# Diving Birds in Cold Water: Do Archimedes and Boyle Determine Energetic Costs?

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*Abstract.*—The volume of air trapped in the feathers and the body density of 36 species of water
bird were determined by water displacement experiments. Body density was higher and the
volume of air trapped in plumage was lower in species that were most reliant on diving for
foraging. Accordingly, we predict that habitually diving species have substantially reduced en-
ergy expenditure while underwater and correspondingly higher aerobic dive limits than infre-
quent divers. This agrees with field observations. Following Boyle's law, aerobic dive limits are
predicted to increase with increasing dive depth due to a reduction in upthrust following volumet-
ric reduction of feather-trapped air caused by hydrostatic pressure. It appears energetically more
costly for diving birds to forage near the surface than at greater depths. Reduced plumage air
to minimize underwater swimming costs, however, probably increases heat loss. The use of fat
for insulation is not compatible with minimized flight costs. Frequent divers have higher flight
costs than infrequent divers. We predict that the amount of air in the feathers and the amount
of subcutaneous fat in aquatic birds are regulated in such a way as to minimize energy expendi-
ture as a function of the temperature of the environment as well as diving and flying rhythms.

Studies on avian energetics (Kendeigh et al. 1977; Whittow and Rahn 1984)
have tended to concentrate on those activities with high energy demands. The
acquisition of food is generally an energy-demanding activity since locomotion is
almost invariably involved (Birt-Friesen et al. 1989). Virtually all waterfowl de-
pend on flight and swimming for effective foraging. Typically, flight energy costs
are around 12 times basal metabolic rate (BMR) (Castro and Myers 1988). Subsur-
face swimming is also energetically costly, even in species that habitually dive to
forage. Penguins, for example, despite being highly specialized for minimum en-
ergy expenditure during underwater locomotion (Nachtigall and Bilo 1980), are
reported to have energy costs approaching 10 times BMR during diving (Nagy et
al. 1984). High energy expenditure underwater is considered to be primarily due
to the resistance of water that results from high viscosity and density compared
to air (Schmidt-Nielsen 1972). However, Butler and Woakes (1984) attributed
the substantial differences in oxygen consumption between Humboldt penguins
(*Spheniscus humboldti*) and tufted ducks (*Aythya fuligula*) to interspecific differ-

ences in buoyancy, whereas Stephenson et al. (1989a) concluded that buoyancy is the dominant force against which ducks have to work during dives and that drag adds little to the overall energy output.

Cessation of underwater swimming in most diving water birds results in immediate passive surfacing (Butler and Jones 1982; Wilson and Wilson 1988; Stephenson et al. 1989a). This buoyancy is primarily due to large volumes of air in the respiratory system and the feathers (Stephenson et al. 1989a). Our experiments indicate that the buoyancy of dead birds is inversely related to depth. Multiple submersions of dead specimens eventually result in feather wetting, but in free-living birds, shot after extensive diving, there is no evidence that water penetrates the outer feather layer (cormorants and anhingas excluded; see below).

In an attempt to assess the importance of buoyancy on a broad spectrum of waterfowl, we present a simplistic model of the energetic costs of working against buoyancy in diving birds. Our model does not purport to be absolutely quantitative, but it serves to indicate how the amount of air in the feathers of different waterfowl groups is linked to their foraging ecology.

## CONSEQUENCES OF AIR-MEDIATED BUOYANCY

This section deals exclusively with the rationale behind the model that considers the consequences of upthrust on bird energetics. The applicability and variability of the parameters used are discussed later. Unless otherwise stated, all units of measurement conform to the Système International d'Unités.

### Variation in Upthrust with Depth

Two vertical forces act on a bird underwater. First is the downward force due to gravity:

$$F_m = g\,m\,,\tag{1}$$

where $g$ is the gravitational acceleration at the surface of the earth and $m$ is the mass of the bird. Second is the upward force, given by Archimedes' principle, which states that the upward force experienced by a body in a fluid, $F_A$, is given by

$$F_A = \rho\,g\,V\,,\tag{2}$$

where $\rho$ is the density of the fluid and $V$ is the volume of fluid displaced. We will define the overall upthrust experienced by a body immersed in a fluid by

$$F_{Up} = F_A - F_m\,.\tag{3}$$

Diving birds experience considerable upthrust when underwater due to air in the lungs and associated air sacs, used for gas exchange (Torre-Bueno 1978), and air trapped in feathers for body insulation (Scholander et al. 1950). The total volume of a bird underwater is

$$V_b = V_L + V_F + V_T\,,\tag{4}$$

where $V_L$ and $V_F$ are the volumes of air in the respiratory system and feathers,

respectively, and $V_T$ is the volume of the remaining body tissue. Boyle's law for gases is

$$p V = \text{constant}, \tag{5}$$

where $p$ is the pressure, so that

$$p_s(V_{Ls} + V_{Fs}) = p_d(V_{Ld} + V_{Fd}), \tag{6}$$

where the subscript $s$ denotes values at the water's surface and the subscript $d$ denotes values at a specific depth. We take $p_s$, atmospheric pressure, to be 1.0 $\times$ 10$^5$ Pa. Pressure varies with depth according to

$$p_d = \rho g d + p_s, \tag{7}$$

where $d$ = depth. Rearranging equations (6) and (7), we find that the air volume associated with the body of a diving bird changes with depth according to

$$V_{Ld} + V_{Fd} = \frac{p_s(V_{Ls} + V_{Fs})}{p_s + \rho g d}. \tag{8}$$

According to equations (1), (2), (3), (4), and (8), we see that the upthrust experienced by the bird is

$$F_{Up} = \rho g \left( \frac{p_s(V_{Ls} + V_{Fs})}{p_s + \rho g d} + V_T \right) - g m. \tag{9}$$

### Energetic Requirements to Counter Upthrust

For a bird to maintain a stationary position underwater, it must exert a force equivalent to and opposing the overall upthrust. In this context, two energetic terms are important: the power output necessary to produce this force and the energy input that the bird needs to produce the requisite power output. We take the power output, $P_O$, to be linearly related to force (see below) so that

$$P_O = \alpha F_{Up}, \tag{10}$$

where $\alpha$ is a proportionality constant.

The actual energetic cost of maintaining a given power output depends on the aerobic efficiency ($n_a$; Stephenson et al. 1989a) of the bird. Data obtained from birds swimming in a water flume strongly suggest that oxygen consumption due to locomotion, $\dot{V}o_2$, is linearly related to $P_O$ (see below) so that

$$\dot{V}o_2 = b P_O + C_1, \tag{11}$$

where $b$ and $C_1$ are constants.

### Energetic Requirements during a Dive

For simplicity, we assume that a bird dives by appearing instantly at a specific depth and then maintains its position in the water column by swimming against upthrust so that there is no horizontal or vertical movement (this situation would be approximated by almost any benthic-foraging bird moving slowly along the

bottom [cf. Stephenson et al. 1989*a*]). This eliminates energy expenditure resulting from forward motion, which would be considerable in fast-swimming pursuit divers. Then, during the dive, the oxygen consumed per second, EE, will depend on the bird's standard metabolic rate, SMR (sensu Prosser 1973), and on the oxygen used for swimming against buoyancy (i.e., EE = SMR + $\dot{V}o_2$). Using equations (10) and (11), EE varies with depth according to

$$EE = SMR + \alpha\, b\, F_{Up} + C_1 .\tag{12}$$

### Maximum Duration of Dive

Essentially two factors determine the aerobic dive limit, ADL (defined later): the oxygen storage capacity of the bird, $O_T$, and the rate of consumption of these stores (West 1981; Woakes and Butler 1983; Hudson and Jones 1986). Oxygen is stored in blood and muscle pigments, $O_P$, and in the lungs and air sacs, $O_L$ (Kooyman 1975, 1989). We define total oxygen stores as

$$O_T = O_P + O_L .\tag{13}$$

Since the ADL is dependent on the rate of oxygen consumption, using equation (12), we obtain

$$ADL = \frac{O_T}{(SMR + \alpha\, b\, F_{Up} + C_1)} .\tag{14}$$

Substituting from equation (9), we have

$$ADL = \frac{O_T}{C_1 + SMR + \alpha\, b \left\{ \rho\, g \left[ \dfrac{p_s\,(V_{Ls} + V_{Fs})}{p_s + \rho\, g\, d} + V_T \right] - g\, m \right\}} .\tag{15}$$

### Parameter Values Used in the Model

In order to examine general trends as a function of bird size and volume of air in the feathers and bird body density, we use standard allometric equations for bird lung and air sac volumes and SMRs as well as assuming that the relationships between $P_O$, force, and EE described above hold true for all species. We expect factors enhancing diving capacity to be more developed in species that rely on diving for foraging. Thus, we expect more specialized divers to be able to reduce air in their plumage on submerging (P. R. Stettenheim, cited in Bédard 1985), to be more efficient at swimming underwater (Nachtigall and Bilo 1980), and to have higher body oxygen stores (Keijer and Butler 1982). For standardization in all future calculations, we assume that all birds are swimming in water of density $1.0 \times 10^3$ kg m$^{-3}$.

*Parameter* $\alpha$.—Parameter $\alpha$ is the conversion value for deriving the power output for working against a particular force that we have simplistically taken as linear. Birds maintaining their position at a specific depth in the water may do so

by swimming down, directly against the force produced by buoyancy (e.g., ducks), or by moving horizontally and using the downward-directed hydrodynamic lift to counteract buoyancy (e.g., penguins). In either case, the force must be identical. The power actually used by birds to overcome the buoyancy force will depend to some extent on the size and shape of the birds (cf. Stephenson 1989a) and on the suitability of the swimming apparatus to perform this acceleration using moving or nonmoving water.

Baudinette and Gill (1985) present data on $P_O$ as a function of an opposing force (the drag) induced by velocity, $F_V$, for both penguins and ducks swimming at the water's surface, where

$$P_O = \alpha F_V - C_2,\tag{16}$$

where $C_2$ is a constant. The $\alpha$ values for penguins and ducks were $\alpha = 0.78$ W $N^{-1}$ ($r^2 = 0.99$) and $\alpha = 0.74$ W $N^{-1}$ ($r^2 = 0.99$), respectively, and $C_1 = 0.08$ W in both cases. The remarkable similarity of the two $\alpha$ values despite substantial morphological differences between the two bird groups makes it likely that other species have similar $\alpha$ values. We fixed $\alpha$ at $0.76$ W $N^{-1}$ and assumed that birds swimming forward against drag or downward against upthrust are similarly efficient although the two situations are not hydrodynamically identical. The concept of power at zero bird velocity appears paradoxical; however, to maintain position the bird must still work to move the water.

*Parameter* b.—Oxygen consumption is an indirect measure of power input. Parameter $b$ is the conversion value for net power input (active power values minus inactive values) to power output. Some workers consider that for flying birds the efficiency is approximately constant over a wide range of power production (Phillips et al. 1985), although precisely how efficiency varies with velocity and limb motion kinematics is not known, and it is probable that efficiency varies considerably with both mode and velocity of locomotion (Rayner 1979). Values for the net aerobic efficiency ($n_a = P_O/\dot{V}_{O_2} - P_{rest}$) of various swimming animals are presented in Stephenson et al. (1989a). Values are, however, complicated by diverse experimental procedures incorporating widely differing water temperatures on animals of very different body sizes. Baudinette and Gill (1985) presented data on $P_O$ with respect to $\dot{V}_{O_2}$ for penguins and ducks of comparable mass (ca. 1 kg) swimming in water at constant temperature (see eq. [11]) in which $b$ values for penguins and ducks were $b = 3.71 \times 10^{-7}$ $m^3$ $s^{-1}$ $W^{-1}$ ($r^2 = 0.99$) and $b = 3.70 \times 10^{-7}$ $m^3$ $s^{-1}$ $W^{-1}$ ($r^2 = 0.92$), respectively, which suggests that under comparable conditions the value for $b$ is relatively invariant. We have assumed that the $b$ values for all species are constant at $3.70 \times 10^{-7}$ $m^3$ $s^{-1}$ $W^{-1}$ but have also attempted to limit $b$-dependent calculations to similarly sized birds in water at constant temperature. Where relevant, changes in predicted parameters with mass are mentioned. Values for $C_1$ from Baudinette and Gill's work (1985) for penguins and ducks are $C_1 = 4.6 \times 10^{-7}$ $m^3$ $s^{-1}$ and $C_1 = 5.9 \times 10^{-7}$ $m^3$ $s^{-1}$, respectively, and correspond to values for SMR (see below).

*Parameter* $V_{Ls}$.—In diving birds, lung and air sac volumes range between $V_{Ls} = 1.6 \times 10^{-4}$ $m^3$ $kg^{-1}$ and $V_{Ls} = 2.2 \times 10^{-4}$ $m^3$ $kg^{-1}$ (Kooyman 1975; Stephenson

et al. 1989*b*). We use the allometric equation presented by Lasiewski and Calder (1971):

$$V_{Ls} = 1.61 \times 10^{-4} m^{0.91}. \tag{17}$$

Free-living divers may actively or passively alter respiratory volume appreciably (Casler 1973; Stephenson et al. 1989*a*), so variation is possible around the values we consider.

*Parameter $O_L$.*—Following Stephenson et al. (1989*b*), we assume that the mean fractional concentration of oxygen in the respiratory system is 17.6% (see Scheid et al. 1974; Torre-Bueno 1978; Butler and Woakes 1979) and that a maximum of 75% of this is usable during dives (Hudson and Jones 1986). The total oxygen stored in the lungs and air sacs is then

$$O_L = 0.13 \, V_{Ls}$$
$$= 2.09 \times 10^{-5} m^{0.91}. \tag{18}$$

*Parameter $O_P$.*—In diving birds, the blood and muscle oxygen capacity (percent by volume) varies between 20% (Lenfant et al. 1969) and 26% (Bohr 1897), although the lower values are more usual (Kooyman 1975). We take the blood and muscle oxygen capacity as 0.209 m$^3$ of oxygen per cubic meter of blood (Stephenson et al. 1989*b;* cf. Weber et al. 1974; Keijer and Butler 1982; Rothe 1983; Viscor et al. 1984) and assume that the relevant oxygen storage volume is $1.0 \times 10^{-4}$ m$^3$ per kilogram of body mass (Kooyman 1975 and references therein). The value of $O_P$ is therefore

$$O_P = 2.09 \times 10^{-5} m. \tag{19}$$

*Standard metabolic rate.*—We derived values for basal metabolic rate, expressed as rate of oxygen consumption (m$^3$ s$^{-1}$), for seabirds using

$$BMR = C_3 m^{C_4}, \tag{20}$$

where $C_3 = 2.29 \times 10^{-7}$ m$^3$ s$^{-1}$ kg$^{-1}$ and $C_4 = 0.744$ (Rahn and Whittow 1984). This is similar to other standard allometric equations for nonpasserines (Lasiewski and Dawson 1967; Dawson and Hudson 1970; Kendeigh et al. 1977). Where relevant, equations for Charadriiformes ($C_3 = 3.17 \times 10^{-7}$ m$^3$ s$^{-1}$ kg$^{-1}$, $C_4 = 1.014$), Procellariiformes ($C_3 = 2.14 \times 10^{-7}$ m$^3$ s$^{-1}$ kg$^{-1}$, $C_4 = 0.68$), Pelecaniformes ($C_3 = 2.40 \times 10^{-7}$ m$^3$ s$^{-1}$ kg$^{-1}$, $C_4 = 0.804$), and Sphenisciformes ($C_3 = 1.98 \times 10^{-7}$ m$^3$ s$^{-1}$ kg$^{-1}$, $C_4 = 0.749$; Rahn and Whittow 1984) were substituted. On the basis of data in Brown (1984), we calculated SMR by multiplying BMR by 1.15.

*Parameters $V_{Fs}$ and $V_T$.*—Where possible, values for the volume of air in the feathers were determined directly. Birds with plumage in good condition, from 36 species (Appendix), comprising 40 freshly dead or frozen specimens, were analyzed. Specimens were fully thawed, weighed, and the feathers smoothed to approximate real-life conditions during diving as closely as possible. Approximate feather depth was measured on the belly, breast, flank, hindneck, back, rump, and crown. Next, birds were immersed, head down, in fresh water in appropri-

ately sized measuring cylinders in which cylinder diameter marginally exceeded maximum bird diameter. The volume of water displaced was read directly from the side of the measuring cylinder within 5 s of immersion. Birds were then plucked, reweighed, and again immersed in water to determine body volume. Finally, the birds were cut open and the lungs and air sacs meticulously destroyed to allow water to enter all respiratory air spaces before the birds were reimmersed. The water displaced was noted as well as the specimen mass in water when the carcasses sank. Errors in displacement estimates were considered to be less than 5%. We made no attempt to prevent loss of air from the lungs and air sacs during plucking, and consequently the calculated volume of air in the feathers may be slightly overestimated. However, specimens were extensively handled for morphometric measurements before volumetric calculations, so that much air likely to escape would already have done so before plucking.

Overall, our estimates of the volumes of air in the feathers are unlikely to be very accurate since we could not simulate the exact plumage condition of living birds. However, feathers are flexible, and it is unlikely that birds are able to control substantially the volume of entrapped air when plumage is subject to hydrostatic pressure (Stephenson et al. 1989a). We assume that the magnitude of our error is approximately the same for all specimens so that derived trends remain essentially unchanged. The mass of the feathers was calculated as the mass difference in the bird before and after plucking. The volume of air enclosed by the feathers was calculated as the difference in the water displacement values pre- and postplucking, minus the mass of the feathers (assuming that keratin in the feathers has the same density as water).

To allow us to assess the applicability of using feather depth as a direct measure of buoyancy for those species in which good specimens could not be obtained, we compared quantities of air in feathers from measured values with predicted values. Predicted values were obtained by multiplying feather depth at the breast by the allometric equation for determining the surface area, $A$, of a bird's body:

$$A = 8.11 \times 10^{-2} m^{0.667} \tag{21}$$

(Walsberg and King 1978).

To examine trends in upthrust as a function of diving activity, we used the classification of seabird feeding methods originally proposed by Ashmole (1971) and subsequently modified by Cramp and Simmons (1983), Harper et al. (1985), and Prince and Morgan (1987).

We compared the estimated cost of level flapping flight with the volume of air entrapped in the feathers per unit mass of our specimens, here termed $\Omega$. Energy expenditure during flight is a complex function of several variables including wing area, wing length, aspect ratio, and bird mass (Pennycuick 1975; Kendeigh et al. 1977). This is further complicated by different tendencies to glide and soar, which change with wing geometry (Pennycuick 1975, 1982, 1983). The few direct measurements of the metabolic cost of flight are highly variable both inter- and intraspecifically depending on measurement conditions (Ellis 1984; Costa and Prince 1987). Generally, though, a higher disk loading necessitates a higher power for

horizontal flight (Pennycuick 1987). Disk loading is given by

$$D_q = \frac{4 \, m \, g}{\pi \, W_i^2},$$  (22)

where $W_i$ is the wingspan (Pennycuick 1987). We used disk loading as a measure of the cost of flight for species for which we had determined values for $V_{F_s}$. If all body dimensions are kept in proportion, scaling effects mean that mass increases by a bigger factor than disk area so that disk loading increases with increasing mass (Pennycuick 1987). To partially correct for this, we performed a multiple linear regression of mass, disk loading, and volume of air contained in the feathers per kilogram of body mass.

<center>RESULTS</center>

Calculated volumes of air contained in the feathers of birds ranged from 5.58 $\times$ $10^{-3}$ m$^3$ in the giant petrel (*Macronectes giganteus*) to 2.4 $\times$ $10^{-5}$ m$^3$ in the white-faced storm petrel (*Pelagodroma marina*; Appendix). The volume of air in the feathers per unit of body mass ($\Omega$) varied according to feeding method (following definitions of Cramp and Simmons 1983 and Harper et al. 1985), with $\Omega$ being lower in birds whose major mode of feeding was either pursuit or surface diving ($\Omega = 2.9 \times 10^{-4}$ m$^3$ kg$^{-1}$, SD $1.0 \times 10^{-4}$, $N = 11$ species; mean values are used for species in which more than one specimen was used) than in species that feed only on the surface or in the air ($\Omega = 6.7 \times 10^{-4}$ m$^3$ kg$^{-1}$, SD $2.5 \times 10^{-4}$, $N = 19$; $t = 5.0$, $P < .001$). Species that plunge dive or occasionally surface dive had intermediate values ($\Omega = 4.5 \times 10^{-4}$ m$^3$ kg$^{-1}$, SD $= 1.4 \times 10^{-4}$, $N = 6$) (fig. 1).

The mass of feathers per unit volume of air in them, $x$, was higher in diving species ($\bar{x} = 252$ kg m$^{-3}$, SD 131, $N = 11$) than in nondiving species ($\bar{x} = 153$ kg m$^{-3}$, SD 55, $N = 19$; $t = 2.91$, $P < .01$). Again, species that plunge dive or occasionally surface dive had intermediate values ($\bar{x} = 232$ kg m$^{-3}$, SD 120, $N = 6$). Calculated body density of divers was higher than that of nondivers ($\bar{\rho}_b = 1.01 \times 10^3$ kg m$^{-3}$, SD 57, $N = 11$ and $\bar{\rho}_b = 9.69 \times 10^2$ kg m$^{-3}$, SD 44, $N = 18$; $t = 2.18$, $P < .05$). When divested of feathers and respiratory air spaces and placed in fresh water, 91% of the divers ($N = 11$), 50% of the partial divers ($N = 6$), and only 35% of the nondivers ($N = 18$) sank ($\chi^2 = 8.14$, df $= 2$, $P < .02$).

Body density plays an increasingly important role in determining the value of upthrust as the volume of the air in the feathers and respiratory spaces decreases. Birds with body densities lower than water are not neutrally buoyant at any depth (table 1). Specific upthrust values occur at shallowest depths in species that have the least air in the feathers and the highest body densities (table 1). Accordingly, the energy expenditure of these birds is predicted to be lowest at all water depths (table 1; fig. 2). Nondiving species, such as gulls and dabbling ducks, have the highest EE values. Diving species, notably cormorants, divers, and penguins, have low EE values and partial divers, for example, petrels, have intermediate
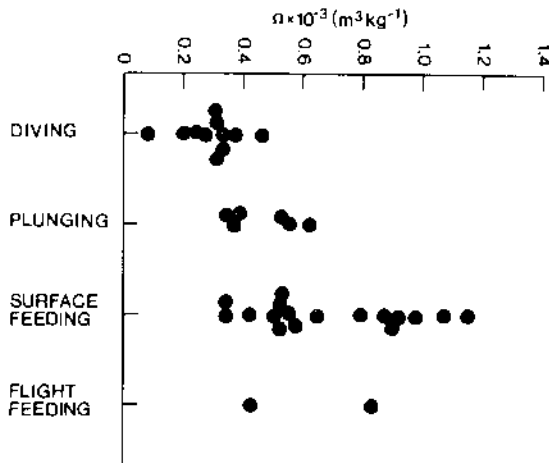
FIG. 1.—Volume of air stored in the feathers per unit body mass ($\Omega$) for various water birds in relation to their principal feeding methods (following definitions of Cramp and Simmons 1983 and Harper et al. 1985).

values (fig. 2). In accordance with this, maximum dive durations of different species are inversely related to the upthrust experienced by the birds (fig. 3).

There was a significant negative correlation between $\Omega$ and disk loading ($D_q$): $\Omega = 8.4 \times 10^{-4} + 9.0 \times 10^{-6} \, m - 4.0 \times 10^{-6} \, D_q$ ($r^2 = 0.37$, ANOVA; $F = 65.9$, $P < .001$) (fig. 4), which indicates that birds that expend relatively little energy during flight expend more for swimming underwater and vice versa.

There was a linear relationship between the predicted volume of air stored in the feathers (predicted volume $V_p = 8.11 \times 10^{-2} \, m^{0.667}$ BFT, where BFT is the breast feather thickness) and the determined volume of air, as estimated by our displacement values, according to $V_{Fs} = 0.44 \, V_p - 1.38 \times 10^{-4}$ ($r^2 = 0.98$, $N = 40$, $P < .001$; fig. 5). The volume of air in the feathers can thus be calculated as

$$V_{Fs} = 0.44 \, (8.11 \times 10^{-2} \, m^{0.667} \, \text{BFT}) - 1.38 \times 10^{-4}, \tag{23}$$

and the volume displaced per kilogram of body mass as

$$\Omega = \frac{(3.57 \times 10^{-2} \, m^{0.667} \, \text{BFT}) - 1.38 \times 10^{-4}}{m}. \tag{24}$$

Owing to induced changes in the volume of air in the feathers and respiratory air spaces, our model predicts that depth has a profound effect on the aerobic dive limit. The ADL is highest and the rate of increase of the ADL per unit increase in depth is fastest when BFT is zero. However, the rate of change of the ratio of the ADL at the surface with respect to the ADL at a specific depth is highest when BFT is high (fig. 6).

TABLE 1

VALUES OF Ω AND ρ FOR DIFFERENT AQUATIC BIRD GROUPS

| Group | $\Omega \times 10^{-4}$ ($m^3$ $kg^{-1}$) | $\rho_b \times 10^3$ ($kg$ $m^{-3}$) | $N$ | $F_{Up}$ (N) | Depth 1: $F_{Up} = 0$ (m) | Depth 2: $F_{Up} = 1$ (m) | EE ($J$ $s^{-1}$) | EE × BMR |
|---|---|---|---|---|---|---|---|---|
| Gulls (Laridae) | 9.8 | .94 | 5 | 11.8 | ... | 275 | 67.8 | 10.6 |
| Dabbling ducks (Anatidae) | 5.1 | .98 | 6 | 6.8 | ... | 74 | 40.0 | 8.7 |
| Petrels (Procellariidae) | 4.9 | .99 | 10 | 6.5 | ... | 62 | 38.0 | 8.8 |
| Diving ducks (Anatidae) | 3.7 | .99 | 3 | 5.3 | ... | 49 | 32.3 | 7.0 |
| Auks (Alcidae) | 3.3 | 1.00 | 2 | 4.8 | ... | 39 | 31.7 | 5.0 |
| Divers (Gaviidae) | 3.1 | 1.06 | 1 | 4.0 | 68 | 19 | 25.4 | 5.5 |
| Penguins (Spheniscidae) | 2.3 | 1.02 | 2 | 3.6 | 185 | 22 | 22.9 | 5.8 |
| Cormorants (Phalacrocoracidae) | 1.8 | 1.03 | 2 | 3.0 | 103 | 16 | 20.8 | 4.3 |

NOTE.—Sample size ($N$) is the number of species sampled. The upthrust at the surface ($F_{Up}$) and calculated depths where upthrust has values of 0 N and 1 N are also shown. Columns designated EE show the theoretical energetic expenditure (in J s⁻¹ and as a multiple of BMR) for the different groups swimming at 1 m below the water surface. All birds are assumed to have a mass of 1 kg.

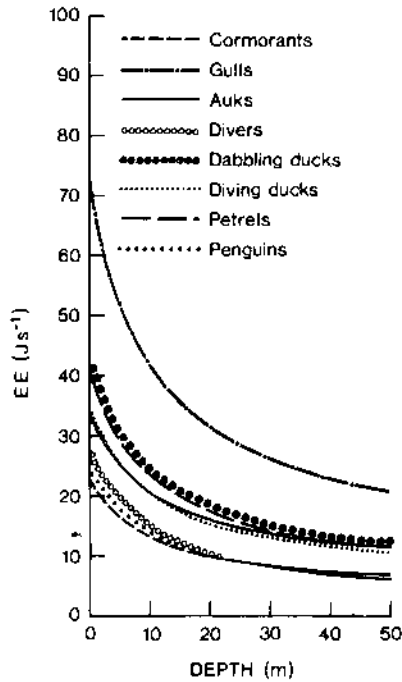FIG. 2.—Theoretical relationship between energy expended per second (EE) and water depth for "typical" 1-kg birds from different families with $\Omega$ and $\rho_b$ values given in table 1. EE is calculated from eq. (12) and does not incorporate any energy expenditure resulting from speed-related drag; see text.
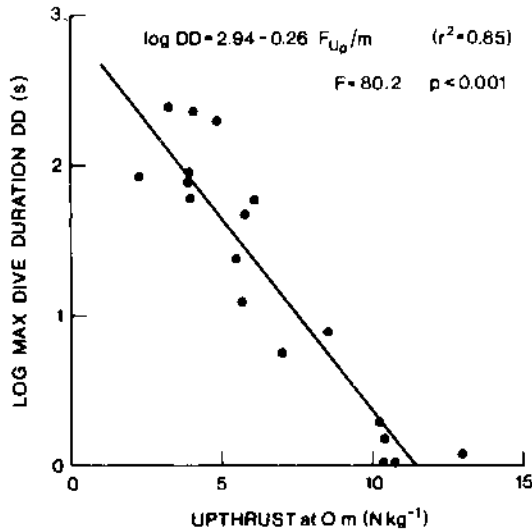


FIG. 3.—The upthrust ($F_{Up}$) per kilogram of body mass experienced by various bird species in relation to their maximum recorded dive durations. Data from Dewar (1924), Kooyman (1975), Wilson (1985), Wanless et al. (1988), Wilson and Wilson (1988), Duffy (1989), C. Bost (unpublished data), T. Chaurand (unpublished data), and Percy FitzPatrick Institute of African Ornithology.
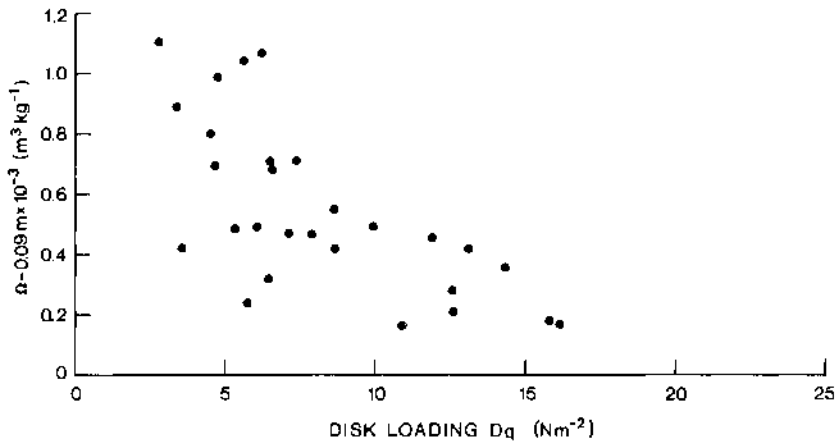
FIG. 4.—Relationship between disk loading ($D_q$) (a measure of the cost of flight) and volume of air in the feathers per unit body mass (and corrected for body mass effects; see text) for different bird species.
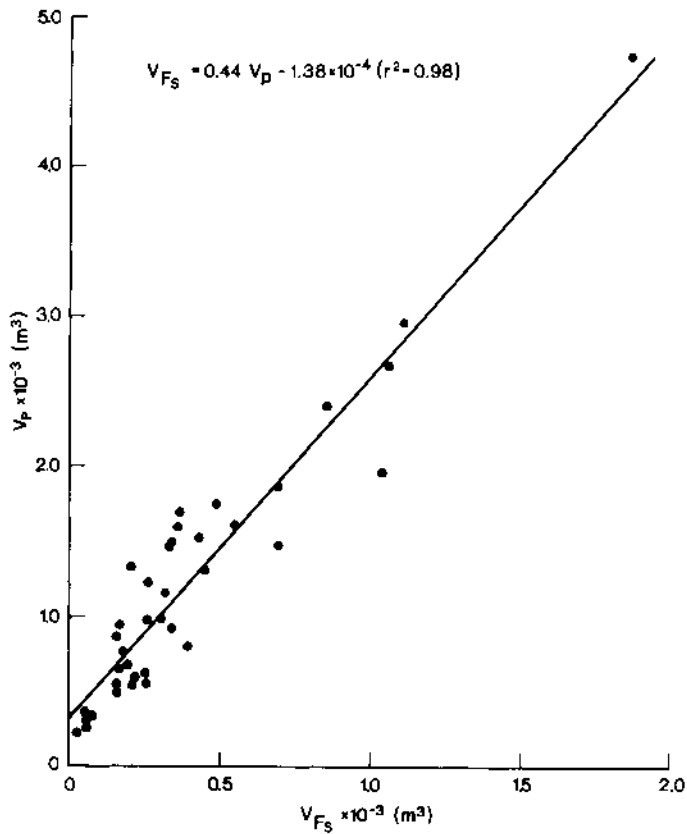


FIG. 5.—Relationship between the determined volume of air in the feathers ($V_{F_s}$ from displacement estimates) and the predicted volume ($V_p = 8.11 \times 10^{-2} \, m^{0.667}$ BFT) for water birds.
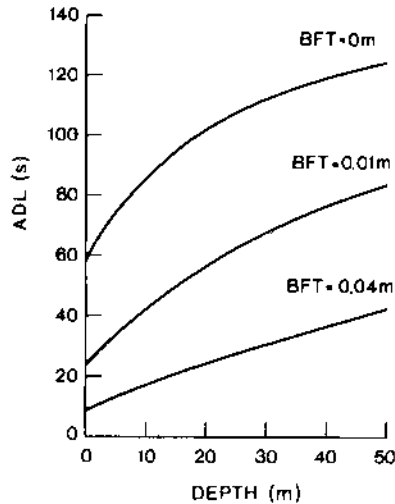
Fig. 6.—Relationship between the theoretical aerobic dive limit (ADL) and depth (eq. [14]; see text) for 1-kg birds with different breast feather thicknesses (BFTs), assuming that the birds incur no energy costs resulting from speed-related drag. The term for the volume of air in the feathers in the equation is calculated from $V_{F_3} \approx (3.57 \times 10^{-2} \, BFT) - 1.38 \times 10^{-4}$ (see text), and bird body $\rho$ is assumed to be $1.0 \times 10^3 \, kg \, m^{-3}$.

## DISCUSSION

Birds have morphological, physiological, and behavioral traits that enable them to minimize energy expenditure (Kendeigh et al. 1977; Whittow and Rahn 1984). Diving species have three major energetic costs: homeothermy, flight, and underwater swimming. The more a bird is adapted to reduce one of these costs, the more energy it expends for the other two.

When body temperatures are maintained higher than ambient temperatures, heat loss can be reduced by insulation through subdermal fat or air in the feathers. Fat has a conductivity approximately 10 times that of air and is 700 times more dense (R. D. Harrison 1972; Chato 1985; Campbell 1986). The densities of the two insulators have important consequences for avian energetics. Flying or underwater-swimming birds must spend more energy maintaining their position (height or depth) when the density of their insulating layer increasingly differs from the density of the medium through which they are traveling. The high density of fat compared with air makes it less suitable for insulation in flying birds because the energetic cost of flight is highly dependent on mass (Pennycuick 1975). Conversely, the low density of air in feathers results in substantial upthrust in diving birds that necessitates a high energy expenditure. Although air volume decreases with increasing depth so that the upthrust also decreases, the insulative capacity also decreases. Water conducts heat 25 times better than air, so heat loss in a submerged bird is potentially particularly high. Fat is essentially incompressible, so its insulative capacity is unchanged by depth. Similar densities of fat and water mean that when fat is used as an insulator, there is little increase in upthrust.

Finally, in species that spend much time sitting on the water surface, air in the plumage will tend to make the bird float higher and thus reduce the surface area in contact with water, which will tend to reduce heat loss (see Stahel and Nicol 1982). Thus, air in feathers for optimal homeothermy and flight is not compatible with minimized diving costs. Subdermal fat for homeothermy and diving is not compatible with minimized flight costs. This clarifies why birds that fly far to forage for chicks do not dive deep and vice versa. Presumably, the optimal strategy for minimizing overall energetic expenditure is dependent on ambient temperatures and the amount of time spent flying, resting on the water's surface, and diving.

Our results show that virtually all birds depend to some extent on air for insulation. Since thermal resistance increases with increasing feather thickness (Chato 1985), we would expect, in both diving and nondiving volant seabirds, the air layer thickness in plumage to increase with increasing latitude. This general trend has been demonstrated for penguins by Stonehouse (1970). Our attempts to correlate BFT with latitude as a function of mass for all our aquatic birds were unsatisfactory mostly due to large variance, presumably caused by highly varied bird life-styles requiring correspondingly varied $\Omega$ values (and hence BFT values). Examination of latitudinal trends would have to be done within narrow taxonomic and ecological groupings. This necessitates an extensive data base for each group. In general, reduced $\Omega$ values for diving birds over all latitudes, compared with nondiving birds, indicate a lower BFT, and hence the insulative capacity of the plumage is presumably compromised. This may be partially compensated by denser plumage, where keratin from the feathers may aid in insulation (Tregear 1965). High feather density and high body densities presumably help compensate for air-induced buoyancy. Both parameters will, however, tend to increase disk loading and thus the energetic cost of flight.

Reduction in feather-entrapped air resulting from increased hydrostatic pressure at depth will diminish the insulative capacity of the feather layer, which will tend to lead to heat loss. This should nominally lead to an increase in metabolic rate (Culik et al. 1989), which in reality may be partially or wholly compensated by muscle-produced heat (Paladino and King 1984). However, heat produced from muscles used in working against buoyancy does not equate directly with heat loss derived from depth-induced changes in feather insulative capacity because the air layer is thickest at the surface where most muscular heat would be produced. Whether depth actually does lead to an increase in metabolic rate as a direct consequence of compromised insulative capacity will depend largely on peripheral heat conservation mechanisms such as vasoconstriction.

Although wing-mediated underwater propulsion necessitates small wings, which leads to high disk loadings and high energy expenditure during flight (Pennycuick 1987), it is not immediately obvious why foot-propelled diving birds should not have larger wings to compensate for the increased mass derived from body $\rho$ values. In our experiments, we did not quantify water displacement by the wings alone; however, all wing surfaces were coated with entrapped air when taken underwater. Diving birds can thus reduce energy expenditure underwater

by having smaller wings. Any features of the plumage that result in increased air retention (e.g., large tail feathers) are expected to have similar effects. Diving species are thus predicted to have smaller tails than nondiving species, and it is perhaps for this reason that feet are often used by diving species as a substitute for the tail in flight.

The reduction in air volume with depth reduces upthrust and therefore the power needed by the bird to swim against it. Thus, with increasing depth, diving birds potentially have more power available. This power may be used to increase swimming speed, which would, however, increase drag. It was found that white-breasted cormorants do indeed increase their traveling speed along the seabed in deeper water (Wilson and Wilson 1988). This behavior may enhance foraging efficiency by enabling birds to search a greater area in a shorter time.

Our dive model assumes that all power output by a diving bird is used to counteract upthrust so that the bird merely maintains its position in the water column. A more realistic approach should take into account the power required for active displacement. These energetic costs must be added to the costs of countering upthrust. Power costs for movement are dependent on the drag coefficient of the bird and on the cube of the swimming velocity (Kooyman and Davis 1987). The overall energy dissipated during a dive can be determined as the integral of the curve of EE against depth over time (fig. 2), plus the energy required for swimming at the given velocity. Energy expended swimming against upthrust is minimized by descending the water column as quickly as possible, but in order to minimize overall power output, the swimming speed must be controlled.

We predict that any reduction in air volume reduces EE in all diving birds and that reduction in air in the feathers will extend the ADL (fig. 6). However, whether a reduction in the volume of respiratory air can result in increases in the ADL depends on the values in equation (15) and is critically dependent on the proportion of air contained in the feathers compared with that in the respiratory air spaces (fig. 7). In general, birds with large $\Omega$ values always extend their ADL by inspiring fully. However, as $\Omega$ decreases to less than $1.0 \times 10^{-4}$ $m^3$ $kg^{-1}$, ADLs can be increased by exhaling (fig. 7). Furthermore, birds with high $\rho_b$ values can substantially extend their ADL by balancing the downthrust due to body density with upthrust due to $\Omega$ plus the respiratory volume. This strategy would be particularly applicable to divers, cormorants, and anhingas. Involuntary reduction in respiratory air space may occur in birds due to distension of the digestive system following food ingestion (Casler 1973), and ADLs may be altered accordingly.

Much literature exists comparing dive durations with dive depths (e.g., Dewar 1924). For bottom-foraging species, dive durations are considered to increase with water depth due to increased transit time (Dewar 1924; Batulis and Bongiorn 1972). However, detailed studies indicate that the time spent on the bottom also increases with water depth (Wilson and Wilson 1988; Stephenson et al. 1989a). This enables birds to maintain transit time and bottom time in similar proportions over a range of depths. However, the physiological consequences of supposed
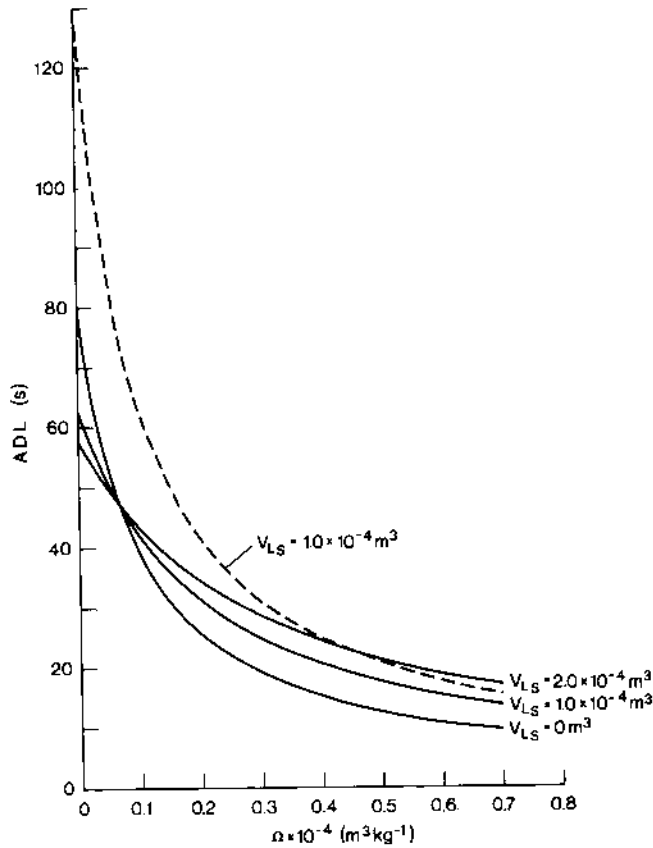
FIG. 7.—Theoretical aerobic dive limit, ADL (s), for a 1-kg pelecaniform that is maintaining a position just beneath the water surface as a function of the air contained in the feathers, $\Omega$, for different respiratory volumes, $V_{L_r}$. The *solid lines* refer to a bird with a body density of $1.0 \times 10^3$ kg m$^{-3}$. The *dashed line* refers to a bird with a body density of $1.1 \times 10^3$ kg m$^{-3}$.

oxygen demands on optimal foraging are unclear (Wilson and Wilson 1988). The reduction in energy necessary for swimming against buoyancy with increasing depth may wholly account for increased dive durations with no change in total oxygen usage per dive, even at greater depths. The premise that it is always energetically favorable for bottom-foraging birds to hunt in shallower water when prey is distributed evenly over all depths (Wilson and Wilson 1988) is thus not tenable. For a fixed prey abundance, the optimum foraging depth will depend on the energetic component described in our model, the total oxygen store, and the ratio of transit time and energetic costs to bottom time and energetic costs.

In general, it is energetically more costly to forage just beneath the surface rather than deeper so that, contrary to conventional thinking, exploitation of

surface-swimming prey may be less rewarding than deeper-dwelling species. Excepting birds with very little air in their feathers, most birds search for surface-swimming prey from the air (terns, gannets, boobies, gulls), the water's surface (gulls), or some vantage point (kingfishers). Only when prey has been sighted can the high cost of underwater forays be justified. Subsequently, kinetic energy, derived from a plunge, can be used to overcome the energetic "hill" constituting submergence at the surface. The high cost of swimming underwater, either via upthrust or heat loss, is probably the reason why most diving birds are carnivorous since poor-quality plant food is not compatible with high energetic expenditure. Aquatic vegetarian birds generally do not dive to forage but can marginally increase the depth of water in which they can effectively feed by "up-ending" (dabbling ducks) or by having long necks (swans).

### Consequences of $\Omega$ and $\rho$ for Different Seabird Groups

Gulls (Lariidae) and albatrosses (Diomedeidae), with high $\Omega$ values and low $\rho_b$ values (table 1; Appendix), are ill adapted for diving. Some species occasionally plunge-dive for a few seconds (Voisin 1981, 1982) but do not descend deeper than 1 m (Coblentz 1985; Prince and Morgan 1987). Large wings make flight costs in both groups particularly low (Baudinette and Schmidt-Nielsen 1974; Costa and Prince 1987), and foraging ranges in breeding birds may be extensive (Weimerskirch et al. 1988). Gannets (Sulidae) have considerably less air in their plumage than either gulls or albatrosses (Appendix). Considerably reduced upthrust, coupled with high momentum derived from high plunge dives, allows these birds to penetrate up to 10 m underwater (Percy FitzPatrick Institute of African Ornithology, unpublished data). Dives may be extended by active swimming at depth (Schreiber and Clapp 1987) where upthrust is minimized. Petrels (Procellariidae) have high variability in $\Omega$ values according to their diving habits ranging from giant petrels ($\Omega = 9.1 \times 10^{-4}$ m$^3$ kg$^{-1}$), which rarely dive (Prince and Morgan 1987), to shearwaters ($\Omega = 5.6 \times 10^{-4}$ m$^3$ kg$^{-1}$; great shearwater, *Puffinus gravis*), which dive regularly (Brown et al. 1978), some species as deep as 20 m (Skira 1979). The Procellariidae cover a large continuum of foraging strategies intermediate in flight costs and diving costs (and hence foraging range and diving depth) between albatrosses and auks. Flight costs in auks (Alcidae) are extremely high due to their small wings adapted for underwater swimming (Pennycuick 1987). Accordingly, foraging ranges of birds with chicks are generally less than 20 km (Bradstreet and Brown 1985). Although auks have further reduced amounts of air in their plumage ($\Omega = 3.3 \times 10^{-4}$ m$^3$ kg$^{-1}$), they are among the most buoyant seabirds that rely exclusively on pursuit diving for foraging. They thus float high on the surface, which presumably reduces heat loss for the months when the birds are pelagic. The energetic cost of diving is, however, predicted to be relatively high near the water's surface (fig. 2), so it is not surprising that auks are exceptionally deep divers (Prince and Harris 1988). Penguins (Spheniscidae) have little air in the feathers ($\Omega = 2.3 \times 10^{-4}$ m$^3$ kg$^{-1}$), much insulation being provided by fat and thick skin (Drent and Stonehouse 1971; Jarman 1973; Kooyman et al. 1976). Although penguins can dive deep (Croxall and Lishman

1987; Croxall et al. 1988), high $\rho_b$ values and low $\Omega$ values, possible as a result of flightlessness, enable penguins to be one of the few seabird groups efficient at pursuit diving in shallow water (see Wilson et al. 1991 and references therein). Cormorants (Phalacrocoracidae) had the lowest $\Omega$ values of any of the birds we examined and appear well adapted to dive in shallow water, where most species are reported to feed (Schreiber and Clapp 1987). The small quantity of air trapped in the plumage results from feather wettability (Rijke 1968, 1971). This will tend to make heat loss high, which may explain why cormorants are entirely coastal (Schreiber and Clapp 1987), only remain in the water for short periods, and are predominantly distributed in warmer water (P. Harrison 1983). Anhingas also have highly wettable plumage. Wettable wing feathers do not contribute to upthrust, so wing size does not impose energetic constraints on diving efficiency. It is notable that both cormorants and anhingas have exceptionally large wings compared to other diving birds, and both groups may soar.

## CONCLUSIONS

This work indicates that $\Omega$ and $\rho_b$ are important parameters in determining the energetics of diving birds. The relationship between $\Omega$, BFT, and mass provides a means by which the energetics of many birds can be examined without plucking. Breast feather thickness is known to be highly correlated with mass (Stonehouse 1970). The reasons for this and the energetic consequences for diving birds, with heat loss decreasing according to surface area (and feather thickness)—that is, volumetric effects—may indicate optimal body masses for divers. Future studies are necessary to address changes in BFT and $\Omega$ with mass over varying latitudes within narrow taxonomic and ecological groups to examine how the necessity of insulation affects diving and flying activities. Ultimately, this work should be put into perspective by experimental assessment of the energy cost of diving birds in relation to upthrust.

## APPENDIX

### TABLE A1

| Species | $\Omega \times 10^{-3}$ $(m^3\ kg^{-1})$ | $\rho_b \times 10^3$ $(kg\ m^{-3})$ | $BFT \times 10^{-2}$ $(m)$ | $F_{U_B}$ per Bird $(N)$ |
|---|---|---|---|---|
| *Anas capensis* | .34 | 1.00 | 1.0 | 1.9 |
| *Anas undulata* | .33 | 1.01 | 1.3 | 4.2 |
| *Aythya fuligula* | .33 | 1.10 | 1.8 | 1.6 |
| *Bucephala clangula* | .46 | 1.01 | 1.5 | 2.1 |
| *Dendrocygna viduata* | .59 | .95 | 1.2 | 3.0 |
| *Eudyptes chrysocome* | .25 | .99 | 1.6 | 6.7 |
| *Fulmarus glacialis* | .53 | .93 | 1.5 | 4.6 |
| *Gallinula chloropus* | .42 | 1.03 | 1.3 | 1.6 |
| *Gavia stellata* | .31 | 1.06 | 1.6 | 7.5 |
| *Halobaena caerula* | .34 | .97 | 1.2 | .8 |
| *Histrionicus histrionicus* | .64 | . . . | 2.8 | . . . |
| *Larus argentatus* | .79 | .89 | 2.5 | 8.9 |
| *Larus dominicanus* | 1.15 | .99 | 3.5 | 11.7 |
| *Larus hartlaubii* | .91 | 1.00 | 1.8 | 2.1 |
| *Larus ridibundus* | .98 | .96 | 2.0 | 3.2 |
| *Macronectes giganteus* | .91 | 1.00 | 4.5 | 89.9 |
| *Morus capensis* | .37 | .95 | 1.7 | 17.2 |
| *Pachyptila vittata* | .26 | 1.00 | 1.4 | .5 |
| *Pelecanoides urinatrix* | .37 | 1.00 | 1.2 | .5 |
| *Pelagodroma marina* | .42 | .98 | 1.0 | .2 |
| *Phalacrocorax capensis* | .27 | 1.04 | 1.2 | 2.2 |
| *Phalacrocorax carbo* | .09 | 1.01 | 1.0 | 8.1 |
| *Phoebetria fusca* | .87 | .96 | 3.5 | 26.0 |
| *Pterodroma brevirostris* | .52 | .95 | 1.7 | 2.0 |
| *Pterodroma incerta* | .51 | .99 | 2.0 | 3.7 |
| *Pterodroma mollis* | .52 | 1.02 | 2.0 | 1.8 |
| *Ptychoramphus aleuticus* | .30 | .99 | 1.2 | .6 |
| *Puffinus gravis* | .56 | 1.01 | 2.0 | 6.8 |
| *Rissa tridactyla* | 1.07 | .85 | 1.9 | 4.6 |
| *Somateria mollissima* | .31 | .87 | 1.5 | 8.9 |
| *Spheniscus demersus* | .21 | .99 | 1.3 | 7.1 |
| *Stercorarius lönbergi* | .83 | .95 | 3.0 | 14.2 |
| *Sula bassanus* | .62 | .92 | 1.7 | 15.9 |
| *Tadorna cana* | .57 | .97 | 1.6 | 9.5 |
| *Tadorna tadorna* | .56 | .97 | 1.8 | 5.6 |
| *Uria aalge* | .33 | 1.00 | 1.8 | 4.2 |

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