# Biomechanical Conflicts Between Adaptations for Diving and Aerial Flight in Estuarine Birds

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ABSTRACT:   Diving and aerial flight place conflicting physiological constraints on diving birds depending on their typical dive depths. The amount by which air volumes in the respiratory system and plumage are reduced by hydrostatic pressure decreases rapidly with depth. Thus, birds diving shallowly, and ascending passively by means of positive buoyancy, contend with greater work against buoyancy as well as more unstable buoyancy as they move vertically in the water column. The buoyancy of air far exceeds that of tissues or blood, whose buoyancy does not change appreciably with depth. Accordingly, experiments on ducks suggest that birds adapt to shallow diving by increasing blood volume and thus blood oxygen stores while decreasing respiratory volume. During dives, increased inertia from greater mass of blood and associated muscle lowers the costs of foraging at the bottom by resisting the upward buoyant force, but raises the costs of descent because of higher inertial work in accelerating the body with each stroke. Thus, average dive depth (compression of buoyant air spaces), stroke kinematics (inertial effects), and the relative time spent descending versus bottom foraging will determine the appropriate balance between buoyancy and inertia for diving.

Greater blood volume also increases wing loading, so elements of dive costs must be balanced against flight costs in optimizing allocation of oxygen stores to blood versus the respiratory system. For example, biomechanical models for ducks suggest that increasing blood volume while decreasing respiratory volume lowers dive costs only for dives to depths <5 m or for dives with extended time at constant depth. If flight costs are also considered, these anti-buoyancy mechanisms reduce daily energy expenditure only if average dive depth is <2 m. High wing-loading in many foot-propelled divers is probably not an adaptation to diving but rather a result of modifications in wing size and shape for high flight-speed. These wing modifications appear possible because competing demands on wing morphology (maneuverability, takeoff ability) are relaxed in open aquatic environments.

## Introduction

Estuarine and pelagic diving birds differ in that the former often dive to much shallower depths. Moreover, among diving birds capable of aerial flight, pelagic marine divers (alcids and diving petrels) swim underwater mainly by wing propulsion, whereas freshwater or shallow inshore taxa (loons, grebes, cormorants, and diving ducks) rely mostly on foot propulsion (Lovvorn 1991).

There are exceptions. Among "inshore" foot-propelled taxa, several cormorants commonly forage at depths of 25–35 m (Wanless et al. 1991) or even 80-100 m (Croxall et al. 1991); and common loons (*Gavia immer*) and some sea ducks (mergini) occasionally dive to 60 m (Schorger 1947; Lovvorn and Jones 1991a). Conversely, among "pelagic" wing-propelled taxa, several auklets, murrelets, and

guillemots (Alcidae) often feed at only 5–10 m (Carter and Sealy 1984; Piatt and Nettleship 1985; Burger and Powell 1990). Regarding habitat type, guillemots often forage around mussel reefs with goldeneyes, scoters, scaups, and grebes (J. R. Lovvorn personal observation), whereas cormorants and loons commonly feed on offshore fish schools with various alcids (Sealy 1973).

Nevertheless, alcids and diving petrels rarely concentrate diving activities in water less than 4 m deep, depths frequently exploited by foot-propelled divers including loons, grebes, cormorants, and sea ducks capable of much deeper dives (Vermeer and Levings 1977; Ross 1974–76; McIntyre 1978; Cooper 1986; Bustnes and Erikstad 1988; Forbes and Sealy 1988; Wilson and Wilson 1988; Daub 1989; Trayler et al. 1989; Wanless and Harris

1991). This propensity for shallow diving appears to distinguish foot-propelled avian lineages that exploit the estuarine environment.

Shallow diving poses unique and important problems. Of three major factors affecting the mechanical work of foot-propelled diving—hydrodynamic drag, inertial work in accelerating the body with each stroke, and buoyancy (Lovvorn and Jones 1991a; Lovvorn et al. 1991)—both drag and inertial work are largely independent of water depth. However, the amount by which air volumes in the respiratory system and plumage are reduced by hydrostatic pressure decreases rapidly with depth (air volume decreases by a factor of $1/n$, where n is the number of 10-m depth increments). Thus, birds diving shallowly, and ascending passively by means of positive buoyancy, contend with greater work against buoyancy as well as more unstable buoyancy as they move vertically in the water column. The latter effect poses challenges for control and maneuverability, and may be especially important for birds pursuing prey throughout the water column versus birds that feed benthically at minimum and predictable buoyancy for a given dive. The buoyancy of air far exceeds that of tissues or blood, whose buoyancy does not change appreciably with depth. Therefore, shallow divers should exhibit adaptations to increase their body density by decreasing their mass-specific air volumes (Lovvorn and Jones 1991b). One means of achieving this is to match decreases in respiratory volume with increases in blood volume and thus blood oxygen stores, so that total oxygen stored in the body stays the same (Stephenson et al. 1989).

However, increasing blood volume to reduce effects of buoyancy also increases body mass and wing loading, which raises the energy costs of flight and reduces lift and maneuverability at low flight speeds (Pennycuick 1989b). During dives, greater body mass might lower locomotor costs by increasing inertial resistance to the buoyant force, but might also increase inertial work in accelerating the body with each stroke (Lovvorn and Jones 1991a; Lovvorn et al. 1991). Because of these opposing considerations for both flight and diving, buoyancy-reducing mechanisms should be more pronounced in shallow divers for which effects of underwater buoyancy are most important. This might be especially true for pursuit divers that must control their buoyancy during rapid and unpredictable depth changes, or spend a large fraction of long dives swimming horizontally so that buoyancy effects at that depth outweigh inertial effects during descent.

In this paper, we use biomechanical models of the locomotor costs of flight and diving to evaluate trade-offs of storing oxygen in the blood versus respiratory system in diving ducks. In particular, we consider effects on these trade-offs of dive depth and the proportion of time spent diving versus flying. We then review published evidence for respiratory and blood volume adaptations to diving in birds, and compare predictions from the biomechanical models to observed dive depths and durations in a variety of species. Finally, we discuss the functional significance and evolution of high wing-loading in foot-propelled diving birds.

## Methods

### MECHANICAL MODEL OF FLIGHT

We evaluated effects of buoyancy-reducing adaptations on energy costs of flight with the aerodynamic models of Pennycuick (1975, 1989b). Pennycuick used actuator disk-momentum jet theory to estimate the mechanical work of steady, flapping flight. An alternative formulation by Rayner (1979, 1986, 1991) models the momentum imparted by wings to the air as vortex rings during slow, flapping flight, and as continuous vortices from the wing tips in fast flight by some species. Flow visualization indicates that Rayner's approach is physically more realistic (Spedding 1986, 1987). However, for slow flight, calculations from his model differ substantially from empirical measurements (Spedding 1986). For fast flight, the continuous vortex model requires a number of parameters unavailable for all but a few species, and at any rate yields results similar to those from momentum jet theory (Spedding 1987). Consequently, we used Pennycuick's more familiar and tractable approach, and restricted our analyses to steady flight at speeds to which this theory applies.

According to Pennycuick (1975), the total mechanical power required by a bird to fly is the sum of the following six components: induced power ($P_{ind}$) to support the bird's weight in air, parasite power ($P_{par}$) to overcome skin friction and form drag of the body, profile power ($P_{pro}$) to overcome drag on the wings during flapping, inertial power to accelerate the wings during each stroke, circulation and ventilation power to pump blood and ventilate the lungs, and basal metabolism ($P_{BMR}$) converted to an equivalent mechanical power to allow addition with the other components.

Induced power is calculated as

$$P_{ind} = k(Mg)^2/2\rho VS_d$$

where the induced power factor k is assumed to equal 1.2, g is gravitational acceleration, $\rho$ is air density, and V is airspeed. The disk area $S_d = \pi b^2/4$ is the area of a circle whose diameter is the wing span b. This area delimits the "momentum jet" of air induced to accelerate downward through the "actuator disk" swept by the flapping

wings. The model assumes that air passes through all parts of the disk at the same speed, and that air outside the momentum jet is not accelerated (Pennycuick 1975); the induced power factor corrects for deviations from those assumptions. Induced power calculated from momentum jet theory is presumed to be equivalent to the power required to overcome the drag of wing-induced vortices that generate lift in Rayner's vortex theory (see above).

Parasite power is calculated as

$$P_{par} = \rho V^3 A_f C_D / 2$$

where $A_f$ is the frontal area (cross-sectional area of the body at its widest point, excluding the wings) and $C_D$ is the parasite drag coefficient. $C_D$ for a given object is determined by measuring the drag force (D) on the object at varying speeds in a wind tunnel and solving the equation $C_D = 2D/\rho V^2 A_f$. The same equation can be used with body surface area substituted for $A_f$, yielding different values for $C_D$. We used values of $C_D$ calculated from the equations of Pennycuick et al. (1988) based on measurements for ducks and geese.

Profile power, the power to overcome drag on the flapping wings, cannot be readily calculated from mechanical principles and relevant data. Pennycuick (1975) estimates profile power as

$$P_{pro} = X_1 P_{am}$$

where the profile power ratio $X_1$ ($P_{pro}/P_{am}$) is assumed to be independent of speed and equal to 1.2. Lower limits to speeds at which Pennycuick's theory applies are determined partly by the validity of this assumed value for $X_1$. The absolute minimum power required for flight is estimated as

$$P_{am} = 0.877 k^{0.75} (Mg)^{1.5} (A_f C_D)^{0.25} / \rho^{0.5} S_d^{0.75}$$

(Pennycuick 1989b). Some formulations incorporate changes in profile power with flight speed (e.g., Blake 1985), but no empirical data exist as a basis for the presumed relationships.

At medium and high airspeeds, inertial power is assumed negligible; aerodynamic lift eliminates the need for muscles to raise the wing, thereby offsetting muscular work required to accelerate the wing during the downstroke (Pennycuick 1975). Circulation and ventilation power are each assumed to be 5% of total mechanical power, and are included by multiplying total mechanical power by 1.10. $P_{BMR}$ is calculated from body mass (M) by the allometric equation of Lasiewski and Dawson (1967) for nonpasserines, $P_{BMR} = 3.79 M^{0.723}$. To convert $P_{BMR}$ to its mechanical equivalent, it is multiplied by a conversion efficiency of 0.23 (Pennycuick 1975, 1989b).

Finally, mechanical power output is converted to actual energy required by applying an aerobic ef-

ficiency, $\eta$ (mechanical power output/aerobic power input). A value of 0.23 is based on respirometry of laughing gulls (*Larus atricilla*) and fish crows (*Corvus ossifragus*) flying in wind tunnels, at a range of work loads induced by varying the airspeed and tilting the tunnels to make the birds fly upward (see Pennycuick 1975). Use of a constant efficiency value for all work loads and flight modes has been criticized (Rayner 1991), but more definitive data are not available.

## MECHANICAL MODEL OF DIVING

Lovvorn et al. (1991) and Lovvorn and Jones (1991a) developed a model of underwater locomotion based on data for canvasbacks (*Aythya valisineria*), redheads (*A. americana*), and lesser scaup (*A. affinis*). Hydrodynamic drag of ducks frozen in a diving posture was measured in a tow tank. Buoyancy was calculated as the difference between body weight and the weight of water displaced by restrained birds submerged head downward in a water-filled cylinder (Lovvorn and Jones 1991a, b). In model calculations, buoyancy is adjusted for compression of respiratory and plumage air spaces with depth (Lovvorn and Jones 1991a). Based on extensive video films of these species (Lovvorn 1994b), we assume that any air lost from the respiratory system or plumage during descent or bottom foraging has negligible effects on total buoyancy.

For kinematic analyses, ducks descending in a tank 2 m deep were filmed at 100 frames s⁻¹ to determine linear displacement at 0.01-s intervals during a stroke cycle (including power and recovery phases). Work during these intervals 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 to yield work per stroke during descent. Work per stroke at the bottom was calculated by multiplying the buoyant force by the distance the bird would float upward during the time required for a stroke (Lovvorn et al. 1991). Counts of strokes required to reach the bottom and remain there (from video films, see Lovvorn 1994b) allowed estimates of total work during dives. Aerobic cost was calculated by dividing mechanical work or power by an aerobic efficiency of 0.17 (Lovvorn et al. 1991).

## EFFECTS OF AIR AND BLOOD VOLUMES ON LOCOMOTOR COSTS

To analyze effects of buoyancy-reducing adaptations, we calculated costs of flight and diving for the dive-trained and dive-untrained (control) ducks in experiments by Stephenson et al. (1989). These birds substantially increased their mass of

TABLE 1.  Blood parameters and blood oxygen stores of diving birds.

| Species | n | Body Mass (kg) | Blood Volume (ml kg⁻¹) | Hct (%) | Hb (g l⁻¹) | Blood O₂ Capacity[a] (ml l⁻¹) | (ml kg⁻¹) |
|---|---|---|---|---|---|---|---|
| *Gavia stellata*[b] | 1 | 1.255 | 132 | 54 | 207 | 277 | 36.6 |
| *Phalacrocorax carbo*[c] | 13 | 2.240[d] | | 45 | 145 | 194 | |
| *Aythya fuligula*[e] | | | | | | | |
| Untrained | 8 | 0.638 | 107 | 43 | 156 | 209 | 22.4 |
| Trained | 7 | 0.740 | 141 | 45 | 155 | 208 | 29.3 |
| *Aythya valisineria* | | | | | | | |
| and *A. americana*[b] | 6 | 0.860 | 111 | 37 | 180 | 241 | 26.8 |
| *Aythya ferina*[c] | 4 | 0.88[d] | | 44 | 146 | 196 | |
| *Uria aalge*[f] | | 0.985[g] | | 50 | 151 | 202 | |
| *Uria lomvia*[h] | 6 | 1.029 | 123 | 53 | 180 | 241 | 29.6 |
| *Eudyptula minor*[i] | | 1.1[j] | | 40 | 180 | 241 | |
| *Pygoscelis antarctica*[k] | 6 | 4.5[j] | | 53 | 196 | | |
| *Pygoscelis adeliae*[f,k] | 8 | 4.85 | 93 | 46 | 165 | 221 | 20.6 |
| *Pygoscelis papua*[k,l] | 5 | 5.8[j] | 79 | 43 | 164 | 220 | 17.4 |

[a] Assuming 1.34 ml O₂ (g Hb)⁻¹ (Keijer and Butler 1982).
[b] Bond and Gilbert (1958).
[c] Balasch et al. (1974).
[d] Palmer (1975).
[e] Stephenson et al. (1989). Untrained birds habitually dove vertically to a maximum depth of 0.65 m; trained birds dove diagonally a distance of 6.0 m to a minimum depth of 1.7 m.
[f] Lenfant et al. (1969).
[g] Spring (1971).
[h] Croll et al. (1992).
[i] Mill and Baldwin (1983).
[j] Stonehouse (1975).
[k] Milsom et al. (1973).
[l] Scholander (1940).

blood and muscle, and decreased their respiratory volume, in response to training (increasing diving activity, details in Results and Tables 1 and 2). Tufted ducks (*Aythya fuligula*) used in those experiments are very similar morphologically to lesser scaup (*A. affinis*) for which wing size and shape, buoyancy, stroke kinematics, and speeds of descent

TABLE 2.  End-expiratory volume of the respiratory system (lung and air sacs) and myoglobin (Mb) content of pectoralis muscle in diving birds.

| Species | Body Mass (kg) | Respiratory Volume (ml kg⁻¹) | Pectoralis Mb (mg per g wet mass) |
|---|---|---|---|
| *Aythya fuligula*[a] | | | |
| Untrained | 0.638 | 232 | 4.7 |
| Trained | 0.740 | 165 | 7.4 |
| *Fratercula arctica*[b] | 0.490[c] | | 12.5 |
| *Uria aalge*[b] | 0.985[c] | | 14.1 |
| *Uria lomvia*[d] | 1.029 | | 19 |
| *Eudyptula minor*[e] | 1.1[f] | | 28 |
| *Pygoscelis adeliae*[e,g,h] | 4.3 | 165 | 28.8, 36 |
| *Pygoscelis papua*[g,h] | 4.9 | 160 | 44.2 |

[a] Stephenson et al. (1989).
[b] Davis and Guderley (1987).
[c] Spring (1971).
[d] Croll et al. (1992).
[e] Mill and Baldwin (1983).
[f] Stonehouse (1975).
[g] Kooyman et al. (1973).
[h] Weber et al. (1974).

and ascent have been measured (Lovvorn et al. 1991; Lovvorn and Jones 1991a; Lovvorn 1994b).

Volumes and buoyancies of air spaces and tissues were calculated with data on the body composition of wild lesser scaup (Austin and Fredrickson 1987). We assumed that the body composition of a 638-g tufted duck (Table 1) is the same as for a 647-g scaup: 66.8% water, 20.8% protein, 5.7% lipid, and 4.5% ash. We assumed all protein was in muscle containing 74% water. We calculated the buoyancy of different body components based on an end-expiratory lung and air sac volume of 232 ml kg⁻¹ (Table 2) and buoyancy values of 9.79 N l⁻¹ for air, 0.729 N kg⁻¹ for lipid, −0.634 N kg⁻¹ for fresh muscle (Lovvorn and Jones 1991a), and −0.140 N kg⁻¹ for ashed bone (J. R. Lovvorn unpublished data). We then estimated the total buoyancy of a scaup weighing 638 g from an equation based on water displacement measurements (Lovvorn and Jones 1991a), and calculated the plumage air volume in addition to the above components required to yield the total buoyancy. This value for plumage air volume (203 ml) was 82% of the value estimated from the data of Dehner (see Lovvorn and Jones 1991a).

We assumed that lipid, ash, and plumage air volume were the same in untrained and dive-trained ducks, the only changes being in blood volume, muscle mass, and respiratory volume. In the dive-

trained ducks, blood volume increased by 36 ml (Table 1). The density of duck blood is 1.056 g ml$^{-1}$ (Sturkie 1976), so 38 g of the 102-g increase in body mass was blood; we assumed the remaining 64 g was muscle. Respiratory volume decreased to 165 ml kg$^{-1}$ (Table 2).

Based on these component values, we linearly interpolated the buoyancies of tissues and air spaces between the extremes for untrained and dive-trained tufted ducks. Adjusting the buoyancy of air spaces for hydrostatic compression, we then calculated the work of diving with the unsteady model described above for dive durations of 20 s to depths of 1–5 m, and of 35 s to depths of 1–10 m. We chose these dive durations based on a mean value of 20 s for wild tufted ducks diving to depths of 1–3 m (Nilsson 1972), and maxima of 30 s (no depth given, Suter 1982) and 34 s (5–6 m, Nilsson 1972) for deeper dives. We used the flight model described above to calculate the maximum range power (P$_{mr}$), which is the power required to fly at the speed that yields maximum distance flown per unit work.

Regarding trade-offs of adaptations for flight versus diving, birds should minimize the total costs over a daily period. Based on radiotelemetry, Suter (1982) found that wintering tufted ducks made up to 650 dives per 24 h, with mean dive duration of 16.9 s (maximum 30 s). These values yield a time spent underwater of 3.05 h per day. Takekawa (1987) reported that lesser scaup on a migration stopover area spent about 4.2 h d$^{-1}$ underwater, which is the value we used in our calculations. Time spent flying has not been quantified adequately in field studies of diving duck behavior; these studies have relied on stationary observers who have not followed birds that flew away from observation sites. The highest value of percent time flying we found was 2.7% for lesser scaup on breeding areas (Siegfried 1974). We used a value of 3%, or 0.7 h d$^{-1}$. These values for time spent diving and flying were multiplied by aerobic power estimates from the mechanical models to yield total daily work in diving and flying.

### BUOYANCIES, FLIGHT COSTS, AND DIVE PARAMETERS OF DIFFERENT SPECIES

We examined variations in flight costs relative to mass-specific buoyancies of different diving birds. Body mass, wing span, and wing area (see Pennycuick 1989b) were measured on common eiders (*Somateria mollissima*), white-winged scoters (*Melanitta fusca*), and common goldeneyes (*Bucephala clangula*) collected by shooting in the fall and winter in New Brunswick; on nonbreeding canvasbacks collected in North Carolina and Lake Erie (Lovvorn 1994a); and on redheads, lesser scaup,

ruddy ducks (*Oxyura jamaicensis*), hooded mergansers (*Lophodytes cucullatus*), and rhinoceros auklets (*Cerorhinca monocerata*) raised in captivity from eggs (ducks) or chicks (auklets) collected in the wild in Manitoba or British Columbia. We also measured eared grebes (*Podiceps auritus*) that died in a storm during fall migration through Utah, and red-throated loons (*Gavia stellata*) salvaged in winter from Monterey Bay, California. Buoyancies of live birds were determined by water displacement as reported by Lovvorn and Jones (1991b).

Frequencies and durations of dives to different depths were taken from Dewar (1924). His data were in fathoms (~2 m), so our table is in depth increments of 0–2 m (<1 fathom), 2–4 m (1–2 fathoms), 4–6 m (2–3 fathoms), and >6 m (>3 fathoms).

## Results

### STRATEGIES FOR REDUCING BUOYANCY

The data of Stephenson et al. (1989) suggest that important trade-offs are associated with buoyancy-reducing adaptations in diving birds. These workers subjected tufted ducks, which closely resemble lesser scaup, to two diving regimes. For 6 mo, an untrained group dived vertically for food in a tank with a maximum depth of 0.65 m, while a second dive-trained group was obliged to dive diagonally a mean distance of 6 m (maximum 10 m) to a minimum depth of 1.7 m. After this period, the calculated usable oxygen store was about the same in both groups (44 ml O$_2$ kg$^{-1}$ versus 42 ml O$_2$ kg$^{-1}$), but the relative amounts of usable oxygen in the three main storage sites—respiratory system, blood, and skeletal muscle—were different. Although hemoglobin content, hematocrit, and blood oxygen capacity (ml l$^{-1}$) were the same in both groups, mass-specific blood volume was 32% larger in the dive-trained ducks (Table 1). This difference increased the fraction of the body oxygen store contained in blood from 35.9% to 49.5%. The dive-trained group also had higher specific myoglobin content in both pectoralis (+57%) and various leg muscles (+38–54%) (Table 2), but this difference accounted for a change from only 3.4% to 5.5% of the body oxygen store. The dive-trained ducks decreased their end-expiratory lung and air sac volume by 29% (Table 2), which decreased the fraction of the oxygen store in the respiratory system from 60.7% to 45.0%.

Thus, tufted ducks adapted to greater diving activity by increasing blood volume and decreasing respiratory volume while maintaining total oxygen stores constant (Stephenson et al. 1989). This strategy reduces buoyancy and the amount of buoyancy change throughout dives. Note that some increase
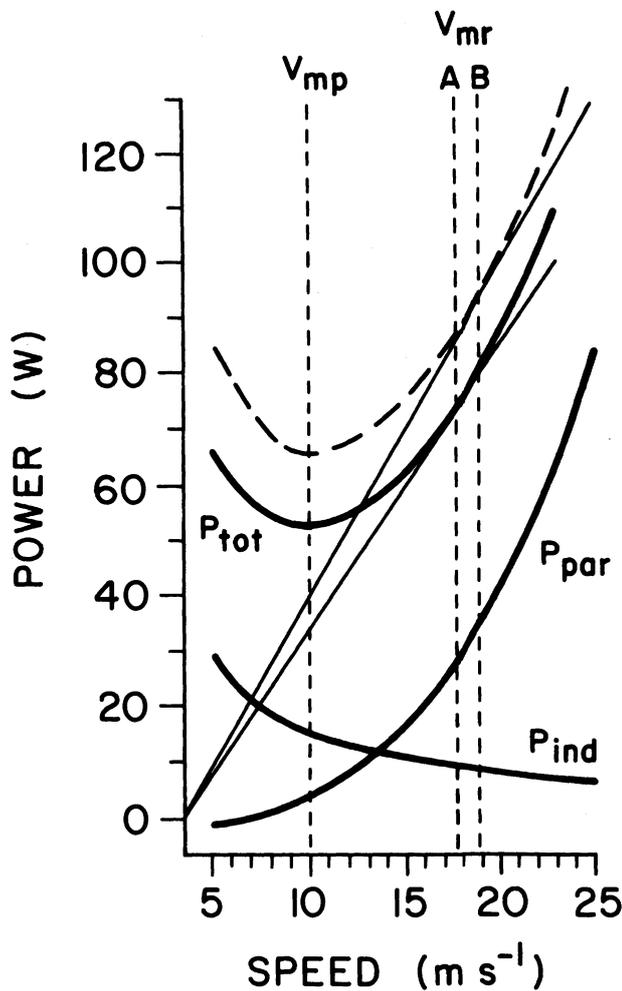
Fig. 1. Total power required for flight in dive-trained (dashed curve) and untrained (solid curve) tufted ducks, based on body masses in Table 2 and wing span of 0.82 m. Minimum power speed ($V_{mp}$) and maximum range speeds ($V_{mr}$, points of tangency of lines from the origin with the power curves) are indicated for (A) untrained and (B) dive-trained ducks. Curves of parasite power ($P_{par}$) and induced power ($P_{ind}$) for untrained ducks are shown; profile power ($P_{pro}$) is assumed constant with speed. Power values are aerobic (mechanical power output/aerobic efficiency of 0.23).

TABLE 3. Effects of buoyancy-reducing adaptations in dive-trained and untrained tufted ducks (see Tables 1 and 2) on optimum speeds and energy costs of fast, flapping flight (Fig. 1). Power values are aerobic (mechanical power output/aerobic efficiency of 0.23). $V_{mp}$ = minimum power speed. $P_{am}$ = absolute minimum power. $V_{mr}$ = maximum range speed. $P_{mr}$ = maximum range power. $CT_{mr}$ = cost of transport at $V_{mr}$.

| | $V_{mp}$ (m s$^{-1}$) | $P_{am}$ (W) | $V_{mr}$ (m s$^{-1}$) | $P_{mr}$ (W) | $CT_{mr}$ (J kg$^{-1}$ m$^{-1}$) |
|---|---|---|---|---|---|
| Untrained | 10 | 53.2 | 18 | 74.2 | 6.46 |
| Trained | 10 | 67.4 | 19 | 93.7 | 6.67 |
| Difference (%) | 0 | +26.5 | +5.6 | +26.3 | +3.2 |

owing to the higher exercise level and larger mass to be transported. The overall increase in body mass substantially raised the power requirements of flight (Fig. 1, Table 3). The speed of minimum power ($V_{mp}$) was the same for both groups, but power at that speed was 26.5% higher in trained ducks. The speed at which maximum distance is traveled per unit work ($V_{mr}$) increased by 5.6%, and the maximum range power was over 26% higher. Cost of transport (J kg$^{-1}$ m$^{-1}$) was only 3% higher in the trained ducks because of their larger body mass.

## EFFECTS OF ANTI-BUOYANCY MECHANISMS ON COSTS OF DIVING

Effects of increased blood and muscle volume and decreased respiratory volume varied with dive depth (Table 4). Accounting for hydrostatic compression of air spaces, buoyancy at the terminal depth was 10.3% to 11.4% lower in trained ducks. For a constant dive duration of 20 s, lower buoyancy and greater inertial resistance to the buoyant force by the larger body mass decreased the power requirements of level foraging at a given depth ($P_b$) by about 30%. However, the greater inertia also increased the work of accelerating the body with each stroke during descent, thereby raising power costs of descent ($P_d$) by 4% to 5%. These opposing trends in effects of buoyancy-reducing mechanisms on descent versus level foraging resulted in varied patterns of total cost with depth (Table 4, Fig. 2). For a constant dive duration of 20 s, the fraction of the dive spent descending versus level foraging increases with dive depth. At depths of 1–3 m, time spent level foraging at the bottom is relatively large, so that buoyancy reduction and increased inertia substantially reduce the total cost of dives. However, at deeper depths, the larger fraction of dives spent descending and ascending makes these anti-buoyancy mechanisms ineffective in reducing total dive costs, and such adaptations actually increase total costs at depths ≥5 m. Thus, inertial effects associated with buoy-

in blood volume is an expected result of exercise training, and is not necessarily an adaptation specifically to reduce buoyancy. However, the outcome is the same. These adaptations did not develop in untrained ducks, which suggests there are disadvantages to high blood volume and/or low respiratory volume that prevent these changes in ducks with lower diving activity.

## EFFECTS OF ANTI-BUOYANCY MECHANISMS ON COSTS OF FLIGHT

Greater blood volume in dive-trained tufted ducks was accompanied by increased muscle mass

TABLE 4. Effects of buoyancy-reducing adaptations in dive-trained and untrained tufted ducks (see Tables 1 and 2) on energy costs of diving to different depths for a dive duration of 20 s. Power values are aerobic (mechanical power output/aerobic efficiency of 0.17). Buoyancy at the water surface is 3.14 N for untrained ducks and 2.83 N for dive-trained ducks. $B_b$ = buoyancy at the bottom. $P_d$ = power during descent. $P_b$ = power at the bottom. $P_{net}$ = net power for a 20-s dive including descent, bottom foraging, and passive ascent.

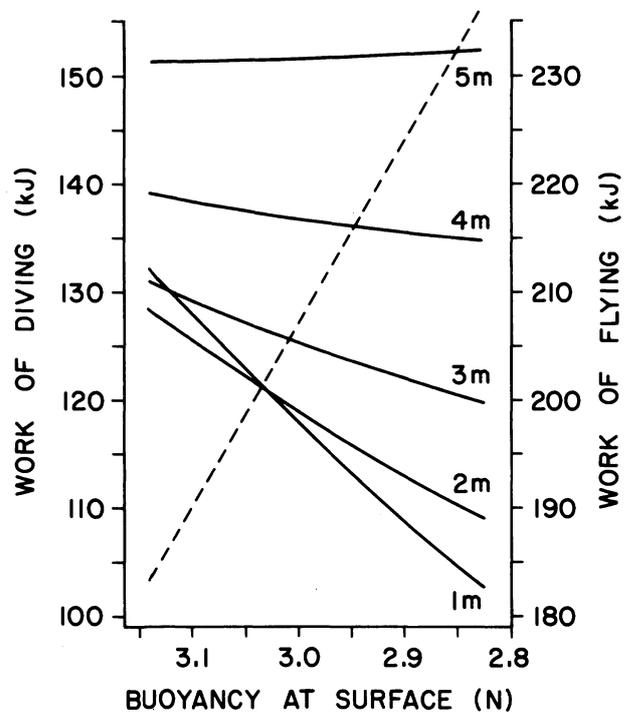| Depth (m) | Group | $B_b$ (N) | $P_d$ (N) | $P_b$ (W) | $P_{net}$ (W) |
|---|---|---|---|---|---|
| 1 | Untrained | 2.83 | 22.62 | 7.97 | 8.75 |
|  | Trained | 2.54 | 23.58 | 5.62 | 6.79 |
|  | Difference (%) | −10.3 | +4.3 | −29.5 | −22.4 |
| 2 | Untrained | 2.58 | 21.33 | 6.83 | 8.50 |
|  | Trained | 2.31 | 22.29 | 4.78 | 7.21 |
|  | Difference (%) | −10.6 | +4.5 | −30.0 | −15.2 |
| 3 | Untrained | 2.36 | 20.99 | 5.75 | 8.66 |
|  | Trained | 2.10 | 21.98 | 4.00 | 7.93 |
|  | Difference (%) | −10.8 | +4.7 | −30.5 | −8.5 |
| 4 | Untrained | 2.17 | 20.70 | 4.90 | 9.20 |
|  | Trained | 1.93 | 21.71 | 3.38 | 8.90 |
|  | Difference (%) | −11.1 | +4.9 | −31.0 | −3.3 |
| 5 | Untrained | 2.01 | 20.44 | 4.21 | 10.01 |
|  | Trained | 1.78 | 21.48 | 2.88 | 10.07 |
|  | Difference (%) | −11.4 | +5.1 | −31.6 | +0.1 |



Fig. 2. Total daily work of diving (solid lines) and flying at maximum range speed (dashed line) for tufted ducks with a gradient of buoyancies from untrained to dive-trained. Dive cost curves for each depth assume all dives in a day are to that depth for a dive duration of 20 s. Daily totals are based on 0.7 h flying and 4.2 h underwater per day. Work values are aerobic.

ancy-reducing mechanisms must be considered in evaluating the net results of such adaptations.

### TRADE-OFFS OF DIVING VERSUS FLYING

In addition to trade-offs between buoyancy and inertia during dives, there are important conflicts between flight costs and diving costs on a daily basis (Fig. 2). The power curve for flight is essentially linear over this interval of maximum range speeds (see Fig. 1). The two ordinates in Fig. 2 are offset but on the same scale, so that the amount of change in costs of flight versus diving with changes in buoyancy can be directly evaluated by comparing slopes. At depths of 1 m and 2 m, decreases in dive costs with lower buoyancy and larger body mass almost offset concomitant increases in flight costs. At these shallow depths, the ducks could probably mediate these opposing trends by increasing their daily diving time relative to time spent flying, or by increasing dive duration (time spent level foraging versus descending). However, at depths >2 m the flight cost curve is much steeper than the curves for diving, so that greater relative increases in flight costs make anti-buoyancy adaptations counterproductive in terms of total cost. For diving alone, increased blood and muscle volume and decreased respiratory volume in dive-

trained tufted ducks significantly reduce costs only at depths <4 m. For total cost including flight, such changes would be quite disadvantageous if average dive depth exceeded 2 m (Fig. 2). These considerations suggest why untrained tufted ducks would not maintain these buoyancy-reducing adaptations, especially considering the metabolic expense of maintaining the extra blood and muscle.

To extend these relations to longer and deeper dives, Fig. 3 shows daily costs of 35-s dives to depths up to 10 m for the gradient of mass-specific buoyancies from untrained to dive-trained tufted ducks. The greater bottom time for these longer dives (35 s versus 20 s in Table 4 and Fig. 2) makes effects of buoyancy reduction especially dramatic at shallow depths. However, even disregarding flight costs, these adaptations are beneficial only to depths of 5–6 m and become increasingly disadvantageous at greater depths.

### BUOYANCIES, FLIGHT COSTS, AND DIVING BEHAVIOR AMONG SPECIES

Mass-specific buoyancies of a variety of diving birds (Table 5) indicate that most benthivores have intermediate buoyancies relative to the range in tufted ducks (about 3.8–4.9 N kg$^{-1}$, Fig. 3). Excep-

TABLE 5. Buoyancy, morphology, and flight characteristics of diving birds. Flight variables are defined in Table 3. Specific buoyancies are from Lovvorn and Jones (1991b).

| Species | Body Mass (kg) | Specific Buoyancy (N kg$^{-1}$) | Wing Span (m) | Wing Loading (Pa) | $V_{mr}$ (m s$^{-1}$) | $P_{mr}$ (W) | $CT_{mr}$ (J kg$^{-1}$ m$^{-1}$) |
|---|---|---|---|---|---|---|---|
| **Foot-propelled benthivores** | | | | | | | |
| Oxyura jamaicensis | 0.468 | 3.57 | 0.58 | 97 | 18.8 | 71 | 8.30 |
| Aythya affinis | 0.617[a] | 4.41 | 0.72 | 91 | 18.0 | 80 | 7.18 |
| Aythya americana | 0.924[a] | 4.11 | 0.83 | 104 | 19.7 | 125 | 6.86 |
| Bucephala clangula | 1.024 | 4.25 | 0.79 | 136 | 21.0 | 158 | 7.35 |
| Aythya valisineria | 1.227 | 4.32 | 0.85 | 130 | 22.0 | 193 | 7.15 |
| Melanitta fusca | 1.519 | 5.29 | 0.95 | 144 | 22.8 | 234 | 6.74 |
| Somateria mollissima | 1.858 | 5.62 | 0.99 | 143 | 24.0 | 301 | 6.75 |
| **Foot-propelled pursuers** | | | | | | | |
| Podiceps auritus | 0.369 | | 0.56 | 101 | 17.4 | 52 | 8.17 |
| Lophodytes cucullatus | 0.582 | 2.92 | 0.66 | 98 | 18.7 | 84 | 7.72 |
| Gavia stellata | 1.248 | | 1.04 | 112 | 20.3 | 150 | 5.94 |
| Phalacrocorax auritus | 1.41[b] | 2.70 | 1.16[b] | 77[b] | 19.6 | 151 | 5.46 |
| **Wing-propelled pursuers** | | | | | | | |
| Cerorhinca monocerata | 0.430 | 4.71 | 0.60 | 100 | 18.9 | 65 | 8.06 |

[a] Mass of individuals that were measured for buoyancy; other masses are for individuals measured for wing parameters.
[b] Pennycuick (1990).

tional are large-bodied white-winged scoters (*Melanitta fusca*) and common eiders (*Somateria mollissima*), which have much higher buoyancies than predicted from the curve for other ducks (see Lovvorn and Jones 1991b). The foot-propelled pursuers, hooded mergansers (*Lophodytes cucullatus*) and double-crested cormorants (*Phalacrocorax auritus*), have very low buoyancies. Rhinoceros auklets (*Cerorhinca monocerata*), which use their wings for both aerial and underwater flight, have specific buoyancies higher than those of diving ducks of small to medium size (Table 5). Unexpectedly, the wing loadings, maximum range speeds ($V_{mr}$), and maximum range powers ($P_{mr}$) of foot-propelled pursuers were similar to or lower than those of foot-propelled benthivores with comparable mass but about twice their buoyancy (Table 5). This pattern suggests that the foot-propelled pursuers we studied decrease their buoyancy near the surface not by increasing blood volume and thus body mass, but by reducing their respiratory and/or plumage air volume.

According to Dewar (1924), benthivorous ducks generally restricted their dives to depths less than 4 m, and some species seldom dove deeper than 2 m (Table 6). White-winged scoters (*M. fusca*) were a notable exception. Foot-propelled pursuers dove more frequently to depths >4 m than did benthivores, although only the great cormorant (*Phalacrocorax carbo*) and common loon (*Gavia immer*) often dove to more than 6 m. Overall, the duration of dives to depths <4 m and >6 m was slightly greater in pursuers than in benthivores (Table 6).

## Discussion

Experiments suggest that birds adapt to shallow diving by increasing blood volume and thus blood oxygen stores while decreasing respiratory volume. These adaptations have important consequences for costs of flight and inertial effects during descent versus level foraging. Increased inertia from greater mass of blood and associated muscle lowers the costs of level foraging by resisting the upward buoyant force, but raises costs of descent because of higher inertial work in accelerating the body with each stroke. Thus, dive depth (hydrostatic compression of buoyant air spaces), stroke kinematics (inertial effects), and the relative time spent descending versus level foraging will determine the appropriate balance between buoyancy and inertia for diving. These elements of dive costs must also be balanced against flight costs over daily activity cycles in optimizing allocation of oxygen stores to blood versus the respiratory system.

### OXYGEN STORAGE PATTERNS IN DIFFERENT SPECIES

Despite definitive experimental results for tufted ducks, descriptive data on blood oxygen storage among species with different diving habits are not clearcut. Varying techniques in different studies confound detailed comparisons, but no clear trends are evident in hematocrit, hemoglobin, or blood oxygen concentration (ml O$_2$ l$^{-1}$) among a variety of diving birds including loons, cormorants, diving ducks, alcids, and penguins with a range of body mass (Table 1). Exceptional are the data for a single (n = 1) red-throated loon (*Gavia stellata*)
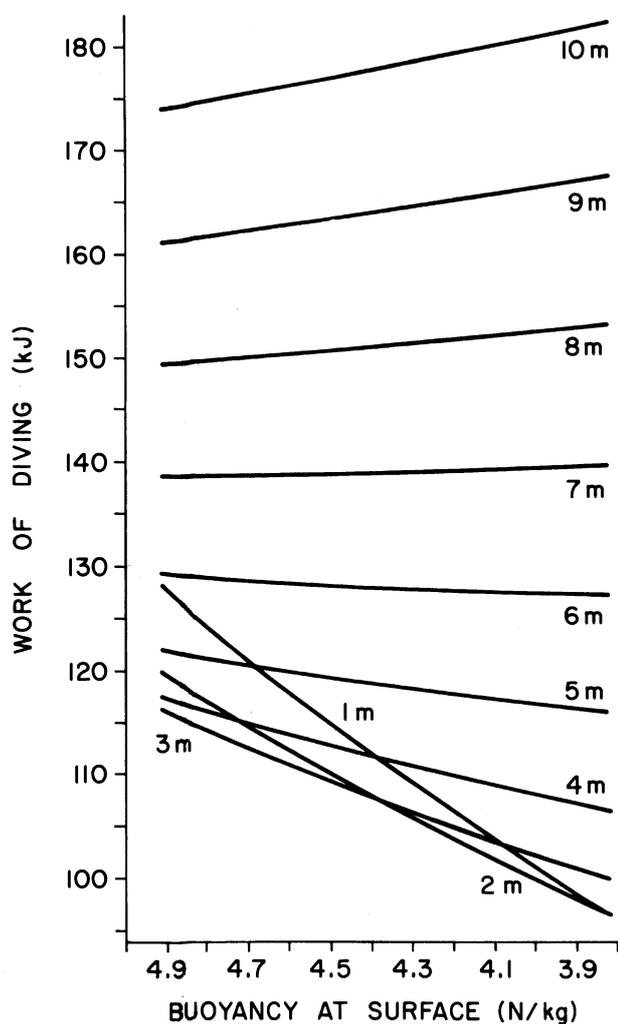
Fig. 3. Total daily work of diving for tufted ducks with a gradient of mass-specific buoyancies from untrained to dive-trained. Curves for each depth assume that all dives in a day are to that depth for a dive duration of 35 s (versus 20 s in Fig. 2 and Table 4). Daily totals are based on 0.7 h flying and 4.2 h underwater per day. Work values are aerobic.

with appreciably higher hematocrit, hemoglobin, and blood oxygen concentration. This loon's specific blood volume was higher than that of untrained diving ducks but less than that of dive-trained tufted ducks. The blood volume of wild penguins with much higher body mass is relatively quite low. In reviewing these data, one must keep in mind the dependence of mass-specific blood volume and blood oxygen capacity on body condition (fatness, muscle hypertrophy), which can vary seasonally and between captive and wild birds.

Data on respiratory volume are available only for dive-trained and untrained tufted ducks and for penguins of different sizes (Table 2). Adélie and gentoo penguins (*Pygoscelis adeliae* and *P. papua*)

have small respiratory volumes similar to those of dive-trained tufted ducks. Although these *Pygoscelis* spp. often dive to depths at which air volumes have negligible effects on buoyancy, they spend a large fraction of their time traveling or diving at depths <5 m (Croxall et al. 1988; Wilson et al. 1991) where air volumes affect dive costs. Their respiratory volumes are also not influenced by considerations of aerial flight. Both little penguins (*Eudyptula minor*) and the *Pygoscelis* spp. have very high pectoralis myoglobin, perhaps in inverse proportion to blood volume (cf., Tables 1 and 2). The myoglobin of Atlantic puffins (*Fratercula arctica*) and common and thick-billed murres (*Uria aalge* and *U. lomvia*) is higher than in ducks but much lower than in penguins.

In summary, specific blood oxygen capacity in diving birds appears to depend mostly on specific blood volume. Blood volume is higher in a shallow pursuit diver (the loon) than in "pelagic" divers, but the loon's value is exceeded by that of a shallow benthivore with high diving activity (dive-trained tufted ducks). The other "inshore" pursuit diver considered, the great cormorant (*Phalacrocorax carbo*), dives rather deeply in some areas (5–20 m, mean 11 m, Ross 1974–76) and may utilize feather-wetting to reduce buoyancy (Rijke et al. 1989). Mass-specific blood volume is relatively low in deep-diving, flightless penguins. Respiratory volume is low in penguins and dive-trained ducks, but data for other species are lacking. Based on existing data and considering the potential for acclimation shown by tufted ducks, it is difficult to relate the diving habits of different species to their oxygen storage strategy.

## CONSEQUENCES OF OXYGEN STORAGE STRATEGY

Increased blood volume and decreased respiratory volume either raise or lower the power and total daily work of diving depending on dive depth (Table 4; Figs. 2 and 3). However, the cost per kilogram of muscle decreases with higher body mass at all depths. This pattern results from increased muscle mass that accompanies the increase in blood volume, owing to the higher exercise level and greater mass to be transported in the trained ducks. However, this lower cost per unit mass will be advantageous only if it enables an increase in absolute food intake to meet the greater absolute cost of higher mass. In this analysis, we are concerned with changes in absolute cost for animals that are already achieving their maximum intake rate at a given food density while level foraging.

In this context, and based on particular time-activity budgets, the models make the following predictions for tufted ducks that shift their alloca-

TABLE 6.  Percentages and mean durations of dives to different depths by foot-propelled diving birds (from Dewar 1924).

| | Percent of Dives | | | | Mean Dive Duration (s) | | | |
|---|---|---|---|---|---|---|---|---|
| | 0–2 m | 2–4 m | 4–6 m | >6 m | 0–2 m | 2–4 m | 4–6 m | >6 m |
| Benthivores | | | | | | | | |
| *Aythya ferina* | 99 | 1 | 0 | 0 | 17.0 | | | |
| *Aythya fuligula* | 94 | 6 | 0 | 0 | 16.1 | 27.0 | 37.3 | |
| *Aythya marila* | 38 | 48 | 13 | 1 | 12.7 | 24.2 | 39.9 | 44.5 |
| *Bucephala clangula* | 13 | 82 | 5 | 0 | 15.1 | 28.3 | 31.4 | |
| *Melanitta fusca* | 15 | 36 | 42 | 7 | 20.0 | 27.3 | 36.6 | 45.6 |
| *Melanitta nigra* | 11 | 81 | 6 | 2 | 18.6 | 25.9 | 33.4 | 45.7 |
| *Somateria mollissima* | 44 | 51 | 5 | 0 | 15.9 | 25.7 | 34.3 | |
| Mean | 44.9 | 43.6 | 10.1 | 1.4 | 16.5 | 26.4 | 35.5 | 45.3 |
| Pursuers | | | | | | | | |
| *Mergus merganser* | 10 | 81 | 9 | 0 | 20.4 | 27.2 | 33.1 | |
| *Mergus serrator* | 10 | 58 | 32 | 0 | 15.7 | 27.7 | 34.2 | |
| *Phalacrocorax carbo* | 4 | 55 | 19 | 22 | 16.5 | 26.3 | 35.0 | 49.4 |
| *Phalacrocorax aristotelis* | 29 | 34 | 35 | 2 | 18.8 | 27.1 | 34.9 | 43.2 |
| *Podiceps cristatus* | 29 | 48 | 20 | 3 | 22.1 | 26.6 | 33.3 | 45.6 |
| *Podiceps auritus* | 71 | 29 | 0 | 0 | 14.9 | 25.2 | | |
| *Gavia immer* | 0 | 8 | 46 | 46 | | 28.2 | 35.5 | 51.8 |
| *Gavia stellata* | 16 | 54 | 24 | 6 | 18.2 | 27.6 | 35.2 | 53.0 |
| Mean | 21.1 | 45.9 | 23.1 | 9.9 | 18.1 | 27.0 | 34.5 | 48.6 |

tion of oxygen storage from the respiratory system to blood.

1a. High body density is probably beneficial only at dive depths up to 2 m. Costs of diving deeper than 5 m increase with increasing body density, owing to higher descent costs caused by greater inertial work in unsteady stroking (Fig. 2). For diving only, high body density lowers energy costs at depths shallower than 5 m; however, these benefits are inadequate to offset the rapid increase in flight costs if mean dive depth exceeds 2 m.

1b. At depths <4 m, birds with high density should extend their time at the terminal depth to maximize the benefits of low buoyancy and greater inertia while level foraging, versus the costs of higher inertia during descent. For the same reason, all birds should increase dive duration with increasing depth.

1c. The ratio of time spent diving to time spent flying should be greater than in diving ducks without these buoyancy-reducing adaptations.

Therefore, in foot-propelled divers with unsteady stroking, adverse inertial effects mean that higher blood mass in ducks is probably not an adaptation to deep diving, but rather to shallow diving (<5 m) or to dives with extended time at the terminal depth.

Conversely, for ducks with low blood volume relative to respiratory and plumage air volume, the models predict the following patterns.

2a. Dive depths should be >3 m, because at shallower depths these birds would be missing substantial advantages of increasing body mass and density.

2b. The ratio of time spent diving to time spent flying should be less than in diving ducks with higher density.

## DIVING PATTERNS IN DIFFERENT SPECIES

The above predictions are based on tufted ducks, whose locomotor patterns differ to varying degrees from those of other foot-propelled divers (Lovvorn 1991). Moreover, Dewar's (1924) data for dive durations at different depths (Table 6) are, like all such data, strongly influenced by observation site and conditions. Nevertheless, broad comparisons may reveal general trends.

Among benthivores, tufted ducks (*Aythya fuligula*) and common pochards (*A. ferina*) made mostly short dives to <2 m (Table 6). At these depths they could substantially decrease their dive costs by increasing their mass and density (Fig. 2), so it appears that flight costs may prevent these species from doing so. As expected, body density is not higher in benthivores that dive frequently to depths >2 m (cf., Tables 5 and 6). The benthivore diving most often to depths over 4 m, the white-winged scoter (*Melanitta fusca*), conformed to prediction 2a by having relatively high buoyancy at the surface, but the shallow diving depths of common eiders (*Somateria mollissima*) were counter to prediction. In some areas common eiders dive much deeper than these data indicate (Dewar 1924), but in other areas their major foods do not occur below 5 m (Bustnes and Erikstad 1988). Both these species are probably capable of the same adaptations of respiratory and blood volumes exhibited by tufted ducks, and the thermoregulatory advantages of thicker plumage air layers should also be considered (Wilson et al. 1992). Despite their high

buoyancies, it is unlikely that white-winged scoters and common eiders spend more time flying than the other diving ducks, but they might spend more time diving (prediction 2b).

Comparisons of benthivores versus pursuers are partly inconsistent with prediction 1a. Foot-propelled pursuers, with generally higher densities than benthivores (Table 5), dived less frequently to depths <2 m and more frequently to depths >4 m than did most benthivores (Table 6). However, pursuers rarely dived to over 6 m where dive costs are increased by higher mass-specific density (Fig. 3), with the notable exception of large-bodied great cormorants (*Phalacrocorax carbo*) and common loons (*Gavia immer*). The latter pattern may correspond to the fact that, although inertial effects increase with increasing body mass for the same structural size, acceleration during strokes decreases with increasing structural size (see Lovvorn et al. 1991).

In general, our field observations suggest that benthivores fly more than pursuers, and mergansers and cormorants fly more than loons and grebes (predictions 1c and 2b). These patterns correspond to measured buoyancies but not to flight costs, which are lower at comparable body masses in pursuers (Table 5). This inconsistency suggests that the relative narrowness of loon and grebe wings may be more important than wing loading in the seemingly greater difficulty they exhibit in taking off. Cormorants (and anhingas) may use feather-wetting as a facultative means of reducing buoyancy for diving without a sustained increase in wing loading (Rijke et al. 1989). The rather high specific buoyancy of rhinoceros auklets probably reflects their relatively deep dives (mostly 8–30 m with a maximum around 65 m, Burger 1991) and the fact that their wing loading is already high due to wing reduction for underwater propulsion (Table 5).

As expected (prediction 1b) birds with high density extended their dive durations (relative time spent level foraging versus descending) compared to birds with lower density (cf., Tables 5 and 6). Also as predicted, all species increased dive duration with increasing depth. The models suggest that the reason for this widely recognized pattern is the need to increase the benefits of inertia and low buoyancy at the terminal depth relative to the costs of inertia during descent.

## LIMITATIONS OF THE MODELS AND AVAILABLE DATA

If plots such as Figs. 2 and 3 were developed for species other than ducks, could they be used to test whether various species are adapted for diving to different depths, and to what extent flight costs

constrain buoyancy adapatations among species? Such analyses will require quantification of the stroke kinematics of each species; the total buoyancy and air volumes, or else the body composition and total volume, of each species; and the total time spent diving and flying over 24-h periods. At present, these data are available only for a few species of diving ducks, and even for them the time spent flying is poorly documented. In particular, the great importance of inertial effects to costs of diving prevents definitive conclusions until the kinematics of swimming strokes is quantified for different locomotor modes.

A more difficult issue is the use of flight models to compare different species. The actuator disk-momentum jet theory used here is very sensitive to variations in body mass for a given wing span. However, large seasonal changes in body mass and composition confound identification of a representative mass for a species. Definitive comparisons among species require that values of body mass used are appropriate for the particular question addressed. Moreover, Pennycuick's models use body mass and wing span as primary input variables, and do not account for changes in wing shape or wingbeat frequency. These shortcomings inhibit detailed interspecific comparisons (e.g., between cormorants with wide wings and slow wingbeats relative to loons). That cormorants fly at speeds substantially below their predicted maximum range speed (Pennycuick 1987, 1989a) emphasizes the problems of comparing species with different morphologies and flight kinematics.

Finally, analyses in this paper concern birds diving to depths at which they remain positively buoyant. Below such depths the birds must work to ascend (about 43 m for birds similar to lesser scaup in ratio of tissue to air volume, Lovvorn and Jones 1991a). Because work against negative buoyancy during ascent would offset savings in work against buoyancy during descent (Hustler 1992), birds that become negatively buoyant during dives (including a number of alcids) should manipulate their buoyancy according to their most common dive depths.

## BUOYANCY, FLIGHT SPEED, AND THE EVOLUTION OF HIGH WING LOADING

Lowering buoyancy by increasing blood volume relative to respiratory volume will increase wing loading if wing area does not also increase. For a given wing span, maximum range speed increases with increasing body mass (Fig. 1). This pattern has led some workers to suggest that high flight speeds in many foot-propelled divers are a consequence of high wing-loading (e.g., Storer 1958), implying that high wing-loading in itself is an adaptation to diving. However, cormorants have

wings with relatively large areas (Table 5), but nevertheless have no higher hydrodynamic drag with their wings folded than many diving ducks (Lovvorn and Jones research in progress). Therefore, the evolution of pointed, low-area wings in loons, grebes, and diving ducks, with consequent high wing-loading, is probably not directly related to diving per se. Such wings in many foot-propelled divers are more likely an adaptation to high flight-speed.

As flight speed approaches and exceeds the maximum range speed for a given body mass and wing span, induced power required to overcome gravity is decreased by the added lift afforded by moving at higher speed (Fig. 1). However, parasite power owing to aerodynamic drag increases much faster than the decrease in induced power (Fig. 1). This unequal change in parasite power versus induced power means that higher speeds must be achieved by flapping faster. However, the tolerance of bones, muscles, and connective tissues to instantaneous inertial forces while the wings are accelerated and decelerated with each stroke places constraints on wing mass and the distribution of mass along the wing (i.e., distal to proximal). Because of these inertial considerations, high wingbeat frequencies require reduced wing mass and more pointed (distally reduced) wings. High wing-loading is thus a consequence of wing modifications for high flight-speed.

But why would loons, grebes, and diving ducks need to fly faster than other birds with lower wing-loading? Rayner (1988) attempted to explain this pattern in terms of the greater need for rapid movements between specialized habitats, particularly during migration. Certainly loons and grebes are incapable of taking off from land, and are entirely restricted to aquatic habitats. However, it is unclear that the benefits of rapid flight are any greater for divers than for many other species—rapid flight is generally advantageous unless other factors prevent its development. We suggest that most foot-propelled divers have evolved high-speed wings not because speed is more important to them, but rather because other constraints on the evolution of high-speed wings and high wing-loading have been relaxed in open aquatic environments.

Development of low-area, pointed wings for fast flight reduces the ability of the wings to generate lift at low speeds. The highly modified wings of loons, grebes, and some diving ducks in fact will not function at low speeds; these birds must run along the surface of the water or take off into a headwind to achieve minimum air speeds at which their wings can provide sufficient lift. Similarly, when these species slow down to land, their wings

stall easily, with loss of lift as well as maneuverability. Hard landings at rather high speeds are certainly more acceptable when landing on water than on a solid substrate. Such wings would be ill-suited for birds that must land on and take off from perches or solid substrates, or that must slow down to maneuver through structurally complex habitats. Accordingly, cormorants, which commonly perch and nest in trees, have wider wings relative to wing length than other diving birds; and cavity-nesting hooded mergansers have lower wing-loading than loons, grebes, or eiders (Table 5).

Moreover, the open aquatic habitats of most divers prevent close approach by undetected predators, thereby reducing the need for rapid, vertical takeoffs to escape (see Lovvorn 1989). The added option of escape by diving if a bird is surprised at close quarters by a predator further reduces the need for wings that provide high lift and maneuverability at low speeds. Thus, high wing-loading in foot-propelled divers does not appear to be an adaptation either to diving or to unusual need for high speed, but rather results from relaxation of forces selecting against high-speed wings. Despite increased power requirements due to high wing-loading (Fig. 1), the high body mass keeps the cost of transport at a reasonable level (Table 5) while the ecological benefits of high speed are retained.

### SHALLOW DIVING, PHYSIOLOGY, AND THE ESTUARINE ENVIRONMENT

From the standpoint of locomotor costs, optimal allocation of oxygen stores to blood versus the respiratory system will depend on dive depth (compression of buoyant air spaces), stroke kinematics (inertial effects of blood and muscle mass), time spent descending versus level foraging, and time spent diving versus flying. Data on these aspects are needed for testing whether various species are adapted for diving to different depths, and to what extent flight costs constrain buoyancy modifications among species. Our models suggest that physiological adaptations to shallow diving may be inappropriate for deeper diving, especially if flight costs are considered. These adaptations to shallow diving may broadly characterize birds frequenting estuaries as opposed to more pelagic environments.

### LITERATURE CITED

AUSTIN, J. E. AND L. H. FREDRICKSON. 1987. Body and organ mass and body composition of postbreeding female lesser scaup. *Auk* 104:694–699.
BALASCH, J., J. PALOMEQUE, L. PALACIOS, S. MUSQUERA, AND M.

JIMENEZ. 1974. Hematological values of some great flying and aquatic-diving birds. *Comparative Biochemistry and Physiology* 49A:137–145.

BLAKE, R. W. 1985. A model of foraging efficiency and daily energy budget in the black skimmer (*Rynchops nigra*). *Canadian Journal of Zoology* 63:42–48.

BOND, C. F. AND P. W. GILBERT. 1958. Comparative study of blood volume in representative aquatic and nonaquatic birds. *American Journal of Physiology* 194:519–521.

BURGER, A. E. 1991. Maximum diving depths and underwater foraging in alcids and penguins, p. 9–15. *In* W. A. Montevecchi and A. J. Gaston (eds.), Studies of High-Latitude Seabirds. 1. Behavioural, Energetic, and Oceanographic Aspects of Seabird Feeding Ecology. Canadian Wildlife Service Occasional Paper 68. Ottawa, Canada.

BURGER, A. E. AND D. W. POWELL. 1990. Diving depths and diet of Cassin's auklet at Reef Island, British Columbia. *Canadian Journal of Zoology* 68:1572–1577.

BUSTNES, J. O. AND K. E. ERIKSTAD. 1988. The diets of sympatric wintering populations of common eider *Somateria mollissima* and king eider *S. spectabilis* in northern Norway. *Ornis Fennica* 65:163–168.

CARTER, H. R. AND S. G. SEALY. 1984. Marbled murrelet mortality due to gill-net fishing in Barkley Sound, British Columbia, p. 212–220. *In* D. N. Nettleship, G. A. Sanger, and P. F. Springer (eds.), Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships. Special Publication, Canadian Wildlife Service, Ottawa.

COOPER, J. 1986. Diving patterns of cormorants Phalacrocoracidae. *Ibis* 138:562–570.

CROLL, D. A., A. J. GASTON, A. E. BURGER, AND D. KONNOFF. 1992. Foraging behavior and physiological adapatation for diving in thick-billed murres. *Ecology* 73:344–356.

CROXALL, J. P., R. W. DAVIS, AND M. J. O'CONNELL. 1988. Diving patterns in relation to diet of gentoo and macaroni penguins at South Georgia. *Condor* 90:157–167.

CROXALL, J. P., Y. NAITO, A. KATO, P. ROTHERY, AND D. R. BRIGGS. 1991. Diving patterns and performance in the Antarctic blue-eyed shag *Phalacrocorax atriceps*. *Journal of Zoology, London* 225:177–199.

DAUB, B. C. 1989. Behavior of common loons in winter. *Journal of Field Ornithology* 60:305–311.

DAVIS, M. B. AND H. GUDERLEY. 1987. Energy metabolism in the locomotor muscles of the common murre (*Uria aalge*) and the Atlantic puffin (*Fratercula arctica*). *Auk* 104:733–739.

DEWAR, J. M. 1924. The Bird as a Diver. H. F. and G. Witherby, London. 173 p.

FORBES, L. S. AND S. G. SEALY. 1988. Diving behaviour of male and female western grebes. *Canadian Journal of Zoology* 66:2695–2698.

HUSTLER, K. 1992. Buoyancy and its constraints on the underwater foraging behaviour of reed cormorants *Phalacrocorax africanus* and darters *Anhinga melanogaster*. *Ibis* 134:229–236.

KEIJER, E. AND P. J. BUTLER. 1982. Volumes of the respiratory and circulatory systems in tufted and mallard ducks. *Journal of Experimental Biology* 101:213–220.

KOOYMAN, G. L., J. P. SCHROEDER, D. G. GREENE, AND V. A. SMITH. 1973. Gas exchange in penguins during simulated dives to 30 and 68 m. *American Journal of Physiology* 225:1467–1471.

LASIEWSKI, R. C. AND W. R. DAWSON. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69:13–23.

LENFANT, C., G. L. KOOYMAN, R. ELSNER, AND C. M. DRABECK. 1969. Respiratory function of the blood of the Adélie penguin *Pygoscelis adeliae*. *American Journal of Physiology* 216:1598–1600.

LOVVORN, J. R. 1989. Food defendability and antipredator tac-

tics: Implications for dominance and pairing in canvasbacks. *Condor* 91:826–836.

LOVVORN, J. R. 1991. Mechanics of underwater swimming in foot-propelled diving birds. *Proceedings of the International Ornithological Congress* 20:1868–1874.

LOVVORN, J. R. 1994a. Nutrient reserves, probability of cold spells and the question of reserve regulation in wintering canvasbacks. *Journal of Animal Ecology* 63:11–23.

LOVVORN, J. R. 1994b. Biomechanics and foraging profitability: An approach to assessing trophic needs and impacts of diving ducks. *Hydrobiologia* 278/280:223–233.

LOVVORN, J. R. AND D. R. JONES. 1991a. Effects of body size, body fat, and change in pressure with depth on buoyancy and costs of diving in ducks (*Aythya* spp.). *Canadian Journal of Zoology* 69:2879–2887.

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

LOVVORN, J. R., D. R. JONES, AND R. W. BLAKE. 1991. Mechanics of underwater locomotion in diving ducks: Drag, buoyancy and acceleration in a size gradient of species. *Journal of Experimental Biology* 159:89–108.

MCINTYRE, J. W. 1978. Wintering behavior of common loons. *Auk* 95:396–403.

MILL, G. K. AND J. BALDWIN. 1983. Biochemical correlates of swimming and diving behavior in the little penguin *Eudyptula minor*. *Physiological Zoology* 56:242–254.

MILSOM, W. K., K. JOHANSEN, AND R. W. MILLARD. 1973. Blood respiratory properties in some Antarctic birds. *Condor* 75:472–474.

NILSSON, L. 1972. Habitat selection, food choice, and feeding habits of diving ducks in coastal waters of south Sweden during the non-breeding season. *Ornis Scandinavica* 3:55–78.

PALMER, R. S. 1975. Handbook of North American Birds, Vol. 3. Yale University Press, New Haven, Connecticut.

PENNYCUICK, C. J. 1975. Mechanics of flight, p. 1–75. *In* D. S. Farner and J. R. King (eds.), Avian Biology, Vol. 5. Academic Press, New York.

PENNYCUICK, C. J. 1987. Flight of auks (Alcidae) and other northern seabirds compared with southern Procellariiformes: Ornithodolite observations. *Journal of Experimental Biology* 128:335–347.

PENNYCUICK, C. J. 1989a. Span-ratio analysis used to estimate effective lift : drag ratio in the double-crested cormorant *Phalacrocorax auritus* from field observations. *Journal of Experimental Biology* 142:1–15.

PENNYCUICK, C. J. 1989b. Bird Flight Performance. Oxford University Press, Oxford.

PENNYCUICK, C. J. 1990. Predicting wingbeat frequency and wavelength of birds. *Journal of Experimental Biology* 150:171–185.

PENNYCUICK, C. J., H. H. OBRECHT, AND M. R. FULLER. 1988. Empirical estimates of body drag of large waterfowl and raptors. *Journal of Experimental Biology* 135:253–264.

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

RAYNER, J. M. V. 1979. A new approach to animal flight mechanics. *Journal of Experimental Biology* 80:17–54.

RAYNER, J. M. V. 1986. Vertebrate flapping flight mechanics and aerodynamics, and the evolution of flight in bats, p. 27–74. *In* W. Nachtigall (ed.), Bat Flight. Biona Report 5. Gustav Fischer, New York.

RAYNER, J. M. V. 1988. Form and function in avian flight. *Current Ornithology* 5:1–66.

RAYNER, J. M. V. 1991. Wake structure and force generation in avian flapping flight. *Proceedings of the International Ornithological Congress* 20:702–715.

RIJKE, A. M., W. A. JESSER, AND S. A. MAHONEY. 1989. Plumage

wettability of the African darter *Anhinga melanogaster* compared with the double-crested cormorant *Phalacrocorax auritus. Ostrich* 60:128–132.

Ross, R. K. 1974–76. A comparison of the feeding and nesting requirements of the great cormorant (*Phalacrocorax corax* L.) and double-crested cormorant (*P. auritus* Lesson) in Nova Scotia. *Proceedings of the Nova Scotia Institute of Science* 27:114–132.

Schorger, A. W. 1947. The deep diving of the loon and oldsquaw and its mechanism. *Wilson Bulletin* 59:151–159.

Scholander, P. F. 1940. Experimental investigation on the respiratory function in diving mammals and birds. *Hvalradets Skrifter Norske Videnskaps-Akademie, Oslo* 22.

Sealy, S. G. 1973. Interspecific feeding assemblages of marine birds off British Columbia. *Auk* 90:796–802.

Siegfried, W. R. 1974. Time budget of behavior among lesser scaups on Delta Marsh. *Journal of Wildlife Management* 38:708–713.

Spedding, G. R. 1986. The wake of a jackdaw (*Corvus monedula*) in slow flight. *Journal of Experimental Biology* 125:287–307.

Spedding, G. R. 1987. The wake of a kestrel (*Falco tinnunculus*) in flapping flight. *Journal of Experimental Biology* 127:59–78.

Spring, L. 1971. A comparison of functional and morphological adaptations in the common murre (*Uria aalge*) and thick-billed murre (*Uria lomvia*). *Condor* 73:1–27.

Stephenson, R., D. L. Turner, and P. J. Butler. 1989. The relationship between diving activity and oxygen storage capacity in the tufted duck (*Aythya fuligula*). *Journal of Experimental Biology* 141:265–275.

Stonehouse, B. 1975. Introduction: The Spheniscidae, p. 1–15. *In* B. Stonehouse (ed.), The Biology of Penguins. University Park Press, Baltimore, Maryland.

Storer, R. W. 1958. Loons and their wings. *Evolution* 12:262–263.

Sturkie, P. D. 1976. Blood: Physical characteristics, formed elements, hemoglobin, and coagulation, p. 53–75. *In* P. D. Sturkie (ed.), Avian Physiology. Springer-Verlag, New York.

Suter, W. 1982. Vergleichende Nahrungsokologie von uberwinternden tauchenten (*Bucephala, Aythya*) und blabhuhn (*Fulica atra*) am Untersee-Ende/Hochrhein (Bodensee). *Der Ornithologische Beobachter* 79:225–254.

Takekawa, J. Y. 1987. Energetics of canvasbacks staging on an upper Mississippi River pool during fall migration. Ph.D. Thesis, Iowa State University, Ames, Iowa.

Trayler, K. M., D. J. Brothers, R. D. Wooller, and I. C. Potter. 1989. Opportunistic foraging by three species of cormorants in an Australian estuary. *Journal of Zoology, London* 218:87–98.

Vermeer, K. and C. D. Levings. 1977. Populations, biomass and food habits of ducks on the Fraser Delta intertidal area, British Columbia. *Wildfowl* 28:49–60.

Wanless, S., A. E. Burger, and M. P. Harris. 1991. Diving depths of shags *Phalacrocorax aristotelis* breeding on the Isle of May. *Ibis* 133:37–42.

Wanless, S. and M. P. Harris. 1991. Diving patterns of full-grown and juvenile rock shags. *Condor* 93:44–48.

Weber, R. E., E. A. Hemmingsen, and K. Johansen. 1974. Functional and biochemical studies of penguin myoglobin. *Comparative Biochemistry and Physiology* 49B:197–214.

Wilson, R. P., B. M. Culik, D. Adelung, H. J. Spairani, and N. R. Coria. 1991. Depth utilisation by breeding Adélie penguins, *Pygoscelis adeliae*, at Esperanza Bay, Antarctica. *Marine Biology* 109:181–189.

Wilson, R. P., K. Hustler, P. G. Ryan, A. E. Burger, and E. C. Noldeke. 1992. Diving birds in cold water: Do Archimedes and Boyle determine energetic costs? *American Naturalist* 140:179–200.

Wilson, R. P. and M.-P. T. Wilson. 1988. Foraging behaviour in four sympatric cormorants. *Journal of Animal Ecology* 57:943–955.