Effects of body size, body fat, and change in pressure with depth on buoyancy and costs of diving in ducks (*Aythya* spp.)

James R. Lovvorn[1] and David R. Jones

Department of Zoology, University of British Columbia, Vancouver, B.C. Canada V6T 2A9

Lovvorn, J. R., and Jones, D. R. 1991. Effects of body size, body fat, and change in pressure with depth on buoyancy and costs of diving in ducks (*Aythya* spp.). Can. J. Zool. **69**: 2879–2887.

Recent studies of diving ducks (*Aythya* spp.) have shown that buoyancy is far more important to locomotor costs of shallow diving than is hydrodynamic drag. Working with Canvasbacks (*A. valisineria*), Redheads (*A. americana*), and Lesser Scaup (*A. affinis*), we investigated factors affecting buoyancy in models of locomotor energetics. Body volume can be accurately estimated from body mass (r^2 = 0.82–0.95), but equations sometimes differ among species, and body volume relative to mass is higher in winter than in summer. Wing molt does not influence body volume or buoyancy. In scaup, an increase in body lipid from 35 to 190 g (from 5.4 to 22.3% of body mass) increases the energy costs of descent more through the inertial effects of higher mass and added mass of entrained water (82.8% of change) than through greater work against drag (12.0%) or buoyancy (5.2%). Costs of foraging at the bottom are 20% lower in the fatter birds because increased inertial resistance to the buoyant force is greater than the increase in buoyancy. Maximal changes in body lipid and associated hypertrophied muscle raise overall costs of diving to a depth of 2 m by only 2%. Such effects can be offset by altering respiratory and plumage air volumes (+15 mL for a 155-g lipid increase) or the relative amount of time spent at the bottom. Hence, diving energetics contrast with the energetics of flight, which are strongly affected by body mass changes. Reduced buoyancy from compression of air spaces with depth lowers costs of bottom foraging in scaup by 24% at 1.2 m and 36% at 2 m. Mass-specific plumage air volume decreases with increasing body mass (slope = 0.12), and body tissues are incompressible relative to air. Thus, buoyancy decreases faster with increasing pressure in smaller birds and they become negatively buoyant at shallower depths (about 43 m for Oldsquaws, *Clangula hyemalis*). Ducks such as eiders (*Somateria* spp.) weighing over 1200 g and diving to less than 60 m probably never become negatively buoyant.

Lovvorn, J. R., et Jones, D. R. 1991. Effects of body size, body fat, and change in pressure with depth on buoyancy and costs of diving in ducks (*Aythya* spp.). Can. J. Zool. **69** : 2879–2887.

Des études récentes sur les canards plongeurs (*Aythya* spp.) ont démontré que la flottabilité contribue beaucoup plus que la traînée hydrodynamique au coût de la locomotion au cours de la plongée. Nous avons tenté de déterminer les facteurs qui affectent la flottabilité en étudiant des Morillons à dos blanc (*A. valisineria*), des Morillons à tête rouge (*A. americana*) et des Petits Morillons (*A. affinis*) et en intégrant nos résultats à des modèles d'énergie locomotrice. Le volume du corps peut être estimé justement d'après la masse corporelle (r^2 = 0,82–0,97), mais les équations diffèrent parfois selon l'espèce et les rapports volume/masse sont plus élevés en hiver qu'en été. La mue des ailes n'influence pas le volume du corps ou la flottabilité. Chez le Petit Morillon, l'augmentation des lipides corporels de 35 à 190 g (5,4 à 22,3% de la masse totale) augmente les coûts énergétiques reliés à la plongée plus par l'effet d'inertie dû à une masse plus grande et à la masse augmentée de l'eau entraînée (82,8% du changement) que par augmentation du travail contre la traînée (12,0%) ou de la flottabilité (5,2%). Les coûts rattachés à la recherche de nourriture au fond de l'eau sont de 20% moins élevés chez les oiseaux plus gras, parce que l'augmentation de la résistance d'inertie à la force de flottabilité est plus grande que l'augmentation de la flottabilité. Les changements maximaux des lipides corporels et l'hypertrophie musculaire qui leur est associée n'augmente que de 2% le coût total d'une plongée jusqu'à 2 m. Ces effets peuvent être compensés par une modification du volume respiratoire et du volume des plumes (+15 mL pour une augmentation de 155 g de lipides) ou par une modification du temps relatif passé au fond de l'eau. La dynamique énergétique reliée à la plongée diffère donc beaucoup de celle qui est reliée au vol, puisque les changements de masse corporelle modifient beaucoup le vol. La diminution de la flottabilité par compression des espaces aériens en eau profonde diminue les coûts reliés à la quête de nourriture au fond de 24% à 1,2 m et de 36% à 2 m chez le Petit Morillon. Le volume d'air du plumage spécifique à la masse diminue à mesure qu'augmente la masse corporelle (pente = 0,12) et les tissus corporels sont incompressibles par rapport à l'air. Donc, la flottabilité diminue plus rapidement sous la pression chez les petits oiseaux puisque leur flottabilité devient négative à des profondeurs moins grandes (environ 43 m chez le Canard kakawi, *Clangula hyemalis*). Chez des canards, tels les eiders (*Somateria* spp.), qui pèsent plus de 1200 g et qui plongent à moins de 60 m, la flottabilité ne devient probablement jamais négative.

[Traduit par la rédaction]

Introduction

The mechanics of horizontal, underwater swimming have been studied in a number of air-breathing vertebrates, including seals (*Phoca vitulina*, *P. groenlandica*, *P. hispida*), sea lions (*Zalophus californianus*), sea otters (*Enhydra lutris*), mink (*Mustela vison*), muskrats (*Ondatra zibethicus*), sea turtles (*Chelonia mydas*), frogs (*Hymenochirus boettgeri*), and a variety of penguins (Prange 1976; Mordvinov 1974; Clark and Bemis 1979; Williams 1983, 1989; Williams and Kooyman 1985; Feldkamp 1987; Fish *et al.* 1988; Gal and Blake 1988; Hui

1988). These studies have all focused on hydrodynamic drag as the major determinant of the energy costs of underwater swimming.

All these animals, however, obtain their food by diving, and so must overcome the vertical force of buoyancy. Recent biomechanical studies of diving ducks (*Aythya* spp.) have shown that buoyancy is far more important than body drag to the locomotor costs of shallow diving. In Canvasbacks (*Aythya valisineria*), Redheads (*A. americana*), and Lesser Scaup (*A. affinis*), work against drag was 10–12%, work against buoyancy 36–38%, and work to accelerate the body during unsteady stroking 49–54% of total work during descent (Lovvorn *et al.* 1991). If inertial (accelerational) effects are ignored, work

---

[1]Present address: Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, U.S.A.

against buoyancy is at least 82% of total work during descent, and at least 95% of work for entire dives (Stephenson et al. 1989a). Based on studies of body drag during horizontal swimming, Williams (1989) suggested that sea otters weighing 19.85 kg will not swim continuously above or below water against a drag force exceeding 4 N. With lung volume after predive exhalation of 189 mL · kg^{-1} (Kooyman 1989, p. 40), body fat content of 2% (Tarasoff 1974), and pelage air volume assumed to be similar to that of muskrats (274 mL · kg^{-1}, Johansen 1962), the buoyancy of sea otters upon submergence approaches 80 N (for methods of calculation see below). Thus, relative to buoyancy, maximal drag work of 4 N is of minor significance for a sea otter traveling between the water surface and benthic food sources. These examples demonstrate that in a natural scenario of vertical diving, analyses of locomotion are incomplete if drag alone is considered.

Buoyancy is strongly affected by the volume of air in the respiratory system and pelage. Fur seals, muskrats, mink, otters, beavers, and the platypus maintain a pelage air layer for thermal insulation underwater, whereas most other aquatic mammals become wet to the skin (Johansen 1962; Grant and Dawson 1978; Costa and Kooyman 1982; Williams 1986; Riedman 1990). Seals and sea lions exhale before submergence and rely for metabolism mainly on oxygen stored in their large volume of blood (Kanwisher 1986), whereas inshore species such as otters, and muskrats probably carry larger volumes of respiratory air during dives (e.g., sea otters, Kooyman 1989, p. 40).

Unlike many aquatic mammals, all birds depend on the plumage air layer for thermal insulation. Molt in at least some species (penguins) strongly disrupts this air layer (Boersma 1975), so molt might also affect buoyancy. Unlike seals (Kooyman 1989), diving birds apparently maintain gas exchange between blood, lungs, and air sacs to depths of at least 68 m (Kooyman et al. 1971, 1973). Some birds dive to great depths, e.g., Common Loons (Gavia immer), Oldsquaws, and eiders (Somateria mollissima, S. spectabilis) dive to 60 m, Common Murres (Uria aalge) to 180 m, and various penguins to 70–265 m (Schorger 1947; Piatt and Nettleship 1985; Kooyman 1989). At such depths, compression of air spaces must greatly reduce buoyancy. However, these and other species often or usually dive to much shallower depths, where the buoyancy of air spaces will be important to dive costs. (For a survey of buoyancies in a variety of species see Lovvorn and Jones (1991).)

Buoyancy of diving birds might also be affected by dramatic changes in body mass and composition during the year (Milne 1976; Chu 1984; Austin and Fredrickson 1987; Jehl 1988). Fresh adipose tissue has a higher buoyancy than muscle (0.52 vs. −0.69 N · L^{-1}, J. R. Lovvorn, unpublished data) but a much lower buoyancy than air (9.79 N · L^{-1} for vapor-saturated air at 35°C). Thus, depending on tissue composition and compensatory adjustment of air volumes, changes in body mass (and thus tissue composition) within individuals might not affect buoyancy in the same way as mass differences among individuals of varying structural size. Fat is essentially incompressible relative to air, so its effect on buoyancy will be greater as depth increases.

Given the importance of buoyancy to the energy costs of diving, there is a need to identify those factors affecting buoyancy that should be considered in studies of locomotor energetics, and to develop equations for estimating their effects. Working with Canvasbacks, Redheads, and Lesser Scaup with mean body masses of about 1.24, 0.99, and 0.80 kg, we examined the effects

on buoyancy of (i) body mass and composition, (ii) simultaneous molt of wing feathers, (iii) pressure change with depth, and (iv) salt water versus fresh water. These variables were also evaluated relative to adjustments in respiratory or plumage air volumes that would offset their effects.

Methods

Study animals

Eggs of wild Canvasbacks, Redheads, and Lesser Scaup were collected from nests near Minnedosa, Manitoba, hatched in an incubator, and shipped to the University of British Columbia. Ducks were kept in concrete ponds 0.5–1 m deep, where they were fed mixed grain and poultry ration (16% protein) ad libitum on platforms. We regularly encouraged ducks to dive by throwing grain into the water.

Body mass, volume, buoyancy, and plumage air volume

After capture from holding ponds, ducks were allowed to dry and preen for at least 2 h before processing. Birds were weighed to the nearest gram with an Ohaus triple-beam balance. Body volume was determined by water displacement. The legs were taped together and, with the bird in an extended prostrate position, the bill and feet were attached with filament tape to a flat steel bar (93 cm long, 3 cm wide, 3 mm thick). The bird was then allowed to breathe freely for at least 15 s, expanding its air sacs, before two strips of masking tape were wrapped lightly around the body (not constricting the plumage) to prevent the bird from flapping its wings. The bird was then immersed head-down in a PVC pipe 70 cm high and 15 cm wide partly filled with water. Change in water height was read within 5 s of immersion by means of a 10-mL pipette connected in parallel with the water column. This apparatus was calibrated with known quantities of water to yield volume of water displaced by the duck, corrected for volume of the bar. Body volume measurements of the same individuals repeated after 2.5 h varied by 1.3 ± 0.8% (mean ± SD) for 10 Canvasbacks and 2.1 ± 1.1% for 14 Lesser Scaup. Buoyancy (in newtons) was calculated as [mass of displaced water (kg) − body mass] × [gravitational acceleration (9.81 m · s^{-2})].

The relation of volume to mass was examined for two time periods. Fourteen Canvasbacks, 17 Redheads, and 34 Lesser Scaup were measured between 26 January and 11 February 1989, and 4 Redheads on 15 June. This sample included birds in mostly Alternate plumage that were molting body feathers lightly, if at all (for terminology and description of annual molt patterns see Palmer 1976). The latter group is termed the "winter" sample. The same individuals (except one Redhead and two scaup that died) were remeasured on 3–4 August 1989 during the period of body and wing molt. Ducks have a complete, simultaneous molt of wing feathers (as do loons, grebes, and auks), separating and overlapping two complete molts of the body plumage. Each bird measured in August was classified as having the remiges complete (flight feathers fully grown and no blood in the quills to indicate growth) or remiges regrowing (missing or partially grown flight feathers with blood in the quills). August measurements are from the group termed the "summer" sample. Regression equations were compared with general linear tests (Neter and Wasserman 1974, pp. 87–89).

Volume of the plumage air layer was estimated from the data of Dehner (1946), who measured the body volume of living Redheads and Greater Scaup (Aythya marila) by water displacement, then killed the birds, plugged their tracheas, plucked their feathers, and remeasured body volume. The difference in initial and final volumes approximated the volume of air in the plumage.

Effects of structural size

We assessed the utility of correcting body mass for structural size in relating mass to volume. Three structural dimensions were measured: bill length (distance from tip to base of the bill at the junction of upper and lower mandibles), tarsus length (from outside the tarsal–metatarsal joint to the tarsal–phalangeal joint when flexed at right angles), and

body length (total length of the bird when flat on its back, minus length of tail feathers).

We performed principal component (PC) analysis of the correlation matrix for lengths of the bill, tarsus, and body for each species separately and for all species combined. Each variable had positive loadings on the first principal component (PC1) from 0.55 to 0.61 for species separate or together. Eigenvalues for PC1 explained 75–81% of total variance for individual species and 96% for all species. PC1 scores for each bird were used as a measure of body size. Body mass, M, was regressed against these PC1 scores to yield equations of the form $M = a + b(PC1)$ for species separate and combined. All regressions were significant ($P < 0.001$) for both individual species ($r^2 = 0.14$–0.39) and species together ($r^2 = 0.79$). Mass adjusted for structural size, M_a, was calculated by the equation $M_a = M - [a + b(PC1)] + \bar{M}$ (Ankney and Afton 1988), using regressions developed for individual species and species combined. Both M and M_a were then regressed on body volume and the results were compared.

To examine further the effects of body condition (mass relative to structural size) on the relation of body volume to mass, we investigated the effects of mass changes within individuals. Body mass and volume of 10 male Lesser Scaup were measured before and after a period of about 56 h without food (1–3 February). The average slope (volume versus mass) of lines connecting points for the same individuals before and after food deprivation was compared with the slope of the regression of volume versus mass among different individuals fed ad libitum.

Biomechanical model

Effects of body fat and change in pressure with depth on the energy costs of descent and bottom foraging were evaluated for Lesser Scaup by means of a biomechanical model of locomotion (Lovvorn et al. 1991). Hydrodynamic drag of ducks frozen in a diving posture was measured in a tow tank and related to body mass and speed. Ducks descending in a tank 2 m deep were filmed at 100 frames/s to determine linear displacement at 0.01-s intervals during a stroke cycle (including power and recovery phases). Work during each interval was calculated by multiplying drag and buoyancy by displacement, and then adding inertial work done in accelerating the body and the added mass of entrained water. Work during all intervals was then integrated over the power phase of the stroke.

Work per stroke at the bottom was calculated by multiplying buoyancy, B, by the distance, D, the bird would float upward during a stroke of duration t, where $D = \frac{1}{2}(B/M_v)t^2$. Virtual mass, M_v, equals body mass plus the added mass of entrained water. Added mass is $\alpha \rho V$, where the added mass coefficient, α, is 0.2, ρ is the density of the water, and V is body volume.

Stroke durations, distance per stroke during descent, and average durations of descent and bottom foraging for each dive were determined from video films of eight Lesser Scaup in the experimental tank ($n = 305$ and 313 dives to depths of 1.2 and 2 m, respectively) (Lovvorn et al. 1991; Lovvorn 1992).

Effects of fat on the costs of diving

To evaluate the effects of body fat on power requirements of descent and bottom foraging, calculations were made from the model for a natural, maximal range of body mass and composition. This range was based on mean values for female Lesser Scaup during the flightless molt period (body mass 647 g, water 432 g, lipid 37 g, protein 134 g, ash 29 g) and fall migration (body mass 842 g, water 463 g, lipid 188 g, protein 149 g, ash 30 g) in southwestern Manitoba (Austin and Fredrickson 1987). The ratio of water to protein did not change, so no relative increase in blood volume occurred. Change in body water and protein resulted primarily from an increase in fresh mass of pectoral muscles (+41 g), whereas leg muscle mass declined (− 10 g).

Lipid gain in birds is usually accompanied by increased muscle mass to accommodate additional weight during flight. Based on the above data, we calculated that a 1-g increase in lipid is accompanied by a 0.1-g increase in protein, and we assumed that all protein gain was in muscle. By water displacement in a graduated cylinder, we determined

the volume of the fresh pectoral muscles of 20 Canvasbacks collected between 7 March and 10 April at Long Point Bay, Ontario. Specific volume of pectoral muscle was 0.939 ± 0.017 mL·g^{-1} (mean $\pm$ SD). If fresh pectoral muscle contains 26% protein by mass (Raveling 1979), then 1 g of muscle protein corresponds to 3.61 mL of fresh muscle, with a density of 1.064 g·mL^{-1} fresh muscle and a buoyancy of -0.634 N·kg^{-1} or -0.674 N·L^{-1}. Density of triglyceride is about 0.93 (DeVries and Eastman 1978), corresponding to a specific volume of 1.075 mL·g^{-1} and buoyancy of 0.729 N·kg^{-1} or 0.678 N·L^{-1}. We first estimated body volume, V, for a Lesser Scaup weighing 645 g (Fig. 2, winter), and calculated buoyancy from estimated volume and body mass, M. Body mass, volume, and buoyancy were then increased by adding body lipid (to the 35 g already present) and associated muscle. Model estimates of locomotor cost were made for different increments of fat and muscle.

We also calculated the change in volume of air required to keep power output constant as lipid and associated muscle increased. Added mass for this difference in air volume was small (<22 g) and was therefore ignored to simplify calculations (see below). Reduction of air volume by pressure with depth (see below) was also ignored for all lipid levels because respiratory and plumage air volumes were uncertain.

To determine the compensatory volume of air during descent to 2 m, the change, Z, in total work per stroke owing to increments of lipid and associated muscle was calculated. We then solved for volume of air, V_a, in the equation

$$Z = D(9.79V_a)$$

where D is the distance per stroke during descent to 2 m (0.152 m per stroke) and 9.79 N·L^{-1} is the buoyancy of air.

For work per stroke to stay constant at the bottom, the following equation must hold:

$$\tfrac{1}{2}(B_1/M_{v1})t^2(B_1) = \tfrac{1}{2}(B_2/M_{v2})t^2(B_2)$$

where B_1 and M_{v1} are buoyancy and virtual mass without addition of lipid, muscle, or compensatory air (i.e., for a 645-g scaup) and B_2 and M_{v2} include additional lipid, muscle, and compensatory air; t is stroke duration, which is not correlated with body mass (J. R. Lovvorn, unpublished data). This equation can be expressed as

$$[1] \quad B_1^2/M_{v1} = (B_1 + B_f + B_m + B_a)^2/[M_2 + 0.2(V_1 + V_f + V_m + V_a)]$$

where B_f, B_m, and B_a are the buoyancy values, and V_f, V_m, and V_a the volumes, of additional (not total) lipid, muscle, and compensatory air, respectively, and 0.2 is the added mass coefficient. As mentioned above, added mass of air ($0.2V_a$ in the denominator of eq. 1) was ignored to simplify calculations (avoiding two solutions to a quadratic expression). Equation 1 was solved for B_a which, when divided by 9.79 N·L^{-1} (the buoyancy of air), yields V_a. V_a is the change in volume of air required to keep work per stroke constant despite addition of lipid and associated muscle.

Effects of water salinity and change in pressure with depth

We calculated buoyancy at different water depths and salinities of "average" Canvasbacks and Lesser Scaup in winter (for 14 Canvasbacks means were 1.238 kg for body mass, 1.764 L for body volume, and 5.15 N for buoyancy above water; for 34 scaup means were 0.798 kg for mass, 1.114 L for volume, and 3.10 N for buoyancy). Respiratory volume at the surface was assumed to be the same, 0.180 L·kg^{-1}, as for Tufted Ducks (Aythya fuligula) (mean mass 0.674 kg) (Keijer and Butler 1982). Plumage air volume was estimated from the data of Dehner (1946) (Fig. 4). Air in the respiratory system and plumage was assumed to be saturated and at 35°C, yielding a buoyancy of 9.79 N·L^{-1} of air. Tissue buoyancy was assumed to be constant and equal to the buoyancy of the entire body minus that of air spaces at the surface. Pressure change with depth was taken to be 9.8 kPa·m^{-1} in fresh water and 10 kPa·m^{-1} in salt water. Compression of air in the respiratory system was assumed to be unopposed by structural resistance of the body wall (Kooyman 1989, p. 41).

We determined effects of buoyancy change with depth on locomotor

costs of scaup at two depths (1.2 and 2 m) for which we had video-film data on duration and distance per stroke. We made model calculations that did and did not consider the change in buoyancy with depth, and compared the results.

Results

Body volume and plumage volume versus body mass

Lesser Scaup were the only species for which sample size (18 males, 16 females) was sufficient to test for sex differences in the relation of volume to mass. Winter samples were used to avoid problems with molt asynchrony beween sexes. Linear regressions for male and female scaup did not differ (general linear test, $P = 0.067$), so sexes were combined in all analyses.

Simple linear regression of body volume on mass, M, yielded r^2 values of 0.90 for Canvasbacks, 0.87 for Redheads, and 0.82 for Lesser Scaup. These r^2 values were 128, 82, and 34% higher than those for regression of body volume on mass adjusted for structural size, M_a. For species combined, the coefficient of determination for M ($r^2 = 0.95$, $s_{y \cdot x} = 61$) was much higher than for M_a ($r^2 = 0.09$, $s_{y \cdot x} = 275$). The need to adjust body mass for structural size was also evaluated in light of weight changes within individual Lesser Scaup (mean $\pm$ SD $= -92 \pm 7$ g, $n = 10$). Slopes of the change in volume versus mass were the same regardless of initial mass (Fig. 1). The average slope ($\pm$SD) for 10 Lesser Scaup (0.953 ± 0.112) did not differ from the slope of the regression relating single points for different individuals fed ad libitum in winter (slope 0.971, Fig. 2A; t-test, $P > 0.25$). We conclude that body volume is best predicted from body mass alone and that adjusting body mass for structural size increases error.

For the winter sample, regressions of body volume versus mass (Fig. 2) were the same for Canvasbacks and Redheads ($P = 0.74$), but both species differed from Lesser Scaup ($P < 0.001$, general linear tests; Neter and Wasserman 1974, pp. 87–89). In summer, regressions of body volume on body mass did not differ between ducks that had complete versus regrowing flight feathers (general linear tests, $P > 0.52$). Sample sizes for the latter tests were 7 and 7 for Canvasbacks, 11 and 8 for Redheads, and 13 and 18 for Lesser Scaup. Summer data for all species were fit by a single regression (Fig. 2).

Summer and winter relations of body volume to mass (Fig. 3) were the same for Canvasbacks ($P = 0.41$) but differed for Redheads ($P = 0.013$) and Lesser Scaup ($P = 0.043$) (general linear tests). The range in body mass was narrower and lower, and Redheads and scaup tended to have lower mass-specific volumes, in summer than in winter.

The relation of plumage air volume to body mass (Fig. 4) was quite variable but indicated a decrease in mass-specific plumage volume with increasing body mass.

Effects of body lipid on the costs of diving

The calculated power requirements of descent in Lesser Scaup increased by almost 19% as body lipid increased from 35 to 190 g (Fig. 5A). This rise resulted from increases of 12.0% in work against hydrodynamic drag, 5.2% in work against buoyancy, and 82.8% in inertial work of accelerational stroking (Fig. 6). In terms of power requirements, decreasing the volume of air in the respiratory system or plumage by 109 mL would compensate for a 155-g gain in lipid plus 60 g of associated muscle (Fig. 5A).

Inertial effects also dominated the response of the power costs of bottom foraging to changing lipid and associated muscle (Fig. 5B, Table 1). The power requirement decreased by almost
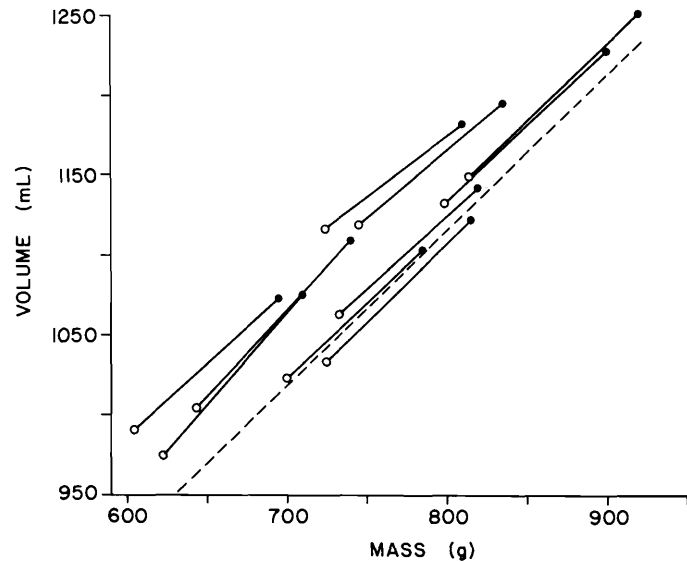

FIG. 1. Change in relation of body volume to mass for individual Lesser Scaup fasted for about 56 h from 1 to 3 February. The broken line is the regression based on points for different individuals fed ad libitum during winter (see Fig. 2).

20% as buoyancy increased by 2.5%. Greater mass and added mass due to more lipid and associated muscle increased inertial resistance to the upward buoyant impulse. The consequent decrease in work against buoyancy lowered total power requirements. Maintaining power output at 1.68 W while lipid increased to 190 g would require expanding respiratory or plumage air volume by 38 mL (Fig. 5B).

Change in buoyancy with water depth and salinity

Compression of respiratory and plumage air volumes with increasing depth decreased the buoyancy of an "average" Lesser Scaup by 20% at 2 m and by 41% at 5 m (Fig. 7). The effect of fresh water versus salt water was negligible, being only 0.6% at 2 m and 1.3% at 5 m. Most dives by *Aythya* spp. in the wild are within this depth range. Reduction in buoyancy with depth decreased the power requirements of descent by <4%, but lowered costs at the bottom by almost 24% at 1.2 m and 36% at 2 m (Table 2).

Simulated buoyancies at depths up to 80 m (Fig. 8) suggest that ducks of the size of Canvasbacks or larger (including eiders) never become negatively buoyant, whereas ducks the size of scaup (including Oldsquaws) become negatively buoyant below a depth of about 43 m (Common Eiders, King Eiders, and Old-squaws are known to dive to 60 m).

Discussion

Because buoyancy is so important to the energy costs of diving (Stephenson *et al.* 1989*a*; Lovvorn *et al.* 1991), factors affecting buoyancy should be considered in studies of under-water locomotion. We found that season, body mass, and changes in pressure with depth substantially affect buoyancy, but that wing molt, fresh water versus salt water, and maximal changes in body composition (see below) have negligible effects on buoyancy and overall dive costs.

Predicting volume from body mass

Body volume of restrained birds at the surface corresponds more closely to body mass than to mass adjusted for structural
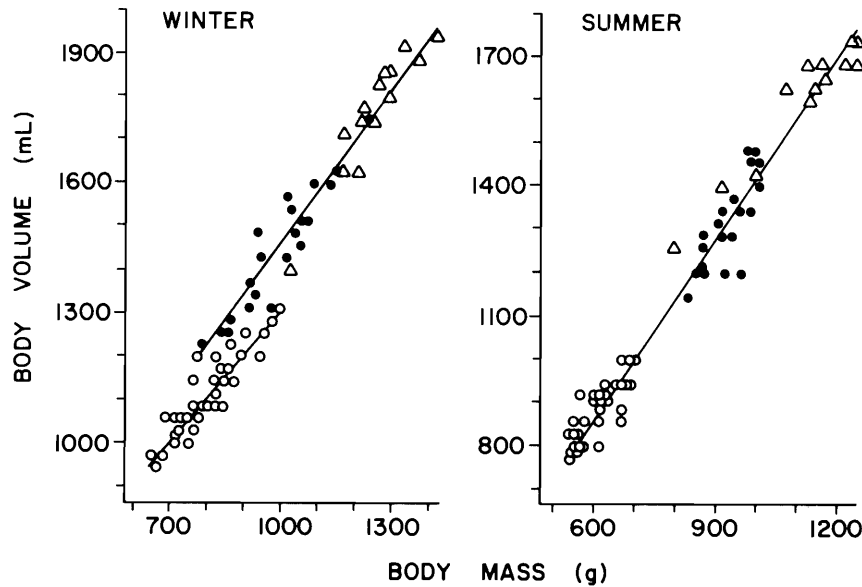
FIG. 2. Relations of body volume, V, to body mass, M, of Canvasbacks ($\triangle$), Redheads ($\bullet$), and Lesser Scaup ($\bigcirc$) during winter and summer. In winter, for Canvasbacks and Redheads $V = 213.6 + 1.2506M$, $r^2 = 0.95$, $P < 0.001$, $s_{y \cdot x} = 49$; for scaup $V = 339.2 + 0.9711M$, $r^2 = 0.82$, $P < 0.001$, $s_{y \cdot x} = 41$). In summer, for all species $V = 42.97 + 1.387M$, $r^2 = 0.97$, $P < 0.001$, $s_{y \cdot x} = 55$).
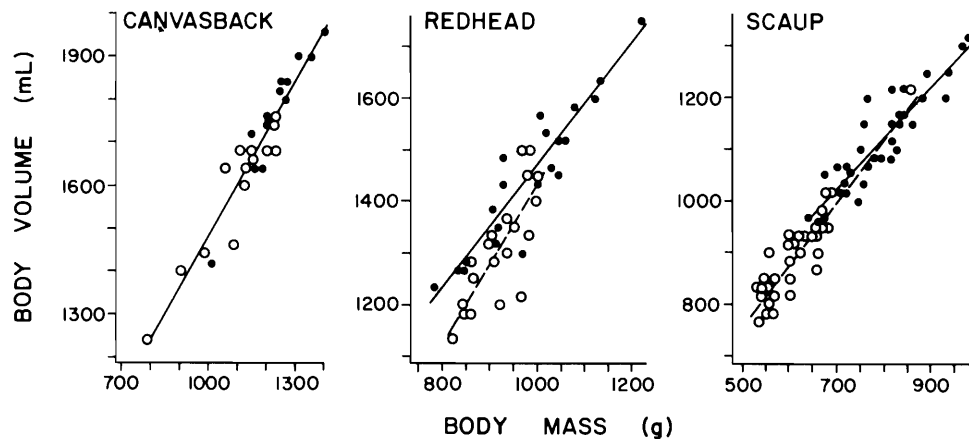

FIG. 3. Relations of body volume to body mass in Canvasbacks, Redheads, and Lesser Scaup in winter ($\bullet$) and summer ($\bigcirc$). Regressions are shown by a solid line for winter and a broken line for summer.
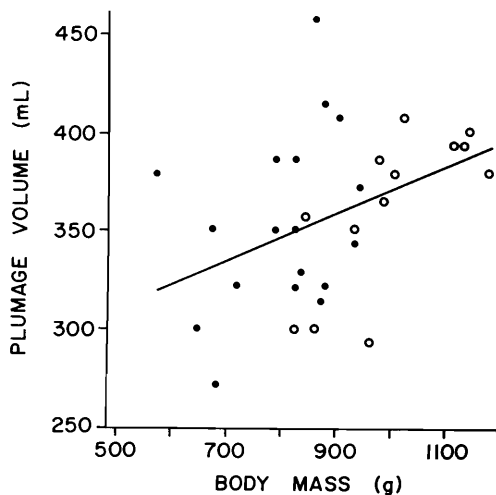

FIG. 4. Relation of plumage air volume, V_p, to body mass, M, in 13 Redheads ($\bigcirc$) and 18 Greater Scaup ($\bullet$) (data from Dehner 1946). ($V_p = 247.8 + 0.1232M$, $r^2 = 0.18$, $P = 0.018$, $s_{y \cdot x} = 39.6$).

size (principal component analysis and Fig. 1). This greatly simplifies estimation of buoyancy for biomechanical analyses (Lovvorn et al. 1991). Volume to mass relations differed between winter and summer for Redheads and Lesser Scaup but not for Canvasbacks (Fig. 3). The body volume of a Redhead weighing 850 g in winter (1288 mL) is about 7% higher than that of an 850-g Redhead in summer (1200 mL). Body composition has negligible effects on the volume to mass relation (Fig. 1), so the seasonal difference in Redheads and scaup probably results from maintaining a thicker plumage air layer in winter. In summer, the volume to mass relation for ducks lacking flight feathers did not differ from that of ducks with complete remiges. This implies that molt itself is less important than other seasonal effects in determining volume and buoyancy, although intensity of body molt does not correspond directly to molt of flight feathers.

Plumage volume was extremely variable (Fig. 4), which emphasizes the difficulty of measuring this important parameter. Experimental compression of the plumage suggests that reduction of the plumage air layer by voluntary ptilosuppression
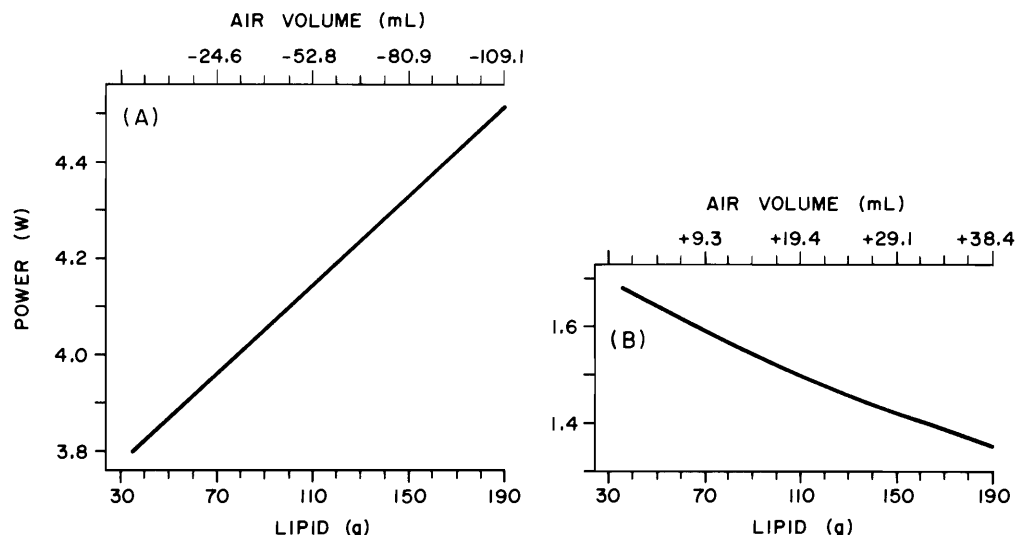
FIG. 5. Power requirements for descent (A) and bottom foraging (B) as a function of body lipid content in Lesser Scaup (based on the model of Lovvorn et al. 1991). Changes of air volume in the respiratory system or plumage that would compensate for changes in lipid and associated hypertrophied muscle are also shown.
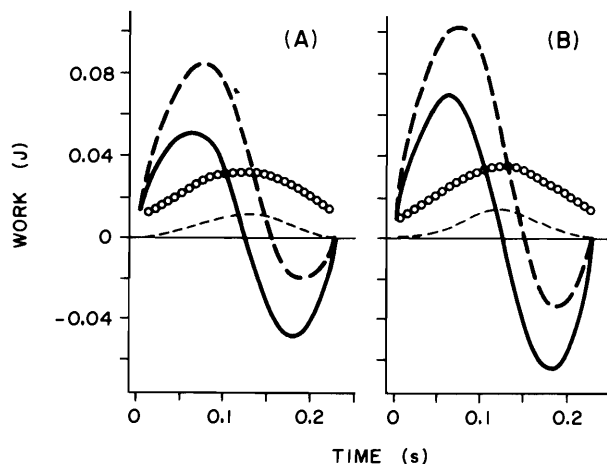

FIG. 6. Work owing to drag (light broken line), buoyancy (O), acceleration (solid line), and all three combined (heavy broken line) during descent in Lesser Scaup with 35 g (A) and 190 g (B) of body lipid. The power phase ends where the curve for total work becomes negative.

reduces buoyancy by <6% (Stephenson et al. 1989a). However, mass-specific plumage air volume decreases rather rapidly with increasing mass (Fig. 4), which has important implications for change in buoyancy with depth for birds of different sizes (Fig. 8).

Effects of body lipid levels on costs of diving

One might think that any increase in a positively buoyant tissue such as fat would result in increased energy costs of descent and staying at the bottom. However, lipid with associated hypertrophied muscle is only slightly buoyant, and has much greater influence on locomotion through the inertial effects of increased mass and added mass of entrained water. Because of these inertial effects, increased costs of descent in fatter birds were higher than those due to buoyancy alone. However, the costs of bottom foraging were lower in fatter birds (Fig. 5B) because the higher inertial resistance to the buoyant force was greater than the increase in buoyancy (Table 1).

For captive Lesser Scaup diving in a tank 2 m deep, average dive duration was 11.2 s, of which 3.0 s were spent in descent, 5.3 s at the bottom, and 2.9 s in passive ascent. These parameters were not correlated with body mass, which allowed the same values to be used regardless of mass change. If the body lipid of a Lesser Scaup increases from 35 to 190 g, its power requirements for locomotion increase by only 2%, from [(3.0 g)(3.80 W) + (5.3 s)(1.68 W)]/(3.0 s + 5.3 s) = 2.45 W to [(3.0)(4.52) + (5.3)(1.35)]/8.3 s = 2.50 W (values were obtained from Fig. 5 and Table 1). The fatter bird could avoid this small increase in overall power requirement merely by increasing the length of time spent on the bottom per dive by 0.34 s (6.5%). The 15–85% quantiles for dive duration in Lesser Scaup diving to 2 m were 8.5–15.1 s, with a range of 3.2–23.8 s (n = 313 dives). Extremely variable dive durations in captivity and in the wild (J. R. Lovvorn, unpublished data) suggest that variations in food intake on different dives overwhelm the energetic importance of small differences in the times spent descending and at the bottom.

The increased power requirement in fatter scaup could also be compensated for by a change in air volume of [(3.0 s)(−109.1 mL) + (5.3 s)(38.4 mL)]/8.3 s = −14.9 mL (values were obtained from Fig. 5). Tufted Ducks habitually diving 6 m for food, rather than 0.65 m, reduced their end-expiratory lung and air-sac volume by about 26 mL (from an average of 148 mL (232 mL·kg⁻¹) to 122 mL (165 mL·kg⁻¹)), with a concomitant increase of 36 mL in blood volume, from 68 to 104 mL (Stephenson et al. 1989b). The ratio of water to protein was the same in both field samples of Lesser Scaup referred to here (Austin and Fredrickson 1987), so no appreciable change in blood volume accompanied the gain in lipid and associated muscle. Plumage air volume in these two groups, with mean mass 645 and 895 g, would be about 327 and 358 mL, respectively (Fig. 4), for which a 6% decrease through ptilo-suppression would be about 20 mL. Tidal volume of scaup is approximately 38 mL (Dehner 1946). Diving ducks use, on average, only about 30% of the oxygen stored in their bodies during voluntary dives to 1.7 m (Woakes and Butler 1983), which suggests some latitude in managing respiratory volume.

In general, it appears that maximal changes in body lipid have

TABLE 1. Effects of body lipid (and associated muscle mass) on power requirements of bottom foraging by Lesser Scaup

Body lipid (g)	Body mass (g)	Body volume (mL)	Buoyancy (N)	Added mass (g)	Virtual mass (g)	Distance/ stroke (m)	Work/ stroke (J)	Power (W)
35	645	966	3.14	193	838	0.153	0.481	1.68
70	693	1016	3.16	203	896	0.144	0.454	1.59
110	749	1073	3.18	215	964	0.135	0.428	1.50
150	804	1131	3.20	226	1030	0.127	0.405	1.42
190	860	1188	3.22	238	1098	0.120	0.386	1.35

NOTE: Distance/stroke = ½(buoyancy/virtual mass)(stroke duration)^2, where stroke duration (at the bottom) at a depth of 2 m is 0.286 s.

TABLE 2. Effects of change in buoyancy with depth on the power requirements of descent and bottom foraging by Lesser Scaup

		Descent				At the bottom			
Depth (m)	Buoyancy (N)	Stroke rate (Hz)	Distance/ stroke (m)	Power (W)	%	Stroke rate (Hz)	Distance/ stroke (m)	Power (W)	%
1.2	2.70	4.5	0.154	4.32	−2.5	3.6	0.103	1.00	−23.6
2.0	2.47	4.4	0.152	4.09	−3.9	3.5	0.100	0.86	−35.7

NOTE: Body mass 798 g, body volume 1114 mL, and buoyancy 3.10 N at the water surface. Percentage decreases in power estimates, if buoyancy change with depth is accounted for (versus being ignored), are given.
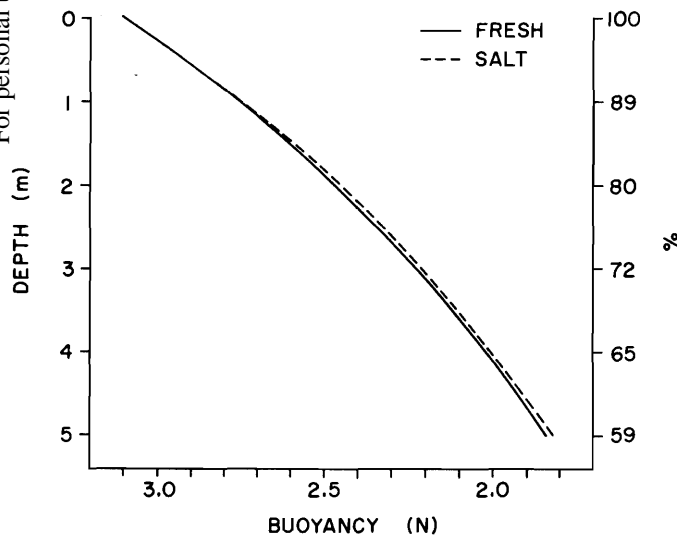

FIG. 7. Effect on buoyancy of water depth and fresh water versus salt water as calculated for an "average" Lesser Scaup (see Methods), and the percentage of surface buoyancy at those depths.
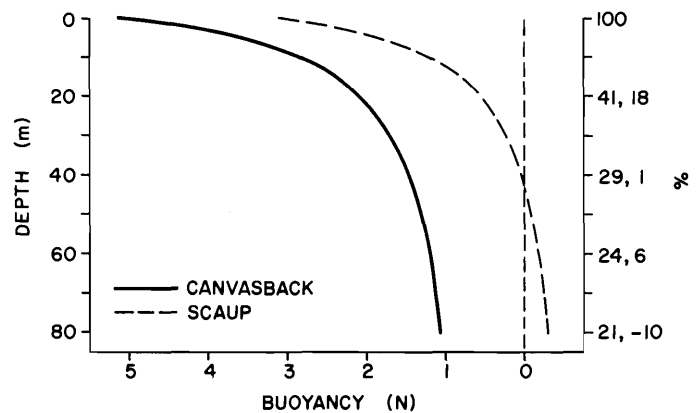

FIG. 8. Change in buoyancy with depth as calculated for "average" Canvasbacks and Lesser Scaup, and the percentage of surface buoyancy at those depths (the first numeral represents Canvasbacks and the second represents Lesser Scaup).

small overall effects on the energy costs of diving to shallow depths, and that most changes can be compensated for by altering air volumes or the relative length of time spent at the bottom. This finding contrasts with the energetics of flight, which are strongly affected by body mass changes (Tucker 1975). However, the effects of air volume and body composition on power requirements are complex, owing to inertial considerations, and are strongly dependent on dive depth and changes in mass-specific plumage volume with body size. Calculations should be made according to the situation of interest.

Body size and change in pressure with depth

In *Aythya* spp. (and probably other aquatic birds), smaller individuals have greater plumage air volumes per unit body mass than larger individuals (Fig. 4). Body tissues are essentially incompressible relative to air, so the greater the fraction of body volume composed of air, the greater the reduction in buoyancy with increased pressure. Thus, smaller birds will become negatively buoyant at shallower depths (Fig. 8). Oldsquaws, which resemble scaup in body mass but dive to depths of up to 60 m (Schorger 1947), may be the only ducks that must routinely ascend by active propulsion. Common Eiders and King Eiders also dive to 60 m, but usually weigh more than 1200 g and probably can always ascend passively by means of buoyancy

(Fig. 8). Frequent negative buoyancy may explain why Old-squaws are apparently the only duck species to depend mostly on wing propulsion underwater (Lovvorn 1991, based on Snell 1985). Auks (Alcidae), which are also wing-propelled, are small and often dive beyond 50 m (Piatt and Nettleship 1985) where negative buoyancy would mandate active propulsion during ascent.

Importance of respiratory and plumage air volumes

Because small changes in air volume have large effects on buoyancy, the most critical variables affecting the buoyancy of diving birds are the volumes of air in the respiratory system and plumage. The importance of other variables considered here cannot be evaluated except in the context of possible adjustments in air volume. Managing air spaces to reduce buoyancy and dive costs is a critical and integral part of managing oxygen stores to avoid anaerobiosis. Unfortunately, no means have been devised for measuring either respiratory or plumage air volumes in birds during natural, unrestrained dives. For example, ducks of the genus *Aythya* are known to exhale before submerging (Butler and Woakes 1979), but the volumes of air exhaled and retained in the respiratory system are unknown. Moreover, different species vary in their manipulation of buoyancy through air-volume adjustments, e.g., loons and grebes versus ducks (Lovvorn 1991). Further understanding of the locomotor energetics of diving birds depends on developing techniques for measuring respiratory and plumage air volumes during voluntary, unrestrained dives.

ANKNEY, C. D., and AFTON, A. D. 1988. Bioenergetics of breeding Northern Shovelers: diet, nutrient reserves, clutch size, and incubation. Condor, **90**: 459–472.

AUSTIN, J. E., and FREDRICKSON, L. H. 1987. Body and organ mass and body composition of postbreeding female Lesser Scaup. Auk, **104**: 694–699.

BOERSMA, D. 1975. Adaptation of Galapagos Penguins for life in two different environments. *In* The biology of penguins. *Edited by* B. Stonehouse. Macmillan Press, London. pp. 101–114.

BUTLER, P. J., and WOAKES, A. J. 1979. Changes in heart rate and respiratory frequency during natural behaviour of ducks, with particular reference to diving. J. Exp. Biol. **79**: 283–300.

CHU, E. W. 1984. Sooty Shearwaters off California: diet and energy gain. *In* Marine birds: their feeding ecology and commercial fisheries relationships. *Edited by* D. N. Nettleship, G. A. Sanger, and P. F. Springer. Spec. Publ., Canadian Wildlife Service, Ottawa. pp. 64–71.

CLARK, B. D., and BEMIS, W. 1979. Kinematics of swimming of penguins at the Detroit Zoo. J. Zool. (1965–1984), **188**: 411–428.

COSTA, D. P., and KOOYMAN, G. L. 1982. Oxygen consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, *Enhydra lutris*. Can. J. Zool. **60**: 2761–2767.

DEHNER, E. W. 1946. An analysis of buoyancy in surface–feeding and diving ducks. Ph.D. thesis, Cornell University, Ithaca, NY.

DEVRIES, A. L., and EASTMAN, J. T. 1978. Lipid sacs as a buoyancy adaptation in an Antarctic fish. Nature (London), **271**: 352–353.

FELDKAMP, S. D. 1987. Swimming in the California sea lion: morphometrics, drag and energetics. J. Exp. Biol. **131**: 117–135.

FISH, F. E., INNES, S., and RONALD, K. 1988. Kinematics and estimated thrust production of swimming harp and ringed seals. J. Exp. Biol. **137**: 157–173.

GAL, J. M., and BLAKE, R. W. 1988. Biomechanics of frog swimming. I. Estimation of the propulsive force generated by *Hymenochirus boettgeri*. J. Exp. Biol. **138**: 399–411.

GRANT, T. R., and DAWSON, T. J. 1978. Temperature regulation in the platypus, *Ornithorhynchus anatinus*: production and loss of metabolic heat in air and water. Physiol. Zool. **51**: 315–332.

HUI, C. A. 1988. Penguin swimming. I. Hydrodynamics. Physiol. Zool. **61**: 333–343.

JEHL, J. R., JR. 1988. Biology of the Eared Grebe and Wilson's Phalarope in the nonbreeding season: a study of adaptations to saline lakes. Stud. Avian Biol. **12**.

JOHANSEN, K. 1962. Buoyancy and insulation in the muskrat. J. Mammal. **43**: 64–68.

KANWISHER, J. W. 1986. The evolution of diving animals. *In* Diving in animals and man. *Edited by* A. O. Brubakk, J. W. Kanwisher, and G. Sundnes. Tapir Publications, Trondheim, Norway. pp. 113–130.

KEIJER, E., and BUTLER, P. J. 1982. Volumes of the respiratory and circulatory systems in Tufted and Mallard ducks. J. Exp. Biol. **101**: 213–220.

KOOYMAN, G. L. 1989. Diverse divers. Springer-Verlag, Berlin.

KOOYMAN, G. L., SCHROEDER, J. P., GREENE, D. G., and SMITH, V. A. 1971. Effects of deep dives on penguins and Blue-eyed Shags. Antarct. J. U.S. **6**: 95.

——— 1973. Gas exchange in penguins during simulated dives to 30 and 68 m. Am. J. Physiol. **225**: 1467–1471.

LOVVORN, J. R. 1991. Mechanics of underwater swimming in foot-propelled diving birds. Proc. Int. Ornithol. Congr. **20**. In press.

——— 1992. Biomechanics and foraging profitability: an approach to assessing trophic needs and impacts of diving ducks. Hydrobiologia. In press.

LOVVORN, J. R., and JONES, D. R. 1991. Body mass, volume, and buoyancy of some aquatic birds, and their relation to locomotor strategies. Can. J. Zool. **69**: 2888–2892.

LOVVORN, J. R., JONES, D. R., and BLAKE, R. W. 1991. Mechanics of underwater locomotion in diving ducks: drag, buoyancy, and acceleration in a size gradient of species. J. Exp. Biol. **159**: 89–108.

MILNE, H. 1976. Body weights and carcass composition of the Common Eider. Wildfowl, **27**: 115–122.

MORDVINOV, Y. E. 1974. The character of the boundary layer in the process of swimming in the muskrat (*Ondatra zibethicus*) and mink (*Mustela lutreola*). (In Russian.) Zool. Zh. **53**: 430–435.

NETER, J., and WASSERMAN, W. 1974. Applied linear statistical models. Richard D. Irwin, Inc., Homewood, IL.

PALMER, R. S. 1976. Handbook of North American birds. Vol. 3. Yale University Press, New Haven, CT.

PIATT, J. F., and NETTLESHIP, D. N. 1985. Diving depths of four alcids. Auk, **102**: 293–297.

PRANGE, H. D. 1976. Energetics of swimming of a sea turtle. J. Exp. Biol. **64**: 1–12.

RAVELING, D. G. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. Auk, **96**: 234–252.

RIEDMAN, M. 1990. The pinnipeds: seals, sea lions, and walruses. University of California Press, Berkeley.

SCHORGER, A. W. 1947. The deep diving of the loon and Old-squaw and its mechanism. Wilson Bull. **59**: 151–159.

SNELL, R. R. 1985. Underwater flight of Long-tailed Duck (Oldsquaw) *Clangula hyemalis*. Ibis, **127**: 267.

STEPHENSON, R., LOVVORN, J. R., HEIEIS, M. R. A., JONES, D. R., and BLAKE, R. W. 1989a. A hydromechanical estimate of the power requirements of diving and surface swimming in Lesser Scaup (*Aythya affinis*). J. Exp. Biol. **147**: 507–519.

STEPHENSON, R., TURNER, D. L., and BUTLER, P. J. 1989b. The relationship between diving activity and oxygen storage capacity in the Tufted Duck (*Aythya fuligula*). J. Exp. Biol. **141**: 265–275.

TARASOFF, F. J. 1974. Anatomical adaptations in the river otter, sea otter and harp seal with reference to thermal regulation. *In* Functional anatomy of marine mammals. *Edited by* R. J. Harrison. Academic Press, New York. pp. 111–141.

TUCKER, V. A. 1975. Flight energetics. Symp. Zool. Soc. Lond. **35**: 49–63.

WILLIAMS, T. M. 1983. Locomotion in the North American mink, a semi-aquatic mammal. I. Swimming energetics and body drag. J. Exp. Biol. **103**: 155–168.

——— 1986. Thermoregulation of the North American mink during rest and activity in the aquatic environment. Physiol. Zool. **59**: 293–305.

——— 1989. Swimming by sea otters: adaptations for low energetic cost locomotion. J. Comp. Physiol. A, **164**: 815–824.

WILLIAMS, T. M., and KOOYMAN, G. L. 1985. Swimming performance and hydrodynamic characteristics of harbor seals *Phoca vitulina*. Physiol. Zool. **58**: 576–589.

WOAKES, A. J., and BUTLER, P. J. 1983. Swimming and diving in Tufted Ducks, *Aythya fuligula*, with particular reference to heart rate and gas exchange. J. Exp. Biol. **107**: 311–329.