

A HYDROMECHANICAL ESTIMATE OF THE POWER REQUIREMENTS OF DIVING AND SURFACE SWIMMING IN LESSER SCAUP (*AYTHYA AFFINIS*)

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Summary

Buoyancy and body drag were measured in lesser scaup (*Aythya affinis*) and the data were used to estimate average power output during diving and surface swimming. Buoyant force (mean \pm s.d.) of fully submerged ducks was 2.89 ± 0.17 N (body mass 0.623 ± 0.089 kg; body volume 918 ± 88 cm³; $N=11$). Buoyancy was decreased by 6.2 % by artificial compression of the feathers during full immersion, but was reduced by 42 % when the ducks were allowed to breathe during head-out immersion. Therefore, voluntary compression of the plumage by the duck appears to have relatively small effects on buoyancy and hence dive costs, whereas alteration of respiratory volume (e.g. by pre-dive expiration) could substantially alter buoyancy and power requirements.

Surface and subsurface body drag (D_{SUR} and D_{SUB} , respectively, in newtons) of frozen duck carcasses increased with velocity (U , m s⁻¹) as follows:

$$D_{\text{SUR}} = 0.239 - 1.292U + 2.027U^2 \quad (r^2 = 0.965),$$

$$D_{\text{SUB}} = -0.144 + 0.562U + 0.622U^2 \quad (r^2 = 0.980).$$

Work required to overcome body drag is greater for a lesser scaup during diving than during surface swimming at average velocities normally attained during these activities (less than 0.7 m s⁻¹). However, the drag force curves merge at 0.8–1.0 m s⁻¹.

It is calculated that the average power output during diving ranges from 1.003 to 1.695 W and that in ducks at least 95 % of the work done during a dive is required to overcome buoyancy. Comparison of these biomechanical estimates with aerobic metabolic power input (\dot{V}_{O_2}) data reported by Woakes and Butler (1983) indicates that, for freely diving ducks, aerobic efficiency (η_{a} =average power output/total aerobic power input) is 0.088–0.149 and net aerobic efficiency [η_{net} =average power output/(total aerobic power input minus resting aerobic power input)] is 0.124–0.209. These values are significantly greater than those during surface swimming at the same velocities (η_{a} =0.004–0.037, η_{net} =0.039–0.063).

Key words: ducks, energetics, hydromechanics, locomotion.

Introduction

The metabolic power requirement of voluntary diving in ducks has been estimated to be 3.5 times resting oxygen consumption (Woakes and Butler, 1983). This estimate, however, may be influenced by water depth, average dive duration and costs of thermoregulation (Fish, 1983; Takekawa, 1987). If it is assumed that voluntary diving metabolism is entirely aerobic and that thermoregulation costs are negligible, then the increased rate of oxygen consumption during diving represents the power required for overcoming body drag and buoyancy.

Eliassen (1960) measured subsurface drag in stuffed guillemots (*Uria aalge*) but at velocities ($1\text{--}3.1\text{ m s}^{-1}$) above the averages recorded for voluntarily diving tufted ducks (*Aythya fuligula*) (Butler and Woakes, 1982; Stephenson *et al.* 1986), lesser scaup, redhead ducks (*A. americana*) and canvasback ducks (*A. valisineria*) (J. R. Lovvorn, unpublished observations). The only value we could find for drag of a duck was that of a hunter's mallard decoy at the water surface measured by Prange and Schmidt-Nielsen (1970). Drag of their 'surface-swimming' decoy was considerable at velocities near those at which ducks swim underwater (0.72 N at 0.55 m s^{-1}). Since drag is a function of the contact area between duck and water, these drag values for a duck only partially submerged at the water surface suggest that the drag force would have a substantial influence on power requirements for underwater locomotion. The only buoyancy values in the literature are those of Dehner (1946), which are about $2.5\text{--}3\text{ N}$ for ducks of the same weight as those used by Woakes and Butler (1983).

To determine power requirements of diving and swimming, we measured the buoyancy of 11 live ducks and the surface and subsurface drag forces of frozen duck carcasses at speeds from 0.3 to 1 m s^{-1} . These data were used to derive an estimate of the efficiency of diving and swimming based on oxygen consumption measurements by Woakes and Butler (1983).

Materials and methods

Adult lesser scaup (*Aythya affinis*) ranging in body mass from 0.49 to 0.78 kg were used in this study. They were kept outdoors in a large tank of water (4.16 m long, 1.87 m wide and 0.65 m deep) located within the animal compound at the University of British Columbia, Vancouver, BC, Canada.

Buoyant force

Buoyant force (in newtons) was calculated by multiplying the difference between body mass (kg) and mass of displaced water (calculated from the volume of fresh water displaced by a submerged duck, assuming a density of fresh water of 1 g cm^{-3}) by gravitational acceleration (9.8 m s^{-2}). The ducks were placed in a dry cage for 2 h before the first measurement and between all subsequent measurements to allow them to preen and to ensure that the plumage was dry. Body mass was measured to 0.5 g using a triple beam balance (Ohaus Scale Corp., Union, NJ, USA).

Body volume was measured by the method of water displacement under four conditions: (1) full submersion, minimal feather depression, head oriented downwards; (2) full submersion, minimal feather depression, head oriented upwards towards the water surface; (3) full submersion, maximal feather depression; and (4) head-out immersion to allow continued lung ventilation, minimal feather depression. In each case, the ducks were attached, by the tip of the bill and by the legs (using filament tape), to a steel bar (93 cm long, 3 cm wide, 3 mm thick). Under conditions of minimal feather depression wing movement was limited by wrapping, as lightly as possible, two lengths of masking tape around the duck and bar. Under conditions of maximal feather depression the wings were held close to the body by two firmly applied strips of masking tape with care taken to ensure that ventilation was not impaired, and the ducks were also fitted with a nylon stocking to effect further depression of the feathers. The duck and bar were lowered into a PVC pipe (15 cm i.d. and 70 cm height) partly filled with water. The change in fluid height was read within 5 s of submersion from the graduations on a 10 ml glass pipette connected in parallel to the water column by means of a right-angle connector tube glued into the side of the main cylinder. The apparatus was calibrated using known volumes of water, and the duck volumes were corrected for the volume of the steel bar.

Drag force

Drag measurements were made on a tow tank located at the BC Research Ocean Engineering Centre. The tow tank is equipped with a manned, instrumented carriage. A computer (LSI 11/23, ADV-11 a/d board, Digital Equipment Corp., Marlboro, MA, USA) mounted on the carriage was used to collect and process data from a load cell (model RUSB no. 200, Hottinger Baldwin Measurements, Framingham, MA, USA) to which a frozen duck carcass was attached by means of an aluminium bar. The load cell was calibrated before measurements by suspending weights of known mass from it. An adjustable mechanical arm, to which the load cell was attached, was positioned so that the duck carcasses were held approximately 30 cm (more than 3 body diameters) below the surface of the water for subsurface drag measurements, and at an estimated 'natural' swimming depth for drag measurements of ducks at the water surface.

Subsurface drag force was measured on five adult scaup carcasses frozen in an extended 'diving' position. Before freezing, metal bars were placed longitudinally and laterally within the carcass to maintain shape and rigidity, and an aluminium bar, used to attach the duck to the force transducer, was placed vertically through the midline of the duck's back. This aluminium bar was 35 cm long, 2.5 cm wide and 0.35 cm thick and was tapered on both the leading and trailing edges. The drag force of the bar was measured and subtracted from the total subsurface drag measurements at each velocity. Surface drag force was measured on five different carcasses positioned in a natural surface-swimming posture. All 10 duck carcasses were frozen in a deep freeze (-18°C) and were kept in a cooler filled with dry ice

during transportation to the tow tank facility. The legs of all birds were amputated at the lower tibiotarsus so that only body drag was measured. Drag measurements were made at constant velocities ranging from 0.3 to 1.0 m s⁻¹. Water temperature was 15°C.

Statistics

All statistics were computed using Systat software (Systat Inc., Evanston, IL, USA). Descriptive statistics used are mean ± standard deviation (s.d.). Buoyancy data were subjected to analysis of matched-pairs (*t*-test), and α for all tests combined was 0.05. For body drag data, curves were compared using the general linear test approach and the 95% joint confidence intervals for the regression coefficients were calculated using the Bonferroni method (Neter and Wasserman, 1974).

Results

Buoyant force

Results obtained from fully submerged ducks are summarized in Table 1. Further depression caused a statistically significant reduction (6.2%) in buoyancy. Both upward head orientation and feather depression increased the variability of the data (Fig. 1).

For head-out body immersion, buoyancy decreased rapidly at first and then more gradually after 10–15 s (Fig. 1). After 5 s of head-out immersion, buoyancy was significantly lower than for full submersion (minimal feather depression, head-down). For head-out body immersion, buoyancy fell to 1.68 ± 0.25 N (58% of the fully submerged, head-down value) after 2 min.

Table 1. *Body mass, volume and buoyancy of lesser scaup measured during full body submergence under different conditions*

Condition	Mass (kg)	Volume (cm ³)	Buoyancy (N)
Minimal feather depression, head-down	0.623 ±0.089 (14.3%)	918 ±88 (9.5%)	2.89 ±0.17 (5.9%)
Minimal feather depression, head-up	0.617 ±0.089 (14.4%)	893 ±117 (13.1%)	2.71 ±0.47 (17.2%)
Maximal feather depression, head-down	0.615 ±0.088 (14.4%)	891 ±83 (9.3%)	2.71 ±0.32 (11.8%)

Values given are mean ± s.d. with the coefficient of variation in parentheses. In all cases *N* = 11.

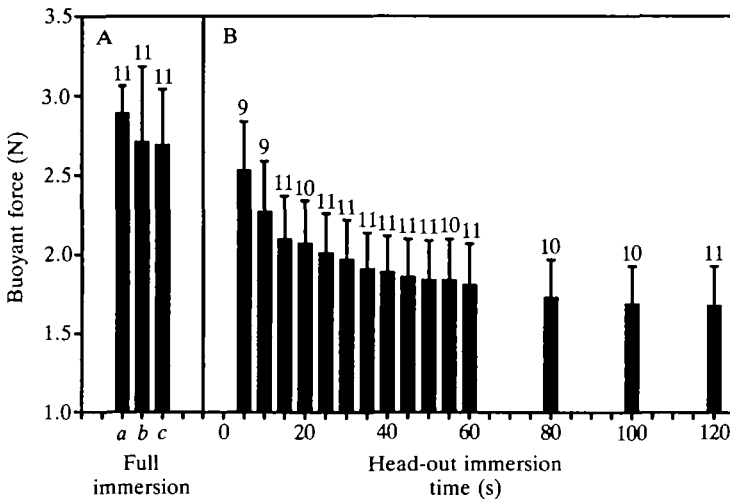


Fig. 1. Buoyancy (N) of lesser scaup. (A) Full immersion under three different conditions: *a*, minimal feather depression, head-down; *b*, minimal feather depression, head-up; *c*, maximal feather depression, head-down. (B) At specific times during head-out body immersion. Mean values \pm s.d. are shown with the sample size indicated above each column.

Drag force

Subsurface drag was obtained by subtracting the drag force of the aluminium bar from the total subsurface drag of the duck and bar. Both subsurface drag (D_{SUB}) and drag of duck carcasses at the water surface (D_{SUR}) increased as a curvilinear function of velocity (Fig. 2). Regression equations for these curves, in which U = velocity in m s^{-1} , are:

$$D_{\text{SUR}} = 0.239 - 1.292U + 2.027U^2 \quad (N = 31; r^2 = 0.965).$$

95 % joint confidence intervals for β_1 (linear effect coefficient) and β_{11} (curvature effect coefficient) are: $-2.136 < \beta_1 < -0.448$ and $1.395 < \beta_{11} < 2.659$, respectively.

$$D_{\text{SUB}} = -0.144 + 0.562U + 0.622U^2 \quad (N = 30; r^2 = 0.980).$$

95 % joint confidence intervals for β_1 and β_{11} are: $-0.333 < \beta_1 < 1.457$ and $-0.078 < \beta_{11} < 1.322$, respectively.

General linear tests (Neter and Wasserman, 1974) indicate that the two curves are statistically significantly different, and it can be seen above that the 95 % joint confidence intervals do not overlap. Intercepts were outside the measured range of velocities, so the intercept coefficients (β_0) were not compared.

Discussion

The buoyant force of fully submerged lesser scaup, corrected for body mass, was similar to that reported previously for greater scaup (*Aythya marila*) and redhead

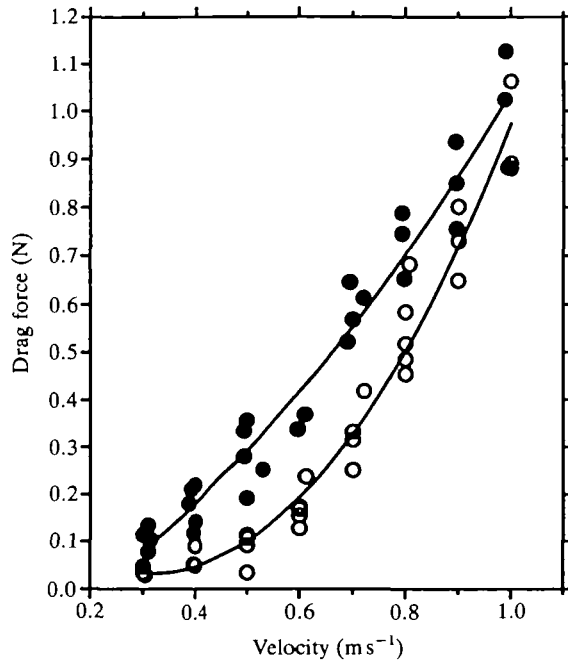


Fig. 2. Drag forces of partly submerged (simulating surface swimming; ○) and fully submerged (simulating the descent phase of a dive; ●) frozen duck carcasses.

ducks (Dehner, 1946). The results indicate, however, that there is potentially much variability within individual birds resulting from changes in the residual capacity of the respiratory system. Dehner's (1946) comparison of plucked and unplucked duck carcasses suggests that up to 50% of the buoyant force may be accounted for by air trapped in the plumage. Furthermore, if respiratory system volume is approximately 120 ml BTPS for ducks of this body mass (Stephenson *et al.* 1988), then at least this much air must reside elsewhere in the body (i.e. mainly trapped in the plumage) to produce the observed buoyant force. It was therefore surprising to find that artificially depressing the feathers had such an insignificant effect on buoyancy in the present study. This result indicates that our volumetric technique for measuring buoyancy is relatively insensitive to handling methods, although the coefficient of variation doubled when plumage was depressed (see Table 1). It also suggests that voluntary depression of the feathers by the duck before natural dives may not have much effect in reducing the buoyant force. An alternative explanation for these results is that the birds may have depressed their feathers as a reflex action during all measurements under all conditions. This question cannot be resolved from the present data.

The reduction in buoyant force during head-out immersion probably results from the effect of water pressure acting on the respiratory system, forcing air out each time the glottis is opened. Ducks are known to exhale before diving (Butler and Woakes, 1979), but it is unlikely that the buoyant force is reduced to the extent

observed during head-out immersion in ducks. Such large respiratory adjustments in buoyancy may, however, occur in other species of diving birds that are observed to swim with only the head and neck above water between dives, such as loons (*Gaviidae*), grebes (*Podicipedidae*), cormorants (*Phalacrocoracidae*), anhingas (*Anhingidae*) and penguins (*Spheniscidae*). It seems reasonable, therefore, to conclude that the buoyant forces measured in this study represent the full range of possible values, and that actual buoyancy during free dives falls between these limits, varying in different dives with variations in respiratory system volume and perhaps, to a lesser extent, with plumage depression.

The most obvious expression of the buoyant effect is seen during passive ascent at the end of a dive. The absence of acceleration as the ducks approach the water surface (R. Stephenson, unpublished observations) indicates that any increase in the buoyant force due to air-sac expansion is accompanied by an equal increase in drag force so that the terminal velocity of ascent remains constant. Since diving ducks passively ascend through the water at the velocity at which the buoyant force is equal and opposite to the drag force, it can be concluded that the drag force during ascent ranges between 1.68 and 2.89 N, according to the range of buoyant forces measured in this study. At velocities of $0.5\text{--}0.6\text{ m s}^{-1}$ (Butler and Woakes, 1982; Stephenson *et al.* 1986), drag force during ascent is approximately 4–8 times that during descent (see Fig. 2). Clearly, body posture (including extension of the feet) has a marked effect on the drag force and it is likely that ducks can use this effect to control their ascent rate at low energetic cost.

Surface drag force of lesser scaup carcasses was found to be much lower than values calculated by Prange and Schmidt-Nielsen (1970) for mallard ducks (*Anas platyrhynchos*). Our values are underestimates of the true drag because the drag of the limbs was not measured, although this was also true of Prange and Schmidt-Nielsen's (1970) measurements. Part of the difference may be due to the large size of the duck models used by Prange and Schmidt-Nielsen (1970). In both studies the drag force increased sharply at velocities of about 0.5 m s^{-1} (Fig. 2). At swimming velocities below 0.5 m s^{-1} , under conditions of laminar flow, the drag force can be attributed mostly to the friction between the duck's wetted surface area and the water. Above that velocity, however, surface drag increases rapidly with increasing swimming velocity as a result of turbulent flow and gravitational surface waves generated by the body (Hertel, 1966; Prange and Schmidt-Nielsen, 1970). The drag associated with the hind limbs during the recovery phase of the leg beat cycle is probably minimized in ducks, as in muskrats (Fish, 1984), by reducing the frontal surface area of the foot through adduction and flexion of the toes (closing the web) and withdrawal of the foot towards the body during the recovery leg stroke (M. R. A. Heieis and J. R. Lovvorn, unpublished observations). Subsurface and surface drag are compared in Fig. 2. It is clear that at speeds normally attained by freely swimming lesser scaup (less than 0.7 m s^{-1}), the drag force during submerged swimming (descent) is approximately twice that during surface swimming.

Woakes and Butler (1983) measured \dot{V}_{O_2} in tufted ducks performing dives of

Table 2. Calculation of work (W_O) and power output (P_O) of lesser scaup diving in a tank 1.55 m deep

W_O descent	W_O buoyancy (max)	$=1.55 \text{ m} \times 2.89 \text{ N}$	$=4.48 \text{ J}$
	W_O buoyancy (min)	$=1.55 \text{ m} \times 1.68 \text{ N}$	$=2.60 \text{ J}$
	W_O drag	$=1.55 \text{ m} \times 0.38 \text{ N}$	$=0.59 \text{ J}$
W_O foraging	W_O buoyancy (max)	$=4.48 \text{ J} \times 9.72 \text{ s} / 2.72 \text{ s}$	$=16.01 \text{ J}$
	W_O buoyancy (min)	$=2.60 \text{ J} \times 9.72 \text{ s} / 2.72 \text{ s}$	$=9.29 \text{ J}$
W_O diving	Maximum	$=4.48 + 0.59 + 16.01$	$=21.08 \text{ J}$
	Minimum	$=2.60 + 0.59 + 9.29$	$=12.48 \text{ J}$
P_O diving	Maximum	$=21.08 \text{ J} / 12.44 \text{ s}$	$=1.695 \text{ W}$
	Minimum	$=12.48 \text{ J} / 12.44 \text{ s}$	$=1.003 \text{ W}$

Dive duration is 14.4 s; the descent phase is 2.72 s, the foraging phase is 9.72 s and the passive ascent phase is 1.96 s. Velocity of descent is 0.57 m s^{-1} . These values are from Butler and Woakes (1982) and Woakes and Butler (1983) (see text).

14.4 s mean duration, at a water depth of 1.55 m. Descent and ascent velocities have been measured in this species (Butler and Woakes, 1982), and the average durations of the descent, foraging and ascent phases of the dive are calculated to be 2.72 s, 9.72 s and 1.96 s, respectively. The work done during a dive is estimated by calculating separately the work done against body drag and buoyancy during the descent phase and the work done against buoyancy during the foraging phase (Table 2). Ascent is largely passive and is therefore ignored in our calculations. Work done against buoyancy and body drag during descent is calculated by multiplying the respective forces (N) by 1.55 m (the distance travelled). The work of foraging is estimated by multiplying the calculated work output against buoyancy during the descent phase by the ratio of the durations of the foraging and descent phases. Thus, the total mechanical work output is between 12.5 and 21.1 J, of which at least 95% is required to overcome the buoyant force, and only 3–5% is required to oppose body drag during descent (assuming steady velocity, Table 2).

The average power output (P_O) during a dive is calculated by dividing the work output (J) by the total duration (s) of the active phases (descent and foraging phases) of the dive. Aerobic efficiency of diving ($\eta_a = P_O / P_{I\text{total}}$) based on the power output (P_O) values of 1.0–1.7 W (Table 2) and the total diving power input ($P_{I\text{total}}$) of 11.4 W (Woakes and Butler, 1983) is 0.088–0.149 (Table 3). Total energetic efficiency (η_{total}) cannot be calculated from the data used above since the work associated with the recovery phase of the leg beat cycle and with acceleration of the body is unknown (resulting in an underestimation of P_O), and the contribution of anaerobic metabolism to power input was not evaluated by Woakes and Butler (1983) (resulting in a possible underestimation of $P_{I\text{total}}$).

Table 3. Power requirements and efficiencies of diving and swimming in several avian and mammalian species

Species	Body mass (kg)	T _w (°C)	U (m s ⁻¹)	P _{rest} (W)	P _{total} (W)	P _{net} (W)	Drag (N)	P _O (W)	η _a	η _{net}	η _{mech}	Source
Subsurface swimming												
Tufted duck (<i>Aythya fuligula</i>)	0.597	13.6	0.57 ^a	3.28	11.38	8.10	0.38	1.695 ^b	0.149	0.209	1.045	Woakes and Butler (1983)
Humboldt penguin (<i>Spheniscus humboldti</i>)	3.780	19.2	1.25	27.40 ^c	55.80	27.40	2.744 ^d	3.430	0.061	0.125 ^e	0.625 ^e	Hui (1988a,b)
Surface swimming												
Tufted duck (<i>Aythya fuligula</i>)	0.613	17.8	0.78	3.60	12.86	9.26	0.46 ^f	0.359	0.028	0.039	0.195	Woakes and Butler (1983)
	0.613	17.7	0.80	4.08	10.93	6.85	0.50 ^f	0.400	0.037	0.058	0.290	Woakes and Butler (1986)
	0.604	-	0.71	4.05	8.90	4.85	0.34 ^f	0.241	0.027	0.050	0.250	Butler <i>et al.</i> (1988)
	0.613	17.8	0.40	3.60 ^g	3.96	0.36	0.05 ^f	0.020	0.005	0.056	0.280	Woakes and Butler (1983)
	0.613	17.7	0.40	4.08	4.56	0.48	0.05 ^f	0.020	0.004	0.042	0.210	Woakes and Butler (1986)
	0.613	17.7	0.50	4.08	4.88	0.80	0.10 ^f	0.050	0.010	0.063	0.315	Woakes and Butler (1986)
Mallard duck (<i>Anas platyrhynchos</i>)	1.081	~23	0.70	7.73	23.38	15.65	1.56	1.090	0.047	0.070	0.350	Prange and Schmidt-Nielsen (1970)
Black duck (<i>Anas superciliosa</i>)	1.100	~21	0.72	6.81	19.89	13.08	1.56 ^h	1.123	0.056	0.086	0.430	Baudinette and Gill (1985)
Little penguin (<i>Eudyptula minor</i>)	1.200	~21	0.72	7.68	13.96	6.28 ⁱ	0.882	0.635	0.045	0.101	0.505	Baudinette and Gill (1985)
North American mink (<i>Mustela vison</i>)	1.000	20.0	0.70	6.81	31.86	25.05	0.648	0.454	0.014	0.018	0.090	Williams (1983)
Muskrat (<i>Ondatra zibethicus</i>)	0.649	25.0	0.75	3.19	10.44	7.25	0.301	0.226	0.022	0.031	0.155 ^j	Fish (1982, 1984)

T_w is water temperature; U is swimming velocity; P_i is aerobic power input calculated from measurements of rate of oxygen consumption; P_O is mechanical power output calculated from measurements of body drag and buoyancy.

Net power input (P_{net}) = P_{total} - P_{rest}; aerobic efficiency (η_a) = P_O/P_{total}; net aerobic efficiency (η_{net}) = P_O/P_{net}; mechanical efficiency (η_{mech}) = η_{net}/η_{muscle}, where η_{muscle} is muscle efficiency and is equal to 0.2 (Hill, 1950).

^b Calculated from the total of drag plus maximum and minimum buoyant forces, this study (see Table 2).
^c Published value (0.68 W; Hui, 1988b) is the estimated basal metabolic rate based on data published by Drent and Stonehouse (1971), not the measured 'resting' metabolic rate.

^d Assuming 15% of swimming time is spent at the water surface (Hui, 1988a,b). Submerged drag value is from the carcass measurements.
^e Published value for η_{net} is 0.247 (Hui, 1988b). This was derived using additional kinematic data and results in η_{mech} = 1.235.
^f Data from this study.

^g Measured with flume motor on.
^h From Prange and Schmidt-Nielsen (1970).
ⁱ Value given by Baudinette and Gill (1985) is 6.82 W.
^j Published value, derived from kinematic data, is 0.33 (Fish, 1984).

If resting \dot{V}_{O_2} is subtracted from the diving \dot{V}_{O_2} to give P_{Inet} , assuming that resting metabolic functions are subserved during diving, the net aerobic efficiency ($\eta_{net} = P_O/P_{Inet}$) of subsurface locomotion is 0.124–0.209 (Table 3). The ducks used by Woakes and Butler (1983) were diving in water at 13.6°C. Takekawa (1987) found that mean standard metabolic rate of lesser scaup was elevated by approximately 50% when the ducks were resting on water at 10–15°C compared with when the water was at 25–30°C. It is not known whether the water at 13.6°C caused an increase in both the resting and the diving metabolic rates of the ducks studied by Woakes and Butler (1983), or whether the excess heat produced by the active leg muscles during submerged swimming is sufficient to supply the requirements of thermoregulation in diving ducks (see Paladino and King, 1984). Subtraction of resting \dot{V}_{O_2} from active \dot{V}_{O_2} for calculation of net aerobic efficiency of locomotion in this and other studies is valid only if water temperature affects resting and swimming oxygen uptake equally. Oxygen uptake values for surface-swimming tufted ducks (Woakes and Butler, 1983, 1986) in conjunction with our surface drag values give surface $\eta_a=0.004$ to 0.037 and $\eta_{net}=0.039$ to 0.063 at speeds from 0.4 to 0.8 m s⁻¹ (see Table 3). Hence, these ducks appear to be more efficient at utilizing their oxygen supply while diving than when swimming at the water surface (Table 3).

Published data pertinent to this study are collated in Table 3. The efficiency values of subsurface swimming ducks are higher than those published for surface swimming ducks and mammalian 'paddlers' such as the muskrat (*Ondatra zibethicus*) and the North American mink (*Mustela vison*). The mechanical efficiency of the diving duck hind limb appears to be similar to that of the pectoral flippers of surface- and subsurface-swimming Humboldt penguins (*Spheniscus humboldti*) (Table 3). It should be noted, however, that calculations of efficiencies rest upon assumptions made in the determination of both P_I and P_O terms, and errors may therefore be large when different methods are used in different studies. For this reason, power requirements and efficiencies given in Table 3 are recalculated from original data, where necessary, so that the same assumptions are applied to all species. Instances in which this has led to different values from those originally published are indicated in the Table footnotes. In all cases power input (P_I) is calculated from oxygen consumption measurements (assuming that 1 W=20.1 ml O₂ s⁻¹), and power output (P_O) data are derived from body drag and buoyancy measurements only, disregarding additional kinematic data where present. Resting power input is taken, unless otherwise noted, as that measured under the same conditions as swimming power input (at zero velocity). This definition of 'rest' may lead to overestimations of P_{Irest} as a result of non-swimming activities of the animals (e.g. Hui, 1988b).

Possible errors associated with the calculation of η_a and η_{net} have already been discussed, and the assumption that η_{muscle} (which is the efficiency of conversion of chemical energy into muscular tension) is 0.2 (Hill, 1950) can also lead to problems, as exemplified by the calculation of η_{mech} greater than 1.0 for diving tufted ducks and Humboldt penguins shown in Table 3 (see footnote e). In his study of the California sea lion, Feldkamp (1987) avoided this problem by

assuming that η_{muscle} is 0.25, based upon data from Cavagna *et al.* (1964) who quoted a value determined by Margaria (1938). In fact, assuming that η_{muscle} is 0.25 instead of 0.2 would result in a 20% reduction in calculated η_{mech} , emphasizing the critical nature of this assumption. Different techniques used to calculate power output can result in different efficiency values, as shown for the η_{mech} value of the muskrat in Table 3 (0.155), which is only half of that obtained by Fish (1984), who based his calculations on kinematic data. Furthermore, directly measured drag forces of towed Harbor seals (*Phoca vitulina*) and California sea lions (*Zalophus californianus*) (Williams and Kooyman, 1985; Feldkamp, 1987) are higher than those calculated indirectly from the rate of deceleration during free glides in the same animals. Obviously, inaccuracies or inconsistencies in measurements of P_O (or P_1) will have direct bearing on the efficiency values calculated. Illustrative of this is the relatively high variability in efficiency values calculated from different sets of P_1 data obtained from surface-swimming tufted ducks under very similar experimental conditions (Table 3). Given these limitations in the data, comparisons among species should be made with utmost caution. It is likely that the efficiencies of different modes of aquatic locomotion can be sensibly compared only when exactly the same techniques are used for all species, and when the efficiency of contraction of muscle has been further investigated, particularly with a view to establishing possible differences between different muscle types and shortening rates (see Kushmerick, 1983).

To summarize, buoyancy is the dominant force against which ducks have to work during dives, while drag adds little to the overall energy output, in contrast to the situation in other species studied. Depression of the plumage and the air layer it contains has minimal effects on buoyancy. However, a reduction in respiratory volume before submersion could substantially reduce the energy required to dive (Dehner, 1946; Schorger, 1947; Owre, 1967; Casler, 1973; Stephenson *et al.* 1988).

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