

Body mass, volume, and buoyancy of some aquatic birds, and their relation to locomotor strategies

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Body mass, volume, and buoyancy of diving ducks, surface-feeding ducks, auklets, cormorants, and gulls were measured by means of water displacement. Relations of volume and buoyancy to body mass in surface-feeding ducks were linear and did not differ from those of diving ducks if scoters and eiders were excluded. These large-bodied sea ducks (scoters and eiders) had buoyancies 22–28% above values predicted by the common linear regression for surface-feeding ducks and smaller diving ducks. Thus, scoters and eiders have larger respiratory or plumage air volumes relative to body mass. Although relations of volume and buoyancy to body mass were similar among most ducks, volumes and buoyancies of gulls were much higher, and those of cormorants much lower, than those of ducks. Volumes and buoyancies of auklets were the same as those of ducks of similar mass. The significance to locomotion of the buoyancy of restrained birds depends on prediving expiration and ptilosuppression, and reduced buoyancy from compression of air spaces at foraging depths typical for the species.

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La masse corporelle, le volume et la flottabilité ont été évalués par mesure des déplacements d'eau chez des canards plongeurs, des canards de surface, des macareux, des cormorans et des goélands. Chez les canards de surface, les relations entre la combinaison volume-flottabilité et la masse sont linéaires et ne diffèrent pas de celles qui prévalent chez les canards plongeurs à l'exception des macreuses et des eiders. Ces canards marins de grande taille (macreuses et eiders) ont des flottabilités de 22–28% plus élevées que les valeurs théoriques obtenues par la régression linéaire calculée chez les canards de surface et les petits canards plongeurs. Les macreuses et les eiders ont donc un volume respiratoire et un volume d'air dans le plumage plus élevés par rapport à la masse corporelle. Bien que les relations volume et flottabilité en fonction de la masse soient semblables chez la plupart des canards, les volumes et flottabilités des goélands sont beaucoup plus élevés que ceux des canards, et ceux des cormorans beaucoup plus faibles. Les volumes et flottabilités des macareux sont égaux à ceux de canards de masse semblable. L'importance de la flottabilité dans la locomotion d'oiseaux à mobilité restreinte dépend de l'expiration et de la ptilosuppression avant la plongée ainsi que de la réduction de la flottabilité par compression des espaces aériens aux profondeurs de recherche de nourriture typiques de l'espèce.

[Traduit par la rédaction]

Introduction

Buoyancy is a major determinant of the locomotor costs of diving in birds (Lovvorn *et al.* 1991). Past comparative studies have focused on body shape and other factors affecting hydrodynamic drag (Prange and Schmidt-Nielsen 1970; Nachtigall and Bilo 1980; Lovvorn *et al.* 1991) and the effects of species and body size on the kinematics and aerobic efficiency of foot-paddling versus underwater "flying" (Clark and Bemis 1979; Baudinette and Gill 1985; Stephenson *et al.* 1989b; Lovvorn *et al.* 1991). However, variations in buoyancy also have important effects on diving costs of different species (Lovvorn 1991; Lovvorn and Jones 1991).

Butler and Woakes (1984) showed that in Humboldt Penguins (*Spheniscus humboldti*), aerobic metabolism during dives was not significantly different from that during resting. This result is in marked contrast to patterns for Tufted Ducks (*Aythya fuligula*), in which oxygen consumption during dives is 3.5 times the resting value (Woakes and Butler 1983). This difference was attributed primarily to the nearly neutral buoyancy of penguins compared with the relatively high buoyancy of Tufted Ducks. Biomechanical measurements and models of underwater locomotion in *Aythya* spp. (Lovvorn *et al.* 1991) indicate that 36–38% of work during descent, and an even greater fraction of work during bottom foraging, is due to buoyancy.

All diving birds, including penguins (Kooyman *et al.* 1971a), are at least somewhat positively buoyant near the surface (but

see Owre (1967) regarding *Anhinga anhinga*). In penguins and cormorants, gas exchange between the air sacs, lungs, and blood apparently continues at depths of at least 68 m (Kooyman *et al.* 1971b, 1973). Air in the plumage is also essential to thermoregulation in water, as shown by greatly enhanced heat loss and metabolism when the insulative layer is damaged by oiling (Erasmus *et al.* 1981; Jenssen and Ekker 1988). Clearly, air in the respiratory system and plumage is important to aerobic metabolism and thermoregulation during diving in birds, but in many species this air has substantial locomotor costs.

Given the importance of buoyancy to the costs of underwater swimming, we explored variation in body volume and buoyancy among various aquatic birds. We were particularly interested in comparing diving with surface-feeding ducks, to infer the relative importance of functional versus anatomical adaptations to underwater locomotion in divers. Detailed studies of the effects of body mass, body fat, and increased pressure with depth on buoyancy and locomotor costs of diving in the genus *Aythya* are described elsewhere (Lovvorn and Jones 1991).

Methods

Double-crested Cormorants (*Phalacrocorax auritus*), Glaucous-winged Gulls (*Larus glaucescens*), and Rhinoceros Auklets (*Cerorhinca monocerata*) were obtained as chicks from Mandarte, Christie, and Pine islands, respectively, of coastal British Columbia, and raised and maintained at the University of British Columbia. Ducks of the genera *Aix*, *Anas*, *Aythya*, and *Oxyura* (Table 1) were removed as eggs from the wild in southwestern Manitoba, hatched and raised at the Delta Waterfowl and Wetlands Research Station, and maintained as adults

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TABLE 1. Body mass, volume, and buoyancy (mean \pm SD), and codes as plotted in Figs. 1–3, for aquatic birds (data for *Aythya* spp. are from summer only)

	n	Mass (g)	Volume (mL)	Buoyancy (N)	Code
<i>Phalacrocorax auritus</i>	6	2318 \pm 121	2958 \pm 175	6.26 \pm 0.91	A
<i>Dendrocygna autumnalis</i>	5	816 \pm 108	1100 \pm 123	2.78 \pm 0.49	B
<i>Aix sponsa</i>	6	559 \pm 45	788 \pm 64	2.24 \pm 0.25	C
<i>Anas platyrhynchos</i>	4	1284 \pm 108	1876 \pm 170	5.80 \pm 1.17	D
<i>A. rubripes</i>	5	1345 \pm 93	1914 \pm 123	5.56 \pm 0.67	E
<i>A. americana</i>	5	578 \pm 34	916 \pm 40	3.32 \pm 0.17	F
<i>A. acuta</i>	5	772 \pm 97	1208 \pm 128	4.27 \pm 0.60	G
<i>A. cyanoptera</i>	7	362 \pm 44	541 \pm 69	1.75 \pm 0.26	H
<i>A. discors</i>	5	362 \pm 27	547 \pm 46	1.81 \pm 0.27	H
<i>A. clypeata</i>	8	484 \pm 69	756 \pm 59	2.66 \pm 0.41	I
<i>Aythya valisineria</i>	14	1104 \pm 131	1591 \pm 147	4.77 \pm 0.49	J
<i>A. americana</i>	20	924 \pm 57	1312 \pm 108	3.80 \pm 0.70	K
<i>A. affinis</i>	32	617 \pm 67	896 \pm 89	2.72 \pm 0.40	L
<i>A. collaris</i>	7	680 \pm 88	983 \pm 143	2.96 \pm 0.69	M
<i>Oxyura jamaicensis</i>	6	482 \pm 60	658 \pm 60	1.72 \pm 0.24	N
<i>Lophodytes cucullatus</i>	4	535 \pm 93	695 \pm 103	1.56 \pm 0.12	O
<i>Bucephala islandica</i>	12	710 \pm 123	1019 \pm 170	3.02 \pm 0.52	P
<i>B. albeola</i>	13	345 \pm 64	487 \pm 76	1.39 \pm 0.22	Q
<i>Histrionicus histrionicus</i>	2	530 \pm 28	782 \pm 9	2.46 \pm 0.36	R
<i>Melanitta fusca</i>	9	1265 \pm 79	1949 \pm 102	6.69 \pm 0.60	S
<i>Somateria mollissima</i>	5	1561 \pm 111	2457 \pm 129	8.77 \pm 0.56	T
<i>Larus glaucescens</i>	8	970 \pm 114	1807 \pm 172	8.19 \pm 0.99	U
<i>Cerorhinca monocerata</i>	5	490 \pm 42	726 \pm 34	2.31 \pm 0.10	V

either at the University of British Columbia (Canvasbacks (*Aythya valisineria*), Redheads (*A. americana*), and Lesser Scaup (*A. affinis*)) or at the Delta Station. Eight adult female White-winged Scoters (*Melanitta fusca*) were captured at nests on Gull Island, Redberry Lake, Saskatchewan. Other ducks were raised from eggs laid in captivity by wild-stock birds.

All birds were measured between 8 July and 22 August, when they were at least 1 year old. The same Canvasbacks, Redheads, and Lesser Scaup were also measured between 26 January and 11 February, when the Canvasbacks and most scaup were only 7–9 months old. If birds were captured on water, they were allowed to dry and preen for at least 2 h before being processed. Birds were weighed to the nearest gram on an Ohaus triple-beam balance or an Ohaus CT-6000 electronic scale. Body volumes were measured 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 3 cm wide and 3 mm thick. After allowing the bird to breathe freely for at least 15 s, expanding its air sacs, we wrapped two strips of masking tape 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 (inside diameter 15 cm) partly filled with water. Change in height of the water column was read within 5 s of immersion by means of a 10-mL pipette connected in parallel with the water column. Calibration of this apparatus with known quantities of water allowed calculation of the volume of water displaced by the bird, corrected for the volume of the mounting bar. Body volume measurements of the same individuals repeated after 2.5 h varied by $2.1 \pm 1.1\%$ (mean \pm SD) for 14 Lesser Scaup and $1.3 \pm 0.8\%$ for 10 Canvasbacks. Buoyancy (in newtons) was calculated as [mass of displaced water (kg) \times gravitational acceleration ($9.81 \text{ m} \cdot \text{s}^{-2}$)].

We did not account for the body condition (mass relative to structural size) of birds in this study, for two reasons. First, shape variations among species made the validity of such adjustments questionable. Second, adjusting body mass of *Aythya* spp. by a principal-component measure of structural size actually decreases the accuracy of body volume estimates (Lovvorn and Jones 1991). Moreover, the volume to mass relation among food-deprived individuals after substantial weight loss is the same as the relation based on different individuals of varying

body mass fed ad libitum. Therefore, body composition has negligible effects on volume to mass relations in *Aythya* spp., and should have little influence on interspecific comparisons made here.

Regression analyses were done with the GLM procedure of the Statistical Analysis System (SAS Institute Inc. 1987). Stepwise selection was used to identify linear versus quadratic relationships.

Results

The relation between body volume, V , and body mass, M , of diving ducks was slightly nonlinear (Table 1, Fig. 1A). When scoters and eiders (codes S and T, Fig. 1) were excluded, the curve was linear ($V = -29.94 + 1.467M$, $r^2 = 0.99$, $P < 0.001$, $s_{y \cdot x} = 30$). The nonlinearity when large-bodied sea ducks are included was magnified in the relation between buoyancy and body mass (Fig. 1B). Mean buoyancies of White-winged Scoters and Common Eiders (*Somateria mollissima*) (Table 1) were 22 and 28%, respectively, above values predicted by the linear regression (Fig. 1B). Buoyancies of Canvasbacks, Redheads, and Lesser Scaup in winter (circled codes J, K, and L in Fig. 1) conformed to the pattern for summer, and fell in the range of points best fit by the linear relation. The allometric equation for all diving ducks, including scoters and eiders, was $B = 8.034 \times 10^{-4} M^{1.253}$, $r^2 = 0.95$, $P < 0.001$, where B is buoyancy. This equation was less satisfactory than the combination of linear and quadratic equations given above and in Fig. 1, as it overestimated data for Redheads and Canvasbacks and underestimated data for scoters and eiders.

Surface-feeding ducks were compared to all diving ducks except scoters and eiders. Both volume and buoyancy were linearly related to body mass (Fig. 2). Separate regressions for diving and surface-feeding ducks were not significantly different (general linear test; Neter and Wasserman 1974, pp. 87–89; $P > 0.53$).

Despite the similarity of mass-specific buoyancy and volume among small to medium-sized ducks, points for cormorants

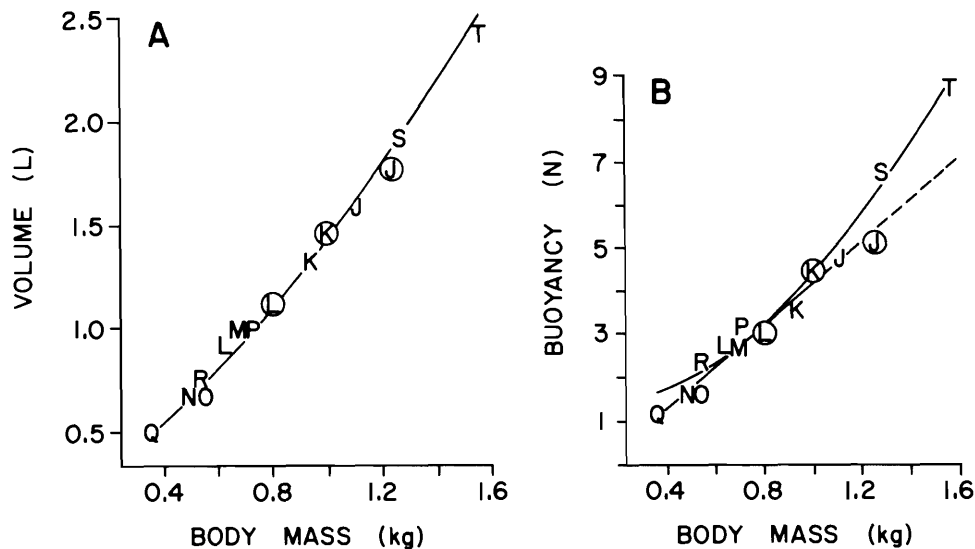


FIG. 1. Regression of body volume V (A) and buoyancy B (B) on body mass M of diving ducks. The broken line extends the linear curve, which is based only on ducks weighing <1200 g. Measurements made in winter (unlike those from summer) are circled and are not included in regressions. For identification of species codes see Table 1. V (mL) = $65.74 + 1.144M$ (g) + $2.495 \times 10^{-4} M^2$, $r^2 = 0.99$, $P < 0.001$, $s_{y \cdot x} = 36$; B (newtons) = $1.21 + 3.17 \times 10^{-6} M^2$, $r^2 = 0.98$, $P < 0.001$, $s_{y \cdot x} = 0.34$; and $B = -0.303 + 4.58 \times 10^{-3} M$, $r^2 = 0.94$, $P < 0.001$, $s_{y \cdot x} = 0.29$.

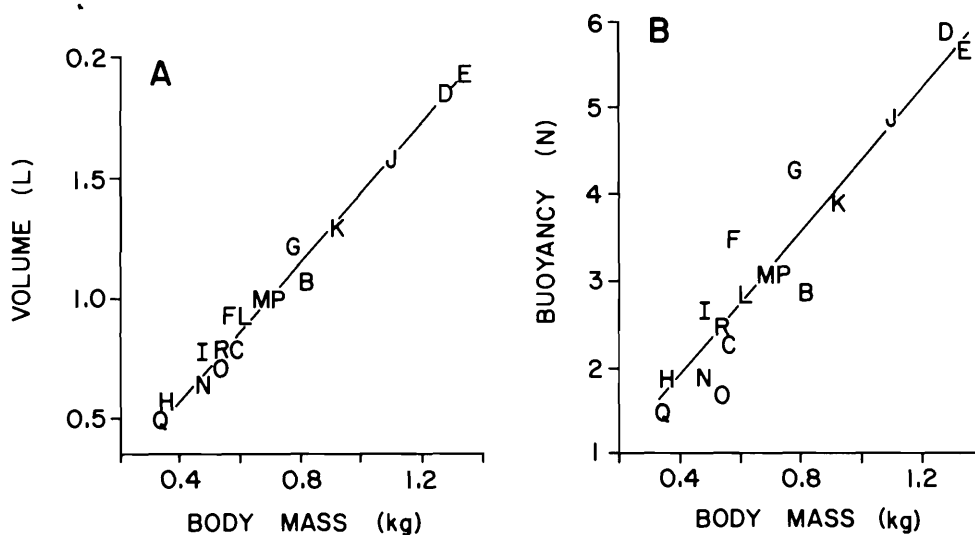


FIG. 2. Regression of body volume V (A) and buoyancy B (B) on body mass M of surface-feeding and diving ducks except scoters and eiders. For species codes see Table 1. V (mL) = $13.7 + 1.43M$ (g), $r^2 = 0.99$, $P < 0.001$, $s_{y \cdot x} = 47$; B (newtons) = $0.131 + 4.18 \times 10^{-3} M$, $r^2 = 0.89$, $P < 0.001$, $s_{y \cdot x} = 0.46$.

(code A) and gulls (code U) diverged dramatically (Fig. 3). Cormorants had lower body volumes and much lower buoyancies than predicted by the curve for ducks, whereas gulls had relatively higher volumes and buoyancies. Volumes and buoyancies of Rhinoceros Auklets (code V) were the same as for ducks of similar mass (Fig. 3).

Discussion

The relation of volume to body mass is the same for most ducks and auklets. Thus, the combined volume of the respiratory system and plumage scales similarly among many species, so that volume (and buoyancy) can often be estimated from general equations. However, large-bodied sea ducks and cormorants

diverge substantially in ways that probably affect the mechanics and energy costs of diving (Lovvorn 1991).

Comparison of diving and surface-feeding ducks

Relations between body mass and either volume or buoyancy did not differ between surface-feeding ducks and diving ducks of small to medium size (Fig. 2). Keijer and Butler (1982) found the end-expiratory lung and air-sac volume of Tufted Ducks ($180 \text{ mL} \cdot \text{kg}^{-1}$) to be 61% greater than that of Mallards ($112 \text{ mL} \cdot \text{kg}^{-1}$), and suggested that this difference results in higher buoyancy in divers. However, Stephenson *et al.* (1989a) reported that Tufted Ducks habitually diving 6 vs. 0.65 m for food decreased their respiratory volumes 41%, from 232 to 165 mL.

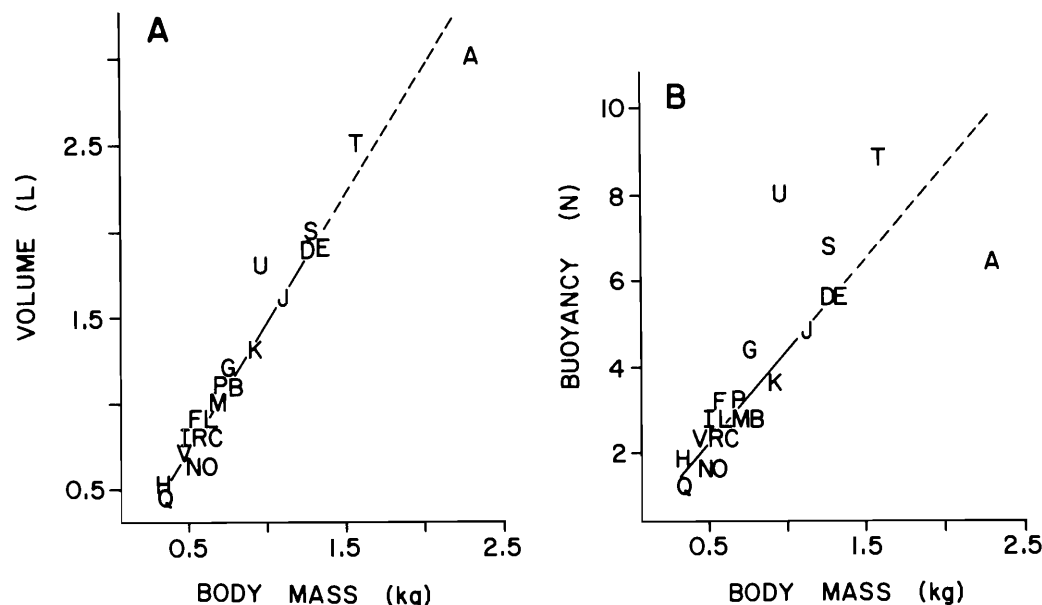


FIG. 3. Plot of body volume (A) and buoyancy (B) versus body mass of aquatic birds. Broken lines extend linear curves based on all ducks except scoters and eiders. For species codes see Table 1.

kg^{-1} , while increasing nonpulmonary oxygen storage (mostly in blood) by a compensatory amount. Although exercise training alone can result in substantial changes in respiratory volume, the large difference between diving and surface-feeding ducks reported by Keijer and Butler (1982) (see above) seemingly should correspond to volume and buoyancy differences.

However, Stephenson *et al.* (1989a) noted that differences in end-expiratory volume might represent a change in compliance of the respiratory system rather than a change in respiratory volume per se. They suggested that respiratory volumes in deep-diving versus shallow-diving Tufted Ducks were similar at the water surface, but that the ducks diving deeper were able to exhale to a lower residual volume immediately before dives. The insensitivity of our method to such mechanisms might explain the lack of differences between surface-feeding ducks and most diving ducks (Fig. 2) and point to more functional than anatomical differences between the two groups. The volume of the plumage air layer might also be lower in diving ducks, thereby offsetting larger respiratory volumes. Dehner (1946) found that plumage volumes of Mallards and Black Ducks were a higher percentage of total body volume (35 and 37%, respectively) than in Redheads and Lesser Scaup (26 and 30%, respectively).

Nonlinearity in diving ducks

White-winged Scoters and Common Eiders differed appreciably from other ducks in the relations of volume and buoyancy to mass (Figs. 1, 3). Mallards (*Anas platyrhynchos*) and Black Ducks (*Anas rubripes*) with body masses similar to that of scoters (Table 1) fell on the linear curve of buoyancy for other ducks (Fig. 2B), which suggests that body size alone does not account for the difference. Divergence of scoters and eiders might result either from substantially higher fat levels than in other species sampled, or from actual differences in scaling of plumage or respiratory volumes.

Regarding fat levels, the average mass (± 1 SD) of three captive female Common Eiders we sampled on 28 July was 1488 ± 65 g, which is the same as for wild females in August, halfway through incubation (Milne 1976; Korschgen 1977).

Body mass in the prelaying period averages about 2500 g, and at the end of incubation 1100–1300 g. Thus, the body condition of female eiders in our study resembled that of wild birds, and their fat content was much lower than the annual maximum. The body mass of the two captive males we sampled (1670 ± 28 g) was well below the mean of about 2170 g for wild males in Scotland in late July (Milne 1976).

Eight of nine White-winged Scoters we measured (Table 1) were wild incubating females which, judging by body mass, were about 5–6 days into their 28-day incubation period (based on data from the same study area in Brown and Fredrickson 1987). Mean body mass during incubation fell from 1408 to 1091 g (Brown and Frederickson 1987). Thus, scoters in our sample (mean mass 1265 g) were not exceptionally fat.

Captive Canvasbacks, Redheads, and Lesser Scaup lost an average of 12, 7, and 29% of body mass from winter to summer, but this loss did not change mass–volume or mass–buoyancy relations by nearly as much as scoters and eiders diverged from the other species (Fig. 1). These and the above data indicate that fat levels do not explain the high buoyancies of scoters and eiders. We conclude that these species have larger respiratory or plumage air volumes relative to body mass than do surface-feeding ducks or smaller diving ducks.

Regarding the high buoyancy of scoters and eiders, it is of interest that these are the only species among those studied that often (scoters) or always (eiders) use their wings (extended alulae) as well as feet in propulsion during descent (Humphrey 1957, 1958; Lovvorn 1991). However, because of compression of air spaces with depth, buoyancy has greater influence on locomotor costs of shallow divers than of deep divers (Lovvorn and Jones 1991). Both Common Eiders and King Eiders (*Somateria spectabilis*) feed at depths up to 60 m (Cottam 1939), where pressure greatly reduces their buoyancy. Diving depths of scoters have not been well studied but are probably much shallower. Oldsquaws (*Clangula hyemalis*), which weigh 750–900 g and dive to 60 m (Schorger 1947), apparently rely on wing propulsion to a greater extent than do scoters or eiders (Snell 1985). This may be an adaptation to negative buoyancy during deep

dives and the need to ascend by active propulsion (Lovvorn and Jones 1991).

Restrained versus freely diving birds

The relation between buoyancy as measured by our technique and the buoyancy of freely diving birds is uncertain. Although at least some penguins dive upon inspiration (Kooyman *et al.* 1971a), most species studied, such as cormorants and ducks, dive upon expiration (Ross 1976; Butler and Woakes 1979; Livezey and Humphrey 1984; Tome and Wrubleski 1988). Based on data from Dehner (1946), we calculated that exhalation of one resting tidal volume would reduce buoyancy by an average of 10% in scaup and 14% in Redheads. By artificially compressing the plumage to an extent similar to that during natural dives, it was shown that voluntary ptilosuppression might reduce buoyancy by up to 6% (Stephenson *et al.* 1989b). Our measurements probably do not include pre-dive respiratory or ptilomotor adjustments.

Buoyancy and locomotion

The avian body is primarily adapted for flight, in which low density (high buoyancy) is strongly favored. The high buoyancy of gulls (Fig. 3), relative to wing span and wing area, corresponds to their slow wingbeats and ability to soar. Cormorants have evolved unusually low buoyancy (Fig. 3), which allows them to submerge without aid from their wings and without first springing upward to gain momentum (Lovvorn 1991). Aside from more posterior placement of larger feet and smaller relative wing areas, most diving ducks perhaps have diverged from surface-feeding ducks primarily in pulmonary compliance and blood oxygen storage, while retaining similar buoyancies above water. Scoters and eiders maintain large air volumes above water, but their effective buoyancy may be lowered substantially by pre-dive exhalation or by pressure during deep dives. Better understanding of buoyancy effects on locomotion will require (i) measuring air volumes after pre-dive exhalation and ptilosuppression, so that accurate values can be used in modelling dive costs (Lovvorn *et al.* 1991), and (ii) evaluating the effects of air-space compression at typical foraging depths, especially regarding the relative costs of descent, foraging, and ascent (Lovvorn and Jones 1991).

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