Scholander, 1940; Eliassen, 1963). The fact that voluntary dives are usually of relatively short duration and involve muscular exercise are clear behavioural clues that metabolic rate might be elevated, not reduced. Observations of physiological variables, such as heart rate and blood flow distribution, support this idea (Butler and Woakes, 1979, 1984; Stephenson and Jones, 1992; Bevan and Butler, 1992*b*). However, very few estimates of diving metabolism have been reported. Woakes and Butler (1983) found that oxygen consumption was elevated to over three times the resting levels during feeding dives in

Key words: diving ducks, *Aythya affinis*, buoyancy, drag, inertia, oxygen consumption.

unrestrained tufted ducks, *Aythya fuligula*. Further studies in the same species have confirmed that, although diving oxygen consumption may vary as a function of dive duration, it is always significantly higher than resting levels (Bevan and Butler, 1992a; Bevan *et al.* 1992).

Butler and Woakes (1984) also investigated freely diving Humboldt penguins, *Spheniscus humboldti*, and found that oxygen uptake was not elevated to the extent seen in diving tufted ducks. They attributed the difference in oxygen uptake between ducks and penguins to apparent differences in buoyancy. Subsequent studies (Baudinette and Gill, 1985; Hui, 1988b; Culik and Wilson, 1991) of aerobic power input in diving penguins have highlighted the importance of swimming speed to dive costs, implying that drag may be more significant than buoyancy in these pursuit divers (Hui, 1988a).

Several studies have concluded that the buoyant force is a major factor determining total power output during dives in ducks of the genus *Aythya* (Dehner, 1946; Stephenson *et al.* 1989a; Lovvorn *et al.* 1991; Lovvorn and Jones, 1991a,b; Wilson *et al.* 1992; Stephenson, 1993). Body drag contributes significantly to power output during the descent phase of the dive but is considered to be relatively less important over the dive as a whole in benthic-feeding species. The importance ascribed to inertial forces associated with the unsteady propulsive action of the hindlimbs varies according to the biomechanical model used. Stephenson *et al.* (1989a) used a simple steady model which assumed the latter to be insignificant, whereas Lovvorn *et al.* (1991) developed an unsteady model and concluded that inertial forces often predominate.

Power input and power output have not yet been measured in the same animals, or even in the same species of ducks. Furthermore, there have been no comprehensive studies of power output in freely diving birds. All previous estimates of buoyant force were obtained using forcibly submerged ducks or cadavers (Dehner, 1946; Stephenson *et al.* 1989a; Lovvorn *et al.* 1991, Lovvorn and Jones, 1991a,b; Wilson *et al.* 1992; Stephenson, 1993). Stephenson (1993) has shown that the methods used to measure buoyancy in those studies are unreliable because there is potentially much variability in the volumes of air in the respiratory system and plumage layer. Body drag data were obtained from frozen duck carcasses with hindlimbs amputated in previous studies (Stephenson *et al.* 1989a; Lovvorn *et al.* 1991). Furthermore, although the kinematic data of Lovvorn *et al.* (1991) were obtained from freely diving ducks, the calculations of work done to accelerate the body in each power stroke were based in part on estimates of body volume obtained from forcibly submerged ducks, so those findings may also be inaccurate.

In the present study, a closed-circuit respirometry system was constructed that enabled simultaneous measurements of oxygen uptake, buoyant force, hindlimb stroke frequency, descent velocity, dive-phase durations and diving behaviour in confined but otherwise unrestrained lesser scaup, *Aythya affinis*. Measurements were made during bouts of voluntary feeding dives. The data were used to re-evaluate the power input, power output, cost of transport and energetic efficiency of diving benthic-feeding ducks.

Materials and methods

Six lesser scaup (five male, one female; body mass range 510–723 g) were trained to

dive for food in a 1.52 m deep glass-sided tank. The surface of the tank (dimensions 262 cm×112 cm) was covered by a black plastic screen held 4.5 cm below the water surface. Eight rectangular holes (37 cm×25 cm) were cut in the screen and these were covered by inverted transparent plastic containers (volume 20 l each). Each container was open to the water below. A vertical mesh screen was placed in the tank to divide it into two approximately equal parts. Throughout the training period, which lasted several months to ensure that the ducks were fully familiarized with the situation, the ducks were kept on the experimental tank and placed in the containers as a group for several hours per day, during which time food was provided on the floor of the tank. Dry food was provided in a bowl each weekend to ensure that the ducks maintained body weight and condition.

During experiments, four diving chambers were placed on one section of the tank and the measurement chamber (respirometer) was placed over the other section. One duck was placed in each chamber concurrently. The duck in the respirometer could see the other four animals both on the surface and while submerged, but it alone was constrained to dive from, and resurface to, the respirometer. The vertical mesh screen prevented access to the respirometer by the other ducks.

During the experimental period, the ducks were housed in a holding tank in an adjacent room (water and air temperatures were identical in both rooms: water approximately 12 °C, air approximately 15 °C). None of the ducks was moulting during experiments. Each day, they were captured in a hand-held net, placed in a carrying box and transported to the laboratory. They were immediately placed in the experimental tank. Water temperature, air temperature within the respirometer and barometric pressure were noted approximately midway through each experiment. Measurements were made in sessions lasting 6 h. At the end of this time the ducks were weighed then returned to the holding tank.

Experimental apparatus

The respirometry system is illustrated in Fig. 1. Two containers, a thermobarometer and a respirometer were used. The entrance to the thermobarometer was closed (but not sealed). Both chambers were connected to a differential pressure transducer (model DP45-14; Validyne Engineering Corp.) and a differential thermometer (BAT-10 multipurpose thermometer; Physitemp Instruments Inc.). The respirometer was also connected to a gas recirculation system incorporating a carbon dioxide scrubber (the gas was bubbled through concentrated sodium hydroxide solution) and an automated oxygen injection system. Thus, carbon dioxide concentration was held below 0.6% at all times and oxygen concentration oscillated (approximately 0.15% peak-to-peak) around an adjustable set point held at approximately 21% in these experiments.

The gas was recirculated at a rate of approximately 16 l min⁻¹ using three vacuum/pressure diaphragm pumps connected in parallel [dual-head 'Air Cadet' pump (Cole-Parmer Instrument Co.) and 'Dyna-Pump' (Neptune Products, Inc.)]. Oxygen and carbon dioxide concentrations were continually monitored using electrochemical fuel cell and infrared analyzers, respectively (models S-3A/1 and CD-3A; Ametek Corp.). The air in the respirometer was rapidly mixed by a single small fan attached to one wall. Dead space in the system was minimized as far as possible, especially between the measurement chamber and the fuel cell of the oxygen analyzer.

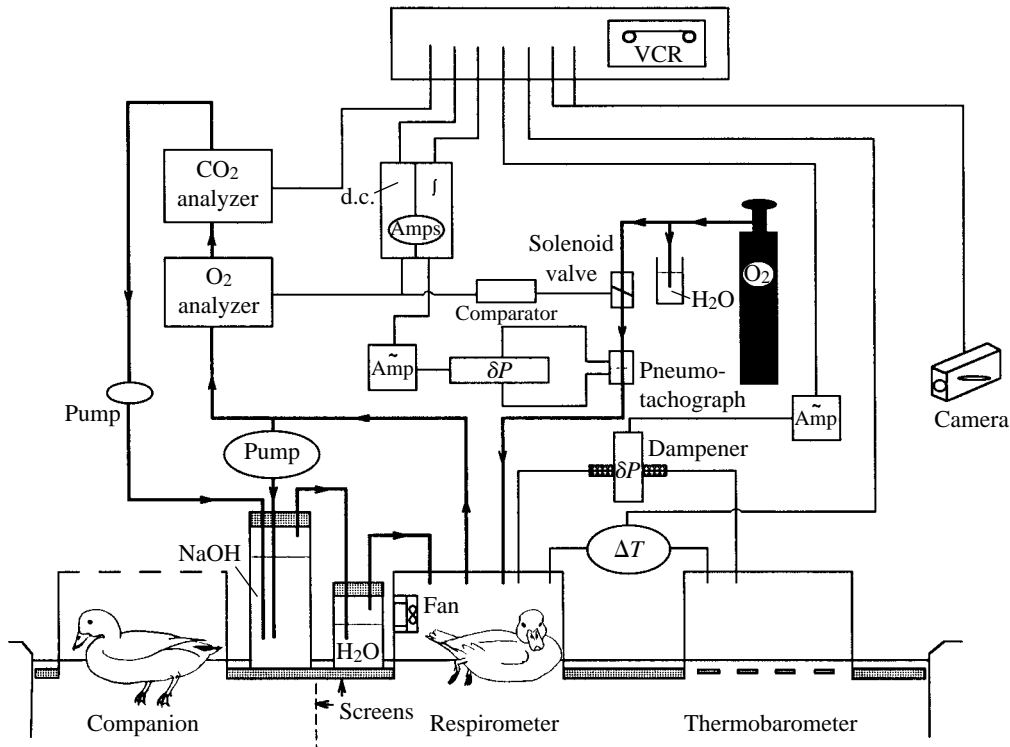


Fig. 1. Closed-circuit system for simultaneous analysis of oxygen consumption, buoyancy and voluntary diving behaviour in lesser scaup. Bold lines represent gas lines and arrowheads indicate direction of gas flow. δP , differential pressure transducer, ΔT , differential thermometer. Amplifiers are depicted as follows: d.c., 'Universal' amplifier; \int , integrating amplifier; \sim , carrier demodulator. See text for further details.

Analogue outputs of the pressure transducers, signal conditioners, gas analyzers and thermometer were recorded, together with a visual record of animal behaviour and a spoken commentary, using a VCR format data recorder (model 820; A. R. Vetter Co.) and camera (model CCD-F77; Sony Corp.). Calibrations for all channels were recorded on each video cassette. The data were later played back *via* a Maclab/8 Interface module (AD Instruments, Inc.) for analysis using a microcomputer and associated software.

Measurement of oxygen consumption

Oxygen consumption by the ducks during the intervals at the surface was measured by closed-circuit respirometry (Fig. 1). Oxygen concentration in the respirometer was held within narrow limits by an automated feedback system. Infusion of oxygen was controlled using a solenoid valve (model V52 LB, Skinner Valve Div.) triggered to open or close by a voltage signal fed from a purpose-built comparator circuit. The latter operated in response to the output from the oxygen analyzer. The voltage output generated by the comparator circuit was switched on or off when the input signal crossed an adjustable threshold. A sub-threshold signal from the oxygen analyzer, indicating low O_2

concentration, caused the comparator to open the valve and allow the infusion of O₂. When O₂ concentration subsequently increased to suprathreshold values, the valve closed. The lag time of the system (approximately 3 s), caused by unavoidable short delays in gas mixing and circulation, obviated the need for an electronic hysteresis in the comparator circuit. The solenoid valve was fitted with Viton parts to ensure safe operation with pure oxygen.

Rate of oxygen infusion was monitored by a differential pressure transducer (DP45-14, Validyne Engineering Corp.) connected to a Fleisch 0000 pneumotachograph, and the volume infused was obtained by passing the flow signal through an integrating signal conditioner (Gould Inc.). The integrator was calibrated by injection of known volumes of pure oxygen through the system using a glass syringe. Tests showed that using air to calibrate caused a 10.2% overestimation of oxygen consumption. The output of the oxygen analyzer was fed into a Gould Universal signal conditioner, which was used to offset the large d.c. voltage and then amplify and filter the signal of interest before recording. Lag time and the proportionality constant relating volume of O₂ injected and O₂ concentration were determined before each experiment in the absence of the duck by injection of known volumes of O₂ *via* the infusion system used in experiments. These data were also used to calculate respirometer volume by oxygen dilution (volume of chamber = volume of oxygen injected/change in fractional O₂ concentration).

Resting oxygen consumption was recorded after at least 30 min had elapsed since the last dive or other activity. The quantity of oxygen injected over a 5 min period was measured by summation of the output of the integrator. During the short intervals between dives, the small oscillations in O₂ concentration were taken into account by measuring the difference between concentrations at the start of the interval and the end of the subsequent dive, after correcting for the lag time of the system.

Measurement of buoyant force

While resting at the water surface, the mass of water displaced by a duck is equivalent to the mass of the duck. Upon immersion, the above-water volume of the duck must displace an equivalent volume of water and the mass of that additional water is proportional to the net buoyant force (the proportionality constant is gravitational acceleration, 9.8 m s⁻²). The net buoyant force was measured at the start and end of each voluntary dive by monitoring the air pressure change in the respirometer caused by the exit and return, respectively, of the above-water part of the duck.

Since the floor of the chamber was liquid, the pressure fluctuations were considerably smaller than would be predicted by Boyle's law at constant volume. Furthermore, pressure oscillations caused by wave action due to movements of the duck were sometimes of the same order of magnitude as the small pressure change of interest (approximately 0.4 kPa). This problem was overcome by incorporating mechanical dampeners into the differential pressure transducer ports. These consisted of short lengths of narrow-bore tubing (truncated 30 gauge hypodermic needles). The time constants of the dampeners were matched ($\tau=1.0$ s). The thermobarometer was used to control for fluctuations in barometric pressure (especially changes due to the building ventilation system), general water level and ambient temperature over the course of an experiment.

The differential pressure signal was calibrated directly in units of buoyant force (newtons, N) at the start of each experiment by introducing standard floats of known buoyancy into the respirometer from below and recording the resulting pressure change. The signal was linearly related to buoyancy over the range tested (1.0–6.0 N). The standard floats used for system calibration were themselves calibrated periodically by weighing in water to the nearest 0.1 g (9.8×10^{-4} N) using an electronic balance (model FX-6000; A&D Co.).

Air lost from the plumage during a dive did not return to the respirometer because the ducks were encouraged to dive to food placed in a patch on the floor of the tank at a point 1 m lateral to the chamber. Therefore, dives were usually not directly vertical and the air escaped from small holes in the surface cover. As a consequence, there was a gradual drift in the pressure signal which was corrected periodically by injection of compensating volumes of air. This procedure took less than 10 s and was usually done following a dive series but dives that occurred during the pressure compensation procedure were not included in analyses.

Buoyancy was also measured in restrained ducks by the volumetric displacement method used previously (Stephenson *et al.* 1989a; Stephenson, 1993) to facilitate direct comparison between methods. After weighing, each duck was restrained by taping it to an aluminium bar in a posture resembling that during the descent phase of a voluntary dive. The legs and bill tip were firmly attached to the bar using filament tape and the wings were restrained by paper tape wrapped loosely around the body. Care was taken to ensure that breathing was not inhibited and that the plumage was not visibly compressed. The duck and bar were then completely submerged by lowering head first into a Plexiglas displacement tube (15.5 cm i.d., 750 cm tall). The rise in water level was observed *via* a transparent side-tube connected in parallel to the main displacement tube. Ducks were submerged for approximately 5 s and each animal was measured once.

Measurement of behavioural variables

The experimental tank was illuminated from above through transparent areas of the surface screen and the remainder of the room was dimmed so that the submerged ducks could not see through the glass window in the tank while diving. A video camera (Sony Corp.) was positioned obliquely in front of the tank and the recording was used to measure hindlimb stroke frequencies during the descent and feeding phases of the dive, and the durations of descent, feeding and ascent phases. The exact start and end of each dive was indicated by the buoyancy signal. The behaviour of the ducks at the water surface was observed, but not recorded on tape, using a second video camera and colour monitor (JVC Canada, Inc.).

Dive trajectories were variable and all were used in calculation of the mean phase durations. Also, in some dives the feeding phase was interrupted by a brief ascent and then the duck returned to the floor of the tank a second time without resurfacing. The ascending and descending phases of these brief excursions were added to the total durations of ascent and descent phases for those dives. The position of the camera, the large distance between the front and back walls of the diving tank and the significant diffraction through the 2 cm thick glass rendered it impossible to make accurate

swimming velocity measurements. Descent velocity was instead estimated from the known direct distance from respirometer to food patch and the observed descent times using only those dives with a linear trajectory.

Data analysis

The following calculations were made using the diving behaviour, oxygen uptake and buoyancy data described above, incorporating previously published values where appropriate.

Oxygen uptake during the interval between two dives ($V_{O_{2up}}$) was calculated as follows:

$$V_{O_{2up}} \text{ (ml ATPS)} = V_{O_2} + c \times \Delta C_{O_2} - c \times \Delta C_{CO_2} \times fC_{O_{2set}}, \quad (1)$$

where V_{O_2} is the volume of oxygen (ml) infused into the respirometer during the inter-dive interval and subsequent dive, ΔC_{O_2} is the difference in oxygen concentration (%) between the start of the surface interval and the end of the subsequent dive, c is the constant relating oxygen concentration (%) change and oxygen volume, ΔC_{CO_2} is the change in CO_2 concentration (%) over a dive cycle and $fC_{O_{2set}}$ is the set-point fractional oxygen concentration.

Total oxygen uptake measured during the intervals between dives ($V_{O_{2up}}$) was subjected to multiple linear regression analysis, as described in detail by Woakes and Butler (1983) and Bevan *et al.* (1992), to resolve the quantities actually used by the duck during the interval ($V_{O_{2i}}$) and the preceding dive ($V_{O_{2d}}$). The partial regression coefficients yield mean oxygen consumptions at mean durations of dive and interval. Volumes were corrected to STPD.

The volume of air lost from the plumage during a dive (ΔV_{pa}) was calculated from the difference in buoyant force at the start and end of each dive (ΔB_{net}):

$$\Delta V_{pa} \text{ (l ATPS)} = \Delta B_{net}/g. \quad (2)$$

Additional variables were calculated as follows:

$$\text{Above-water body volume } (V_{net}; \text{ l}) = B_{net}/g, \quad (3)$$

$$\text{Diving body volume } (V_{tot}; \text{ l}) = (M_b/\rho_w) + V_{net}, \quad (4)$$

$$\text{Added-mass of entrained water } (M_a; \text{ kg}) = \alpha \times \rho_w \times V_{tot}, \quad (5)$$

$$\text{Virtual-mass } (M_v; \text{ kg}) = M_b + M_a, \quad (6)$$

$$\text{Respiratory system/plumage air volume } (V_{r+p}; \text{ l BTPS}) = V_{tot} - (M_b/\rho_{t+f}), \quad (7)$$

where g is gravitational acceleration (9.8 m s^{-2}), M_b is body mass (kg), α is the added-mass coefficient (assumed to be 0.2; Daniel, 1984; Lovvorn *et al.* 1991), ρ_w is the density of water (assumed to be 10^3 kg m^{-3}), and ρ_{t+f} is the air-free tissue density of the fully feathered bird (assumed to be $1.036 \times 10^3 \text{ kg m}^{-3}$; Stephenson, 1993).

The values of buoyant force used in calculations of work done during the descent and feeding phases of a dive (B_d and B_f , respectively) were corrected for time submerged and hydrostatic pressure at depth. In correcting for time submerged, it was assumed that the

rate of loss of plumage air is a linear function of active dive time ($t_{\text{active}}=t_{\text{descent}} + t_{\text{feeding}}$), noting that no air was observed to escape from the plumage during the passive ascent phase.

Following Wilson *et al.* (1992), pressure at depth (P_d) was calculated as:

$$P_d = P_s + \rho_w \times g \times d, \quad (8)$$

where P_s is pressure at the water surface (approximately 100 kPa) and d is depth. In this study, mean depth during descent was 0.76 m and depth during feeding was 1.52 m. Therefore, factorial increases in pressure at these depths (ΔP) were 1.074 and 1.149, respectively. Compression of bodily air spaces was assumed to be unhindered. After calculation of time-corrected V_{r+p} (at mid-descent phase and mid-feeding phase), the decrease in volume of gas in the respiratory system and plumage due to compression (ΔV_{r+p}) was calculated as:

$$\Delta V_{r+p} = V_{r+p} - (V_{r+p}/\Delta P). \quad (9)$$

Buoyant force was then corrected for pressure as follows:

$$\text{Pressure-corrected buoyancy } (B_d \text{ or } B_f) = \text{time-corrected } B - (\Delta V_{r+p} \times g). \quad (10)$$

The equation given by Lovvorn *et al.* (1991), which relates percentage stroke distance to percentage stroke duration in lesser scaup, was used to calculate bill tip displacement (m), forward velocity (m s^{-1}) and acceleration (m s^{-2}) at 0.01 s intervals through a leg-beat cycle during the descent phase of a dive. Mean stroke distance was calculated for each duck as mean descent speed/leg-beat frequency during descent. Mean stroke duration was taken as the reciprocal of stroke frequency. Acceleration was multiplied by M_v to give the force (G) required to accelerate the body and entrained water in each 0.01 s interval (Daniel, 1984). It was assumed that the power phase constitutes 70 % of the leg-beat cycle (Lovvorn *et al.* 1991), and inertial forces were calculated for both the power (G_p) and recovery (G_r) phases.

Drag of the body minus hindlimbs (D_b) was calculated at average velocity during each 0.01 s interval using the equation given by Stephenson *et al.* (1989a). Drag of the body plus hindlimbs (D) was estimated in each 0.01 s interval of the recovery phase by subtraction of the average buoyant force during descent (B_d) from the inertial force of deceleration (G_r). Drag of the hindlimbs (D_h) during recovery was then estimated as $D_h = D - D_b$.

Work (joules, J) done against inertia, drag and buoyancy in each 0.01 s interval was calculated by multiplying the respective forces (G , D , D_b , D_h and B_d) by bill tip displacement. Total work done against each force [$W(G)$, $W(D)$, $W(D_b)$, $W(D_h)$, $W(B_d)$] was then obtained by summation (Lovvorn *et al.* 1991). Total mechanical work per leg-beat cycle was calculated as the sum of $W(G)$, $W(D)$, $W(D_h)$ and $W(B_d)$. The above calculations apply to the descent phase of the dive only and represent the unsteady biomechanical model adopted in this study for calculation of mechanical power output.

In calculations of work done during a leg-beat cycle in the feeding phase of a dive, it was assumed (a) that the duck is stationary and therefore G and D_b are zero, and (b) that the 'distance' travelled per stroke and the hindlimb drag (D_h) are equivalent to those

during the descent phase. Thus, total mechanical work per leg-beat cycle was $W(D_h)+W(B_f)$.

For comparative purposes, total work per leg-beat cycle was also calculated using a steady model. In this model, $W(B_d)$ was estimated as $B_d \times$ average stroke distance. Total drag (D) was estimated as the sum of average body drag (D_b) at mean descent velocity (from Stephenson *et al.* 1989a) and mean hindlimb drag (D_h) calculated from the unsteady model above. $W(D)$ was then $D \times$ average stroke distance. D_b was assumed to be zero during the feeding phase.

In both models, total work done in a dive was obtained by multiplying the work per leg-beat cycle, calculated as described above, by the mean number of leg-beats executed during the descent and feeding phases. Mechanical cost of transport ($\text{J kg}^{-1} \text{m}^{-1}$) was calculated for descent and feeding phases as mass-specific power output/velocity. Velocity was taken as the product of stroke distance and stroke frequency.

Between 47 and 79 feeding dives were analyzed for each animal. To avoid bias, all calculations were done for each duck separately and then individual results were averaged to yield the summary statistics presented in Results. Therefore, unless otherwise stated, sample size is six.

All statistics were computed using Data Desk software (Data Description, Inc.) and graphics were generated using Sigma Plot (Jandel Corp.). Normal probability plots and Pearson product-moment correlations between variables and their respective normal scores were tested before using parametric statistics to confirm that the data exhibited a near normal distribution. Data sets were compared using independent-sample or paired-sample t -tests, as appropriate. Differences are considered significant at the 95 % confidence level ($P < 0.05$).

Results

Diving behaviour

The behavioural variables measured during voluntary feeding dives are presented in Table 1. Mean dive durations (t_d) varied between birds from 9.0 to 17.4 s and were usually variable within individuals (coefficients of variation were 19–36 %). Durations of inter-dive intervals (t_i) also varied within and between individuals (range of means 10.6–24.75 s). Although mean t_d and t_i were strongly correlated among individuals ($r=0.903$, $P < 0.01$), correlation coefficients within individuals were generally low, varying from -0.035 to 0.648 . Nevertheless, given the large sample sizes ($N=47-79$), correlation was significant at $P < 0.05$ in four of the ducks. Mean t_d and t_i were not significantly correlated with body mass ($r=0.40$ and 0.32 , respectively).

Feeding dives were usually performed in bouts, often preceded or followed by non-feeding dives. The average number of feeding dives per bout did not vary much between individuals (mean \pm S.E.M. = 6.7 ± 0.6 dives per bout) but it was very variable within individuals. For example, one animal performed between 1 and 36 feeding dives per diving bout. The t_d/t_i ratios ranged from 0.70 to 1.03 and on average the ducks were submerged for 46 % of a feeding bout. However, only 27 % of the time was spent actually feeding at the bottom, indicating that approximately 41 % of each dive and

Table 1. *Behavioural and locomotor variables in diving lesser scaup*

Variable	Mean value \pm S.E.M.
Dive duration (s)	13.5 \pm 1.4
Interval duration (s)	16.3 \pm 2.2
Descent phase duration (s)	3.1 \pm 0.3
Feeding phase duration (s)	8.1 \pm 1.1
Ascent phase duration (s)	2.3 \pm 0.4
Stroke frequency (descent) (Hz)	4.44 \pm 0.06
Stroke frequency (feeding) (Hz)	3.54 \pm 0.07
Stroke distance (m)	0.14 \pm 0.01
Swimming speed (descent) (m s ⁻¹)	0.63 \pm 0.04

Based on measurements on six individuals.

18.5 % of a foraging bout were spent in transit between the water surface and the food patch.

All animals were observed to engage in prolonged non-feeding bouts, during which between 30 and 150 short dives occurred in quick succession. The animals appeared to be attempting to gain contact with the companion ducks in the other section of the tank on those occasions. The response times of the recording system were too long to permit reliable measurements of buoyancy and oxygen uptake during those sequences.

Descent trajectories were variable and the ducks sometimes explored all parts of the tank, apparently in search of food. This occurred despite the fact that excess food was always available and clearly visible in a single small patch on the floor of the tank. With the exception of one animal, ascent trajectories were usually direct to the measurement box. The ducks were observed to steer themselves during ascent by adjusting the position of the feet and by the occasional leg-beat. One duck consistently veered away from the entrance and swam in a short circle just beneath the surface screen before entering the respirometer.

Oxygen consumption and aerobic power input

The variable diving behaviour of the individual ducks facilitated multiple regression analysis of oxygen uptake data. The regressions of $V_{O_{2up}}$ on t_d and t_i for each duck were highly significant (F -ratios indicated $P < 0.001$) and partial regression coefficients were all statistically significantly different from zero (t -ratios indicated $P < 0.001$). The adjusted r^2 statistic ranged from 0.52 to 0.78. The data are summarized in Table 2.

Resting rate of oxygen consumption ($\dot{V}_{O_{2r}}$) varied little within and between animals (Fig. 2). On average, diving oxygen consumption ($\dot{V}_{O_{2d}}$) increased to 3.6 times resting levels (Fig. 2). $\dot{V}_{O_{2d}}/\dot{V}_{O_{2r}}$ ratios varied from 3.2 to 4.5 among individuals. Surface interval oxygen consumption ($\dot{V}_{O_{2i}}$) was 1.4–3.3 times (mean 1.9) resting levels and 0.4–1.0 times (mean 0.6) the diving level. Mean diving oxygen consumption tended to be inversely related to mean dive duration (Fig. 2), but the linear regression coefficient (slope = $-0.019 \text{ ml O}_2 \text{ s}^{-2}$) was not statistically significant (t -ratio = -0.88 , d.f. = 4, $P = 0.45$). $\dot{V}_{O_{2d}}$ was not significantly correlated with body mass ($r = 0.3$), and accounting for

Table 2. *Body mass, ambient temperature and oxygen consumption in resting and diving lesser scaup*

Variable	Mean value \pm S.E.M.
Body mass (kg)	0.591 \pm 0.30
Air temperature ($^{\circ}$ C)	16.6 \pm 0.7
Water temperature ($^{\circ}$ C)	13.0 \pm 0.9
Oxygen consumed between dives, $V_{O_{2up}}$ (ml STPD)	18.6 \pm 2.2
Rest $\dot{V}_{O_{2r}}$ (ml s $^{-1}$ STPD)	0.237 \pm 0.008
Dive cycle $\dot{V}_{O_{2c}}$ (ml s $^{-1}$ STPD)	0.630 \pm 0.020
Dive $\dot{V}_{O_{2d}}$ (ml s $^{-1}$ STPD)	0.862 \pm 0.066
Surface interval $\dot{V}_{O_{2i}}$ (ml s $^{-1}$ STPD)	0.463 \pm 0.073

$\dot{V}_{O_{2c}}$, $\dot{V}_{O_{2d}}$ and $\dot{V}_{O_{2i}}$ are mean rates of oxygen consumption at mean durations of dive cycle, dive and surface interval, respectively.

Observations on six individuals.

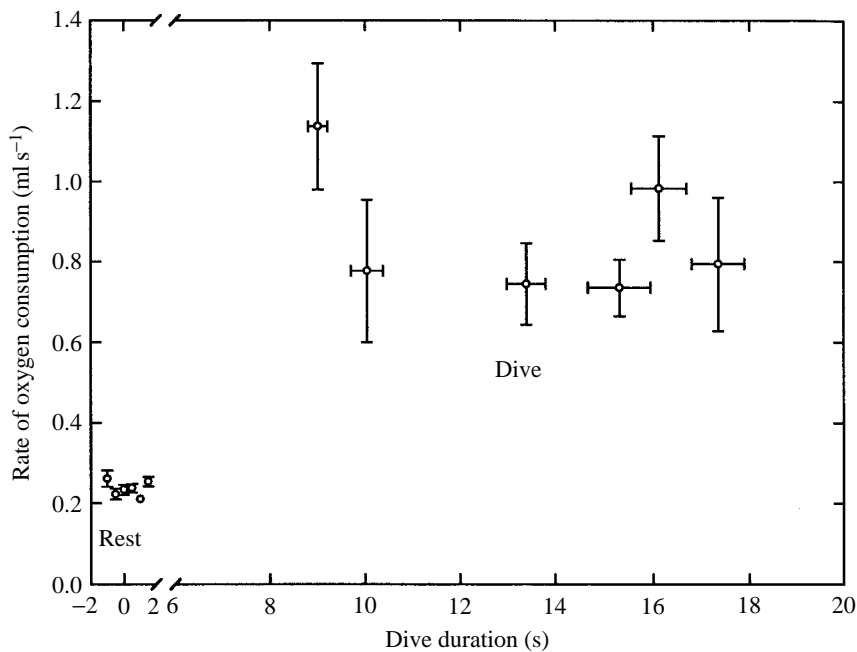


Fig. 2. Relationship between mean (\pm S.E.M.) diving rate of oxygen consumption ($\dot{V}_{O_{2d}}$) and mean (\pm S.E.M.) dive duration (t_d) for six lesser scaup. Resting rate of oxygen consumption ($\dot{V}_{O_{2r}}$) is plotted at $t_d=0$ s.

body mass by multiple regression of $\dot{V}_{O_{2d}}$ on t_d and body mass, or by regression of mass-specific $\dot{V}_{O_{2d}}$ on t_d , did not yield a significant regression coefficient.

Buoyancy, drag, inertia and power output

Buoyant force was found to decrease progressively during the descent and feeding

Table 3. *Buoyancy, body volume and air volumes in restrained and unrestrained submerged lesser scaup*

Variable	Voluntary dives	Involuntary immersion
Buoyancy, start dive (N)	3.62±0.12	2.90±0.10*
Buoyancy, end dive (N)	2.88±0.09†	–
Body volume, start dive (l)	0.963±0.035	0.894±0.034*
Body volume, end dive (l)	0.886±0.029†	–
Respiratory and plumage air volume, start dive (l)	0.391±0.012	0.317±0.010*
Respiratory and plumage air volume, end dive (l)	0.314±0.009†	–
Plumage air loss during dive (l)	0.077±0.007	–

*Significantly different from voluntary dive value (paired sample *t*-test, $P<0.01$).

†Significantly different from start dive value (paired sample *t*-test, $P<0.01$); $N=6$.

phases of voluntary dives (Table 3, Fig. 3). Air was seen not to escape from the plumage during the ascent phase, nor did it appear to escape from the respiratory system at any stage of the dive. Under the present experimental conditions, air was lost from the plumage at an average rate of 7.8 ml s^{-1} , causing on average a total decrease in buoyancy of 0.76 N. The reduction in buoyancy caused by compression of the remaining air by hydrostatic pressure was calculated to be 0.4 N. Thus, buoyant force decreased by 32 % from $6.20 \pm 0.35 \text{ N kg}^{-1}$ at the start of the dive to $4.24 \pm 0.33 \text{ N kg}^{-1}$ at the end of the feeding phase (i.e. before ascent).

Changes in respirometer air temperature at the start ($\Delta T = -0.117 \pm 0.025 \text{ }^\circ\text{C}$) and end ($\Delta T = -0.012 \pm 0.012 \text{ }^\circ\text{C}$) of a dive were insignificant and did not cause detectable changes in pressure (Fig. 3). Any radiant or convective heat loss from the duck to the respirometer was counteracted by evaporative cooling associated with splashing and agitation of the water surface.

Buoyant force measured in restrained ducks using a volumetric water displacement method was significantly lower than that measured at the start of the dive in unrestrained ducks (Table 3). Calculated buoyancy at the end of the feeding phase (i.e. at a depth of 1.5 m) was significantly lower (paired samples *t*-test, $P<0.05$) than that measured in restrained animals.

Fig. 3. Representative record of buoyant force and respirometer gas analysis over two complete dive cycles in a foraging male lesser scaup. Traces from top to bottom are as follows. V_{O_2} , volume of oxygen injected into the respirometer each time the solenoid valve was activated. Buoyancy, changes in pressure in the respirometer, calibrated in newtons, after diving (descending arrows) and resurfacing (ascending arrows); the scale zero position was set arbitrarily and buoyant force at the start and end of the dive was determined from the change in signal. ΔT , difference in temperature between respirometer and thermobarometer; temperature oscillations due to diving activity were insignificant. O_2 flow, rate of flow of oxygen into respirometer each time the solenoid valve was activated; overshoot was due to water pressure in the gas overflow line and oscillations were undamped pressure fluctuations caused when the duck submerged. $[O_2]$, oxygen concentration in the respirometer oscillating around the set point. $[CO_2]$, carbon dioxide concentration in the respirometer.

The forces generated through a leg-beat cycle are illustrated in Fig. 4A. In the absence of any forward thrust by the hindlimbs during the recovery stroke of the leg-beat cycle, the deceleration calculated from the data given by Lovvorn *et al.* (1991) is a direct measure of the total drag and buoyant force opposing forward motion (force = virtual mass \times acceleration). Virtual mass, the sum of body mass and the mass of entrained water, was calculated to be 0.776 ± 0.037 kg during voluntary dives using the buoyancy

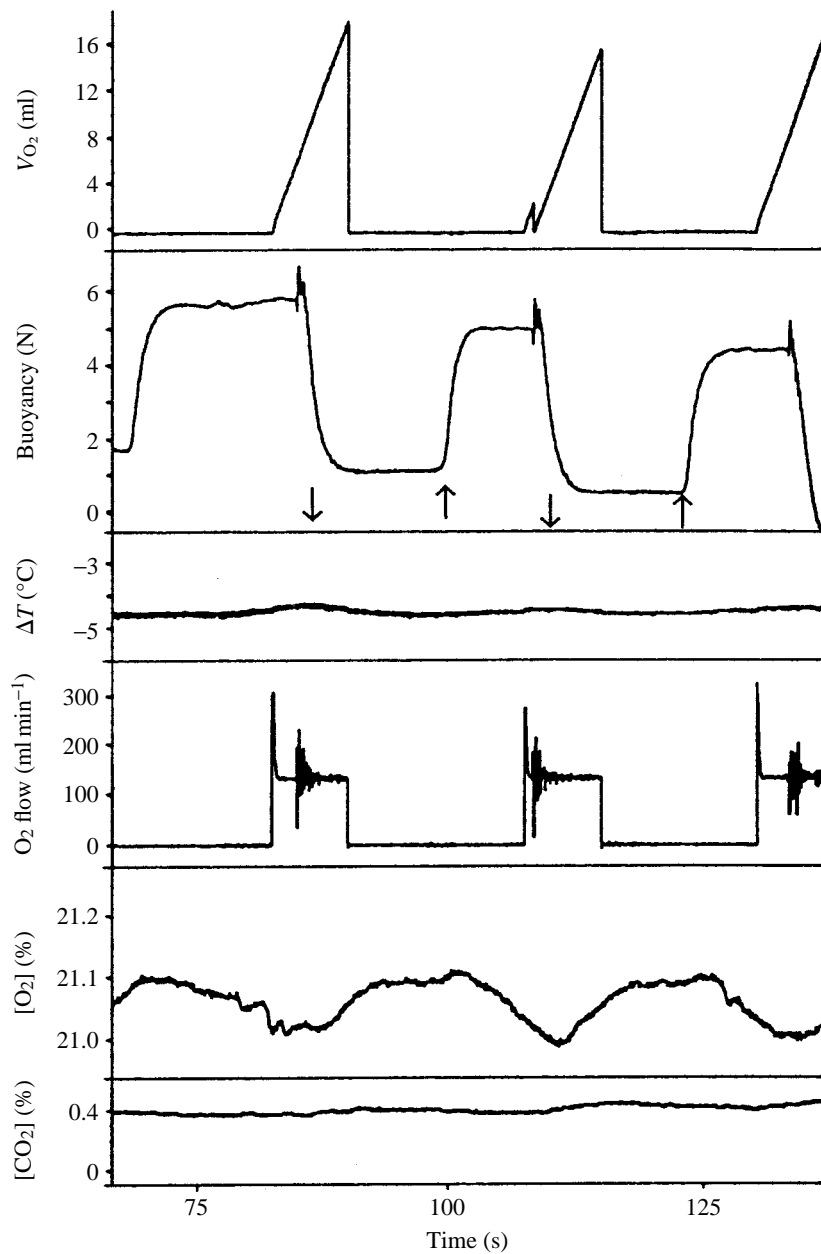


Fig. 3

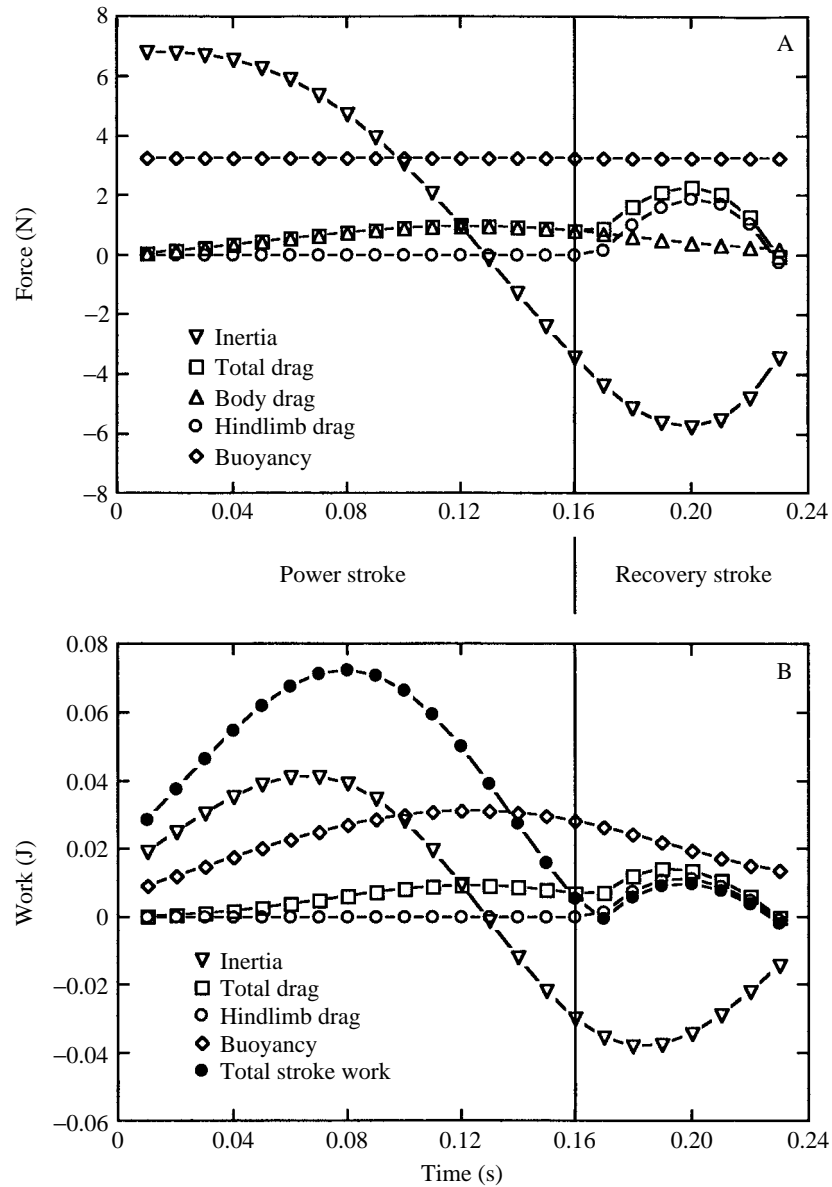


Fig. 4. (A) Buoyant, drag and inertial forces opposing (positive values) and augmenting (negative values) forward motion of a lesser scaup during a leg-beat cycle in the descent phase of a voluntary dive. Total drag is the sum of body drag and hindlimb recovery drag. (B) Calculated work done through a leg-beat cycle against buoyancy, drag and inertia during the descent phase of a voluntary dive. Total work in a leg-beat cycle is given by the area under the combined curve (solid circles) and represents the unsteady model used in the present study. The equation relating percentage stroke distance and percentage stroke duration for diving lesser scaup (Lovvorn *et al.* 1991) was used to calculate displacement, velocity and acceleration of the ducks at 0.01 s intervals. Body drag was calculated using data from Stephenson *et al.* (1989a).

Table 4. Work (J) per leg-beat cycle against buoyancy, drag and inertia and mechanical power output (W) during the descent and feeding phases of a voluntary dive in lesser scaup

	Descent phase	Feeding phase
Buoyancy, $W(B)$	0.517±0.022	0.385±0.020
Total drag, $W(D)$	0.166±0.031	0.056±0.019
Body drag, $W(D_b)$	0.108±0.014	0*
Hindlimb recovery drag, $W(D_h)$	0.058±0.019	0.056±0.019
Inertia (net acceleration), $W(G)$	0.090±0.011	0*
Total work done per stroke	0.831±0.074†	0.441±0.034‡
Power output	3.63±0.38	1.51±0.10

*Assumed value.

†Calculated as $W(B)+W(D)+W(D_h)+W(G)$.

‡Calculated as $W(B)+W(D)$. See text for details.

Observations on six individuals.

measurements in Table 3. Total drag, estimated as the difference between the inertial and buoyant forces, increased sharply during the recovery stroke but never exceeded the buoyant force. The difference between total drag force and body drag, estimated from tow-tank experiments (Stephenson *et al.* 1989a), was assumed to represent drag of the forward-moving legs.

The work associated with displacing these forces is shown in Fig. 4B. Approximately 93 % of the muscular work of the hindlimbs is done during the power stroke of the leg-beat cycle. By the unsteady biomechanical model used in the present study, hindlimb recovery drag accounts for approximately 14 % of the total mechanical work of descent (see Fig. 5), half of which is done by the flexor muscles of the hindlimb (see Discussion). Hindlimb drag accounted for 13 % of the work of staying at the bottom during the feeding phase, all of which is done by the flexor muscles. Inertial forces associated with net acceleration accounted for approximately 11 % of the work done during descent. Body drag accounted for 13 % of total work during descent. The buoyant force accounted for approximately 62 % of the work of descent and 87 % of the mechanical work of staying at the bottom while feeding (see Fig. 5).

Total work per leg-beat cycle was 1.9 times greater during descent than during the feeding phase (Table 4, see Fig. 5). As a result of the higher stroke frequency (Table 1), however, power output was 2.4 times greater during descent (Table 4). Overall dive costs and energetic efficiencies are presented in Table 5. Two lines of evidence support the assumption that the effective stroke ‘distance’ during the feeding phase is unchanged from actual stroke distance during descent. The ratio of total force opposing descent and force opposing staying at the bottom is 1.3. This is the same as the ratio of stroke frequencies in descent and feeding phases. Furthermore, calculation of the distance that a duck of known virtual mass and buoyant force would rise during the period of a leg-beat cycle if it were to stop paddling in the feeding phase (Lovvorn *et al.* 1991) yields a value of 0.15 m, which is close to the stroke distance observed during descent in the present study (Table 1).

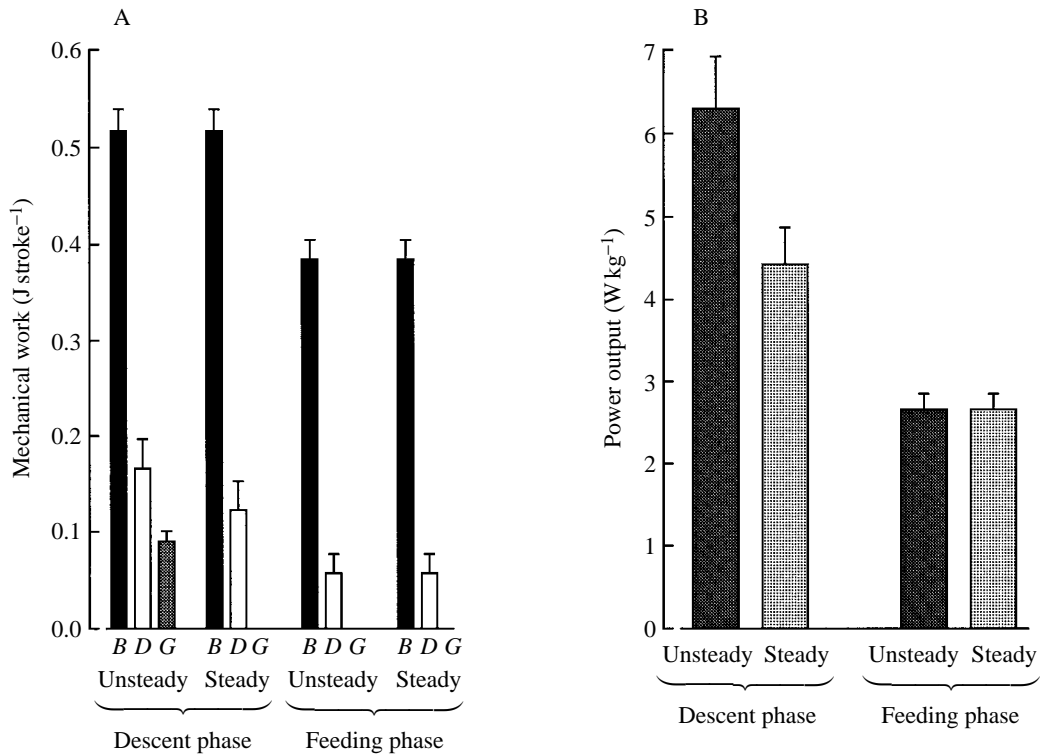


Fig. 5. A comparison of estimates of mechanical costs of diving using unsteady and steady biomechanical models. Data are mean values (+ S.E.M.) for six animals. (A) The contributions of buoyancy (*B*), drag (*D*) and inertia (*G*) to mechanical work per leg-beat cycle during descent and feeding phases of a voluntary dive. (B) Mass-specific power output during the descent and feeding phases of dives to 1.5 m depth in lesser scaup.

Discussion

Diving behaviour

Dive and interval durations and swimming speeds of the lesser scaup in this study were similar to those recorded previously for Aythyini diving under similar experimental conditions (Woakes and Butler, 1983; Takekawa, 1987; Bevan and Butler, 1992a; Bevan *et al.* 1992) and from ducks diving to comparable depths in open water (Dewar, 1924; Draulans and De Bont, 1980; Stephenson *et al.* 1986). However, the number of dives in each dive bout was lower than that typically observed in free-living ducks.

Takekawa (1987) found that canvasback ducks would not dive readily from a respirometer when measurements were attempted on individual animals. He found it necessary to use pairs of ducks and this protocol rendered his oxygen consumption data difficult to interpret. The tendency of the ducks to dive from the respirometer also varied widely between individuals in the present study. One animal appeared to be completely unaffected by handling and confinement within the chamber, whereas seven lesser scaup and five redhead ducks not used in the study refused to dive at all. Five of the ducks used

Table 5. *Locomotory performance of lesser scaup diving and feeding at 1.5 m*

Measure of energetic cost	Mean \pm S.E.M.
Resting aerobic power input (W kg^{-1})	8.13 \pm 0.37
Diving aerobic power input (W kg^{-1})	29.32 \pm 2.47
Mechanical power output (W kg^{-1})	3.69 \pm 0.24
Aerobic cost of transport ($\text{J kg}^{-1} \text{m}^{-1}$)	54.8 \pm 6.2
Mechanical cost of transport ($\text{J kg}^{-1} \text{m}^{-1}$)	6.9 \pm 0.3
Aerobic efficiency (%)	12.6 \pm 1.3
Net aerobic efficiency (%)	17.4 \pm 2.1

Mechanical power output and mechanical cost of transport are specific to the dive phase durations observed.

Aerobic efficiency is mechanical power output/diving aerobic power input.

Net aerobic efficiency is mechanical power output/(diving aerobic power input minus resting aerobic power input); $N=6$.

in this study would dive only when fasted overnight before experiments and only when accompanied by other ducks. Unaccompanied ducks were reluctant to perform feeding dives even after a 36–48 h fast. Under those circumstances, the ducks were continually alert, indicating a trade-off between foraging and vigilance behaviours. The compromise used here, allowing visual and auditory contact combined with mild food deprivation, appeared to tip the balance in favour of foraging. It is unknown whether these effects of experimental conditions on motivation and behaviour were accompanied by changes in energy expenditure.

Power output

This paper reports the first measurements of buoyant force in unrestrained diving animals. Buoyancy at the onset of a voluntary dive was significantly higher than that measured in restrained ducks and cadavers (Dehner, 1946; Stephenson *et al.* 1989a; Lovvorn *et al.* 1991; Lovvorn and Jones, 1991a,b; Wilson *et al.* 1992; Stephenson, 1993), supporting the suggestion that previous measurements may be unreliable (Stephenson, 1993). However, since buoyancy estimated by water displacement in restrained ducks was greater than the minimum buoyancy measured during voluntary dives, the water displacement method probably provides a reasonable rough estimate in benthic feeding ducks and it certainly has advantages in terms of simplicity, cost and convenience. Nevertheless, lack of accuracy limits its application somewhat.

Comparisons between congeners that were made using the water displacement method (Dehner, 1946; Lovvorn and Jones, 1991b; Stephenson, 1993) are likely to be qualitatively correct. However, conclusions based on comparisons between species that differ significantly in normal dive durations and depths, or in pursuit divers (Lovvorn and Jones, 1991b; Wilson *et al.* 1992), must be treated with caution since the effects of plumage air loss and hydrostatic pressure may be significantly different in different types of divers. In particular, it was noted in the present study that air was not lost from lesser scaup plumage when body position became horizontal. When vertical, there is a hydrostatic pressure gradient from head to tail and this, together with the anterior-to-

posterior feather orientation, probably facilitates air loss in descending and feeding ducks. These factors are likely to be much reduced in pursuit divers swimming horizontally.

By measuring buoyant force at the start and end of voluntary dives, the technique developed here enabled quantification of the volume of air lost from the plumage layer. It was found that the reduction of buoyant force due to release of air was approximately twice that caused by compression by hydrostatic pressure at the dive depths studied here (1.5 m). Clearly, the relative importance of the two effects will vary as a function of dive depth and duration, although the depth studied here was within the normal preferred range for these ducks (Dewar, 1924). Since the water displacement method provides no information about these effects, it cannot be used to model the effects of water depth reliably (Lovvorn and Jones, 1991a; Wilson *et al.* 1992).

Although it was assumed for the purposes of calculations that the rate of air loss from the plumage was constant, this was not confirmed by subjective visual observations. It appeared that the rate of air loss decreased progressively through the dive, but further experiments are needed to test that hypothesis and to quantify the dependence of buoyancy on dive time and depth more accurately. Nevertheless, there must be a time when the feathers become sufficiently pressed together to prevent further air loss, because if plumage air volume is generously assumed to be 260 ml (Stephenson, 1993), at a rate of loss of 7.8 ml s^{-1} all air would be gone within 34 s and ducks have been observed to dive for longer than that without becoming wetted (e.g. Stephenson *et al.* 1986, 1989b; Bevan *et al.* 1992).

Measurement of buoyancy using respirometer pressure fluctuations is strictly accurate only if the mean respiratory system and plumage air volumes during inter-dive intervals are the same as those during dives. If the diving volumes are different from the mean non-diving volumes, there will be an error. This would occur, for example, if the ducks dive at end-expiration or end-inspiration, or if ptiloerection or ptilosuppression occurs immediately before the dive, or if air is lost from the respiratory system or plumage during a dive. The magnitude of the error is proportional to the net volumes lost or accumulated by the respiratory system and plumage before and after a dive. The error is caused by warming and humidifying the inhaled air and the air drawn into the plumage in the case of a net gain, and *vice versa* in the case of a net loss. Note that the long time constant of the apparatus prevented detection of rapid changes associated with lung ventilation and only changes in the average lung volume are significant here.

The potential magnitude of the error was estimated (Chapin, 1954) by assuming that barometric pressure (P_b) was 100.6 kPa, that recirculating air was 50 % saturated at 17 °C (290 K, $P_{\text{H}_2\text{O}}=1.0 \text{ kPa}$), inhaled air was saturated at 41 °C (314 K, $P_{\text{H}_2\text{O}}=7.4 \text{ kPa}$) and plumage air was saturated at 30 °C (303 K, $P_{\text{H}_2\text{O}}=4.2 \text{ kPa}$). For each 1 ml net increase in mean respiratory system volume after resurfacing, the above-water body volume was overestimated by $(107/100.6) \times (314/290) = 0.15 \text{ ml}$. For each 1 ml net increase in plumage air volume, the above-water body volume was overestimated by $(103.8/100.6) \times (303/290) = 0.08 \text{ ml}$. Thus, if the ducks dive at end-expiration (Butler and Woakes, 1979), then mean respiratory system volume will expand by half a tidal volume (approximately 10 ml; R. Stephenson, unpublished observations) after resurfacing.

Furthermore, in this study it was found that 77 ml of plumage air was lost during an average dive and it was assumed that this was completely replaced during the subsequent surface interval. V_{net} was measured at end-dive to be 293 ml, implying that the total overestimation was $293/[293-(10 \times 0.15 + 77 \times 0.08)] = 1.027$ or 2.7%. This estimated error is less than the variability in the data (coefficient of variation was 7.5%) and therefore no corrections were attempted.

The present study has found that buoyancy is the dominant factor determining mechanical costs of diving in lesser scaup (see Fig. 5). It accounted for 62% of the cost of descent and 87% of the cost of staying at the bottom. The drag force was found to play a more significant role (27% of total mechanical work of descent) in determining dive costs than was described in previous studies (Stephenson *et al.* 1989a; Lovvorn *et al.* 1991). The net contribution of inertia was only 11% in descent and was assumed to be zero during the feeding phase.

Approximately 38% of locomotory muscle work during descent is directly involved in acceleration of the duck and entrained water during the power stroke, and 7% is involved in active deceleration during the recovery stroke. Acceleration in the power stroke is an essential intermediate stage in momentum transfer between duck and environment, but most of the work done to accelerate the body during the power stroke ultimately serves to overcome buoyancy and drag during the subsequent recovery stroke (see Lovvorn *et al.* 1991).

Steady and unsteady models of locomotion

Stephenson *et al.* (1989a) estimated mechanical costs of diving using a simple steady model of locomotion in which dive velocity was assumed to be constant. Lovvorn *et al.* (1991) extended that work by incorporating kinematic measurements of acceleration during each leg-beat cycle of descent. They concluded that for diving lesser scaup a steady model underestimates descent phase power output by 43% compared with an unsteady model. The present study builds upon previous work by incorporating buoyancy and body volume measurements from unrestrained ducks and by reinterpreting the kinematic data of Lovvorn *et al.* (1991). Power output during descent was found to be underestimated by 28% using a steady model compared with an unsteady model (see Fig. 5), thus confirming that the steady model is an inadequate description of mechanical dive costs in ducks. Both the unsteady and steady models used in the present paper differ from those in previous studies (Stephenson *et al.* 1989a; Lovvorn *et al.* 1991) in that the work of the flexor muscles during the recovery stroke is included.

In their analysis of the unsteady model, Lovvorn *et al.* (1991) quantified power output for the power stroke of the leg-beat cycle only, reasoning that 'the work against drag and buoyancy during the recovery phase is done passively by means of momentum and is experienced by the duck's muscles as work to accelerate the body during the power phase'. However, in the absence of any net acceleration during descent, the 'negative' work of deceleration is exactly equal to the 'positive' work of acceleration in each leg-beat cycle. Therefore, the net contribution of inertial forces to overall dive costs must be zero, if recovery is passive (Daniel, 1984). This means that when the recovery stroke is passive the total work done during the power stroke against buoyancy, drag and

acceleration (unsteady model of Lovvorn *et al.* 1991) must be equivalent to the total work done during the whole leg-beat cycle against only buoyancy and drag (steady model).

Therefore, by ignoring work done during the recovery stroke of the leg-beat cycle, the unsteady model of Lovvorn *et al.* (1991) underestimated total power output and as a result should have been quantitatively identical to the steady model. However, following Stephenson *et al.* (1989a), they also underestimated power output using the steady model by using drag data acquired from duck cadavers with hindlimbs amputated (Stephenson *et al.* 1989a; Lovvorn *et al.* 1991). Those data therefore quantify the drag force of the body only and neglect that of the hindlimbs during the recovery stroke. This limitation was acknowledged by both Stephenson *et al.* (1989a) and Lovvorn *et al.* (1991), but the latter authors did not take advantage of the fact that their more comprehensive kinematic study provides the means by which to estimate reverse thrust of the hindlimbs during the recovery stroke (see Materials and methods).

The two models are better compared if one abandons the assumption that the recovery stroke is passive. The work done to accelerate the duck during the power stroke of a leg-beat cycle in the descent phase of a dive involves the expenditure of sufficient energy to give the duck the momentum needed to counteract hindlimb drag (in addition to body drag and buoyancy) during the subsequent recovery stroke. Furthermore, if the hindlimbs are retracted actively, then additional energy is expended by the locomotory muscles during the recovery stroke. Therefore, work done to overcome hindlimb drag during the recovery stroke must be added to work done during the power stroke to yield total work in a leg-beat cycle during descent. In other words, the work of hindlimb recovery is done twice in each leg-beat cycle: by the extensor muscles of the hindlimb during the power stroke then by the flexor muscles during the recovery stroke. This is a mechanism by which the unsteady model yields higher estimates for dive descent costs than does the steady model (Daniel, 1984).

A different situation exists during the feeding phase of the dive. It was observed on video recordings in the present study that the body of the duck oscillates in the vertical plane with each leg-beat cycle. Thus, the body ascends during each recovery stroke, indicating that the power stroke does not generate enough momentum to overcome hindlimb drag during the subsequent recovery stroke. Therefore, work against hindlimb drag is done only once per leg-beat cycle (i.e. by the flexor muscles) during the feeding phase. Therefore, when total drag is included, the unsteady and steady models yield identical mechanical costs in the feeding phase (Fig. 5). In the absence of a kinematic analysis of locomotion during the feeding phase, this interpretation is likely to be oversimplified and the assumptions of zero net contribution of inertial forces and the magnitude of D_h during the feeding phase require empirical validation.

A second factor contributing to a difference between models during descent is net acceleration. The calculated positive work of acceleration during the power stroke and negative work during the recovery stroke (Lovvorn *et al.* 1991) do not sum to zero; there is a net positive quantity, signifying that the ducks accelerate from stroke to stroke during descent. Calculations indicate that this is not fully explained by decreasing buoyant force due to loss of air from the plumage and compression of air spaces with increasing hydrostatic pressure. Net acceleration was also a feature of the equations summarizing the

kinematic data for canvasback and redhead ducks (Lovvorn *et al.* 1991), which argues against the possibility that it was a statistical artefact and suggests that swimming velocity actually does increase during descent. Failure to incorporate the effects of net acceleration caused the steady model to underestimate power output by approximately 11 %.

Therefore, the steady model was inadequate because it failed to account for the cost of active deceleration (hindlimb drag) during the recovery stroke and the cost of net acceleration. The steady model also underestimated the true mean value of D_b . This occurred because drag increases approximately as the square of velocity. In the present study, instantaneous velocity ranged from approximately 0.2 to 1.0 m s⁻¹ over the course of a leg-beat cycle and true mean D_b was 6.2 % higher than that calculated from average velocity.

Power input

Power input of diving lesser scaup (Tables 2 and 5) was approximately 42 % higher than that predicted from the relationship between oxygen consumption and dive duration for tufted ducks (Bevan *et al.* 1992). This difference was significant (*t*-test, $P=0.0125$). It is unlikely that the difference between studies can be explained by species differences given the close structural and behavioural similarity between *Aythya affinis* and *A. fuligula*. Dive depths, dive and surface interval durations, ambient temperatures, inhaled oxygen and carbon dioxide concentrations and respirometer dimensions were virtually identical in the two studies. However, three differences were identified. Tufted ducks were all carrying implanted radiotransmitters, they were studied in an open-circuit respirometry system and they were subjected to operant conditioning techniques in an effort to prolong or control dive duration. None of these conditions applied to the lesser scaup in the present study, but none can convincingly explain the differences in calculated power input.

Interestingly, $\dot{V}_{O_{2r}}$ of lesser scaup (Table 2) was a significant 45 % higher (*t*-test, $P<0.001$) than that of the tufted ducks studied by Woakes and Butler (1983), suggesting that lesser scaup had a higher overall metabolic rate. However, the sample of mean values of $V_{O_{2up}}$ for the lesser scaup in this study (Table 2) was not statistically significantly different (*t*-test, $P=0.315$) from the overall mean value published by Woakes and Butler (1983). Furthermore, $\dot{V}_{O_{2r}}$ of tufted ducks studied by Bevan *et al.* (1992) was similar to that of lesser scaup (*t*-test, $P=0.062$). Thus, the higher $\dot{V}_{O_{2d}}$ values obtained in the present study may simply be an artefact of the multiple regression analysis of $V_{O_{2up}}$ on t_d and t_i . Numerous diagnostic tests [partial regression plots, probability plots of residuals and leverages, and two distance measures (DFFITS and Cook's distance)] were performed for this regression of data from each animal to identify individual cases with unusually high influence on the regression. Such cases were surprisingly rare and their exclusion usually had little or no effect on the value of the partial regression coefficients.

Since power output is strongly affected by dive depth and duration, it may be predicted that power input will also be altered in response to changes in these behavioural parameters. Bevan *et al.* (1992) concluded that oxygen consumption is inversely related to dive duration, supporting the suggestion by Woakes and Butler (1983), and in the

present study there was a similar trend among individuals (Fig. 2). However, it should be pointed out that only the study by Bevan *et al.* (1992) has specifically addressed this question and the correlation they observed was not significant. Only by pooling their data with those of Woakes and Butler (1983) was a significant regression coefficient obtained. Unfortunately, the force of the argument in favour of a significant relationship between dive duration and power input is weakened somewhat by invoking the regression obtained by combining data from two studies to explain the differences in diving power input between those studies (Bevan *et al.* 1992).

The contribution of anaerobic metabolism to total power input during dives is generally assumed to be negligible (Woakes and Butler, 1983), but has not yet been measured. Indirect evidence in support of the above assumption was reported by Stephenson *et al.* (1992), who found that plasma lactate concentration was maintained at a fairly constant level above resting values in rhinoceros auklets, *Cerorhinca monocerata*, during bouts of escape diving. Even under those apparently strenuous diving conditions there was no continuous lactate accumulation, indicating that rates of lactate production were matched by rates of aerobic removal. However, this must be confirmed for voluntary dives in ducks.

Cost of locomotion and energetic efficiency

Mechanical cost of transport during descent ($9.97 \pm 0.41 \text{ J kg}^{-1} \text{ m}^{-1}$) was about 25% higher than previous estimates for lesser scaup (Stephenson *et al.* 1989a; Lovvorn *et al.* 1991), mainly because of the inclusion of hindlimb drag in calculations of power output in the present study. Aerobic efficiency was also lower than previous estimates for diving ducks (Stephenson *et al.* 1989a).

Unlike penguins (Hui, 1988b) and sea otters (Williams, 1989), which experienced a marked reduction in aerobic cost of transport upon submergence (compared with surface-swimming at the same speed), the aerobic cost of transport of diving lesser scaup (Table 5) was more than three times that calculated for tufted ducks swimming at the same speed at the surface ($16 \text{ J kg}^{-1} \text{ m}^{-1}$: calculated from data in Woakes and Butler, 1986; Stephenson *et al.* 1989a). Aerobic cost of transport in diving lesser scaup was 4–7 times greater than that of submerged swimming penguins (Baudinette and Gill, 1985; Hui, 1988b; Culik and Wilson, 1991). These species differences are likely to be a result of different relative contributions of buoyant force to diving energetics.

Given the progressive changes in mechanical work done by diving ducks as a result of decreasing buoyant force, calculations of cost of transport and diving efficiency (Table 5) must be interpreted with caution. These measures of locomotory performance may be significantly affected by changes in diving behaviour. Any environmental factors, such as water depth or prey density (Dewar, 1924; Draulans, 1982), that alter the absolute and relative durations of dive phases may profoundly affect diving energetics (Lovvorn *et al.* 1991) and further work is needed to model such factors in different species. The techniques developed in this study provide the means to examine more effectively such interactions between energetics, behaviour and environment in diving birds.

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