Fur does not fly, it floats: buoyancy of pelage in semi-aquatic mammals

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Abstract

The transition from a terrestrial to an aquatic lifestyle in mammals required the evolution of specific adaptations for locomotion and stability in water. We postulated that the non-wettable fur of semi-aquatic mammals is an important adjunct to buoyancy control. Fur buoyancy characteristics and hair morphology were examined for two terrestrial mammals (opossum, *Didelphis virginiana* and Norway rat, *Rattus norvegicus*), and seven semi-aquatic mammals, (beaver, *Castor canadensis*; sea otter, *Enhydra lutris*; Australian water rat, *Hydromys chrysogaster*; river otter, *Lutra canadensis*; American mink, *Mustela vison*; muskrat, *Ondatra zibethicus*; and platypus, *Ornithorhynchus anatinus*). We determined buoyancy hydrostatically, measured hair density on histological skin samples, and hair length and diameter. Buoyancy was positively correlated with hair density, but was not with hair length or thickness. As expected, buoyancy was considerably greater in aquatic mammals than in terrestrial mammals. *Enhydra* displayed the greatest hair density (1188.8 hairs/mm^2) with a buoyant force of 0.94 N, whereas *Rattus* had the lowest hair density (95.2 hairs/mm^2) and *Didelphis* had the lowest fur buoyancy of 0.12 N. High hair density of non-wettable fur traps large amounts of air and thus provides semi-aquatic mammals with positive buoyancy and decreases the effort needed to float.

Key words: buoyancy, fur, semi-aquatic, hair density, flotation

Introduction

The transition from a terrestrial to an aquatic lifestyle in mammals required adaptations for enhanced locomotor performance and stability of the animal in water (Howell, 1930; Fish & Stein, 1991; Fish, 2001). Specific adaptations include changes in body shape towards greater streamlining and modifications in the propulsive appendages (Fish, 1993*a, b*; 1996). However, relatively few studies have examined adaptations that affect buoyancy of mammals in water (Johansen, 1962; Kooyman, 1973; Clarke, 1978; Domning & de Buffrénil, 1991; Fish & Stein, 1991; Webb *et al.*, 1998; Skrovan *et al.*, 1999). Buoyancy control is an important determinant of energetic costs of swimming, diving, stability at rest, and associated behaviours, such as escape from predators and foraging in water (Clarke, 1978; Skrovan *et al.*, 1999; Williams *et al.*, 2000).

Marine mammals, such as grey seals, *Halichoerus grypus* (Beck *et al.*, 2000) and northern elephant seals, *Mirounga angustirostris* (Webb *et al.*, 1998), exhibit significant seasonal changes in body mass and composition that affect buoyancy. In bottlenose dolphins (*Tursiops truncatus*) changes in buoyancy are associated with lung compression at depth (Skrovan *et al.*, 1999). In these animals, changes in swimming behaviour appear to compensate for any marked changes in buoyancy that could affect dive performance.

Semi-aquatic mammals carry large volumes of air in both the respiratory tract and the pelage during dives. Air trapped in the pelage is a property of the dense waterproof fur possessed by semi-aquatic mammals (Sokolov, 1962, 1982; Reynolds, 1993). The waterproof fur will confer protection against heat loss in water and also contributes to the positive buoyancy of individual animals. Muskrats possess an air layer representing 21% of the body volume, which reduces the animal's specific gravity to 0.79 (Johansen, 1962). Positive buoyancy is expected to greatly increase energetic and mechanical costs of diving and prolonged submergence (Stephenson *et al.*, 1989; Alexander, 1990; Taylor, 1994). Biomechanical studies of diving waterfowl

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suggest that buoyancy contributes significantly more to the locomotor costs of shallow diving than does body drag (Lovvorn & Jones, 1991*a*, *b*).

The purpose of this study was to investigate the relationship between buoyancy and fur properties for a variety of semi-aquatic mammals.

Materials and Methods

We measured buoyancy of pelage (skin and hair) samples from the mid-dorsum of seven species of semi-aquatic mammals: beaver (*Castor canadensis*), sea otter (*Enhydra lutris*), Australian water rat (*Hydromys chrysogaster*), river otter (*Lutra canadensis*), mink (*Mustela vison*), muskrat (*Ondatra zibethicus*), and platypus (*Ornithorhynchus anatinus*); and two terrestrial species: Virginia opossum (*Didelphis virginiana*) and Norway rat (*Rattus norvegicus*). The pelage samples for *Castor*, *Lutra*, *Mustela*, and one specimen of *Ondatra* had been tanned. All other pelage samples were from air-dried pelts that were removed from carcasses of live-caught or stranded animals.

According to Archimedes' principle, the buoyant force on an object immersed in a fluid at rest is equal to the weight of the fluid displaced (Giancoli, 1985; Wilson *et al.*, 1992). Consequently, we calculated the buoyant force (F_{bf} , N) of the entrapped air layer of the fur as:

$$F_{bf} = F_{bt} - F_{bs} \qquad (1)$$

where, F_{bt} is the total buoyant force of the intact fur sample, and F_{bs} is the buoyant force of the sample with fur removed. The buoyant forces F_{bt} and F_{bs} were:

$$F_{bt} = m_{af}\, g - m_{wf}\, g \qquad (2)$$

$$F_{bs} = m_{as}\, g - m_{ws}\, g \qquad (3)$$

where, m_{af} is the pelage mass (kg) in air, m_{wf} is the pelage mass (kg) in water, m_{as} is the skin mass (kg) in air with hair removed, m_{ws} is skin mass (kg) in water, and *g* is gravitational acceleration (9.8 m/s^2). Therefore:

$$F_{bf} = g\, (m_{af} - m_{wf} - m_{as} - m_{ws}) \qquad (4)$$

Because the buoyant force of the fur is equal to the weight of water displaced by the entrapped air, the volume of air in the fur (V, m^3) is:

$$V = F_{bf}/\rho g \qquad (5)$$

where, ρ is density of water (1000 kg/m^3).

To obtain buoyancy measurements, we mounted circular, 12-cm diameter mid-dorsal fur samples on circular glass plates. Samples were glued onto the plate with silicon adhesive, then flattened with a roller to remove air bubbles trapped between the skin and the glass plate. Mass of the pelage and glass plate in air (m_{af}) was measured to the nearest 0.01 g with either an Ohaus E400 or Mettler AE 200 electronic balance. The pelage mass in water (m_{wf}) was obtained by suspending the sample plate with a monofilament sling to the bottom of the balance and weighing the sample plate under water (Fig. 1). A 100 g ballast weight was attached to provide sufficient negative buoyancy to submerge the pelage sample. The sample was submerged to a depth of 10 cm in 20 l of water and water temperature was 20°C. Underwater weight was determined in less than 30 s to minimize buoyancy changes resulting from air bubbles escaping from the fur. The sample was then air-dried for 24-h and reweighed. This procedure was repeated twice to determine measurement error associated with the procedure. The sample was then completely air-dried and the hair shaved from the skin. The entire procedure was repeated for the shaved samples to determine m_{as} and m_{ws}.

Length and width of guard hairs and underfur were measured for 10 randomly-selected hairs of each type, that were wet-mounted on glass slides. Hair length was measured to the nearest 0.1 mm with a Bausch and Lomb dissecting microscope equipped with an ocular micrometer. Hair width was measured at the hair base to the nearest 0.001 mm at 400 × magnification with a Nikon Alphaphot 2 compound microscope and ocular micrometer.

Hair density was estimated from histological sections of the epidermis obtained from each pelage sample. Skin samples with hair attached were fixed in Zamboni's fixative for 12 h, and then dehydrated in ethanol and chloroform. Samples were embedded in blocks of Paraplast wax and sectioned with a microtome at 14 μm intervals parallel to the skin surface. Representative sections were stained with haematoxylin and eosin. Fur density (hairs/mm^2) was estimated by counting the hair stubs within 10 randomly selected ocular grid squares (grid square area = 0.52mm^2) at 100 × magnification; the number of hairs was averaged for the 10 grid fields.

Means and standard deviations (SD) were calculated when two or more samples for a given species were available. We estimated linear associations between variables by Pearson's correlation and least squares regression (Zar, 1984).

Results

Fur properties
Underhair length was positively correlated with guard hair length across all species considered in
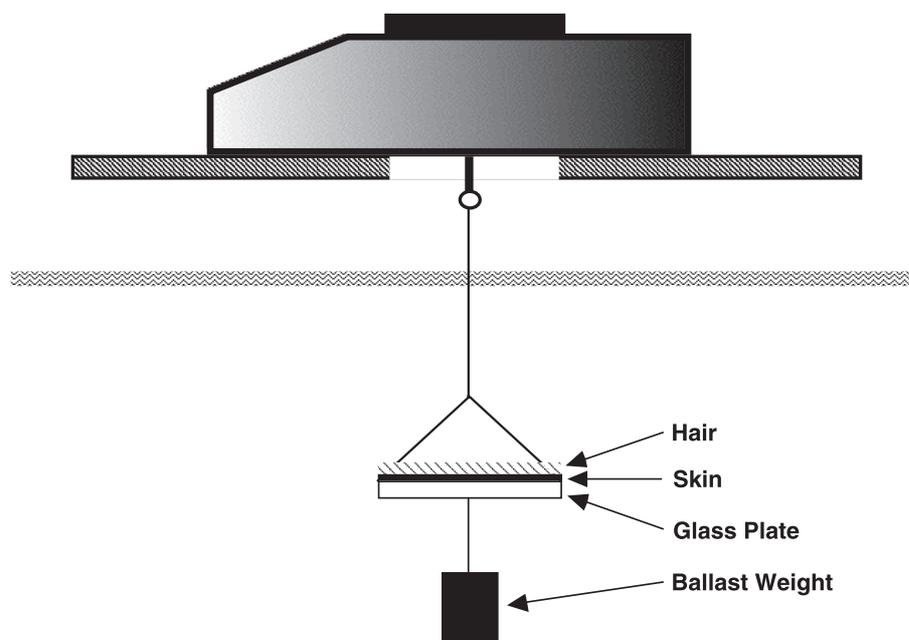
Figure 1. Schematic of apparatus for weighing pelage samples in water. To determine the buoyancy due to the fur and entrapped air layer, the skin was weighed with the hair removed.

this study (r=0.76, *P*=0.018). However, the ratio of guard hair to underhair length was greater (Fig. 2) for the two terrestrial species (3–4) in comparison with the semi-aquatic species (1.4–2). Underhairs of semi-aquatic species were finer (0.009 ± 0.001 mm) and more dense (>300 hairs/mm^2) than those of the two terrestrial species considered (>0.022mm and <150 hairs/mm^2, respectively) (Table 1, Fig. 3). Consequently, there was a weak negative relationship between underhair diameter and hair density (r= − 0.64, *P*=0.06). There were no significant correlations between other fur properties.

Fur buoyancy
Buoyant force, F_{bf}, and calculated fur air volume, of semi-aquatic mammals was 3 to 8 times greater than those of the two terrestrial species examined in this study (Table 1). Buoyancy F_{bf} (N) increased linearly with hair density ρ_h (hairs/mm^3) (Fig. 4) according to the relation:

$$F_{bf}=0.155+0.0007\rho_h \ (r=0.91, \ P<0.001),$$

and was negatively correlated with underhair diameter (r= − 0.72, *P*=0.025).

Discussion

Numerous studies have examined the relationship between mammalian pelage characteristics and insulation and the effects of wetting on insulative properties of fur (Scholander *et al.*, 1950; Johansen, 1962; Frisch *et al.*, 1974; Morrison *et al.*, 1974; Doncaster *et al.*, 1990). In this study, we demonstrated explicitly that the volume of air trapped between hair fibres also is related to the effectiveness of fur as an agent of enhanced buoyancy. These observations suggest that there are important implications of fur structure for energetic and biomechanical cost of swimming and diving in semi-aquatic mammals.

Our laboratory experiments with pelage samples from semi-aquatic and terrestrial mammals suggested that air volume, and consequently buoyancy of fur, was dependent primarily on hair density. Hair of semi-aquatic mammals was considerably finer and denser than that of the two terrestrial species examined in this study. There was also greater similarity of hair length between the hair types in semi-aquatic species compared with the terrestrial species. Additional studies have demonstrated that other morphological fur properties are important in minimizing compression of the pelage and water infiltration as a result of hydrostatic pressure changes during diving (Ling, 1970; Romanenko & Sokolov, 1987). For example, the underfur hairs of semi-aquatic mammals are typified by a large number of kinks (Sokolov, 1962; Grant & Dawson, 1978), and interlocking cuticular scales of adjoining hairs (Williams *et al.*, 1992),
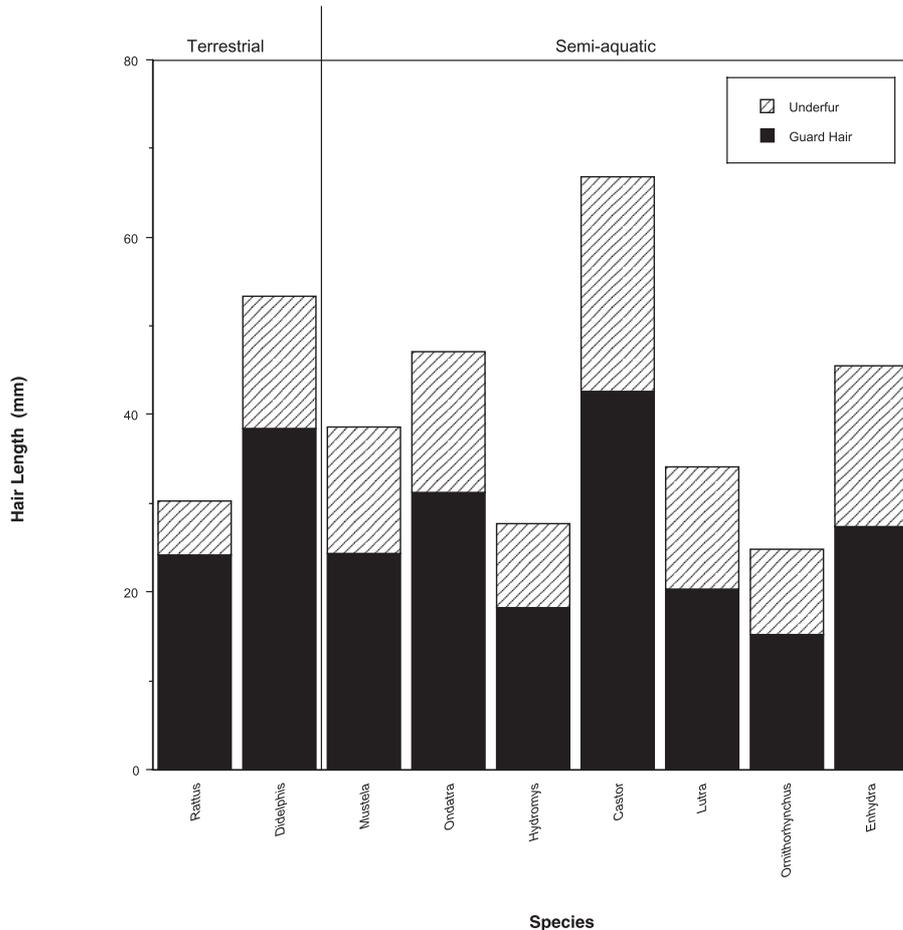
Figure 2. Comparison of guard hair lengths and underfur hair lengths among different species examined in this study.

characteristics that could act mechanically as a spring, and thus aid to resist compression of the air layer (Sokolov, 1962). Water penetration and disruption of the entrapped air volume are further prevented by the interaction of high hair density and water surface tension (Sokolov, 1962, 1982; Romanenko & Sokolov, 1987; Williams *et al.*, 1992). Because water also reduces the insulative properties of the fur (Scholander *et al.*, 1950; Johansen, 1962; Frisch *et al.*, 1974; Morrison *et al.*, 1974; Doncaster *et al.*, 1990), it is evident that specific adaptations of the fur that minimize heat loss will also contribute to enhanced buoyancy.

Hair densities for *Rattus*, *Castor*, *Enhydra*, and *Ornithorhynchus* were close to or within the range of previously reported data (Table 2). Hair density values estimated from tanned skins of *Lutra*, *Mustela*, and *Ondatra* and dried skins of *Hydromys* were higher than reported in previous studies. As

the techniques used to measure fur density were often not reported in these studies, it is difficult to determine if differences are due to preparation of the pelage sample. A potential source of error was the comparison of tanned and dried skins. Because the tanning process could stretch the skin, hair density would be expected to be underestimated; whereas shrinkage due to drying of the skin would produce an over-estimate of hair density. In addition, differences in hair density may be a function of the location on the body, season, climate, geographic location, age, and sex (Sokolov, 1962; Kaszowski *et al.*, 1970; Ling, 1970). We have no information on the extent of variability of hair density in the species in this study.

We observed a general positive association between the aquatic habits of a given species with water and fur buoyancy. For example, the buoyancy of the fur from the mink was lower than that

Table 1. Mean buoyancy and hair measurements ($\pm$ SD) by species with terrestrial (T) or semi-aquatic (S) habits.

Species	Habit	N	F_{bf} (N)	V ($\times 10^{-3}$m)	Guard hair length (mm)	Underfur length (mm)	Guard hair diameter (mm)	Underfur diameter (mm)	Hair density (hairs/mm²)
Didelphis virginiana	T	1	0.12 (0.00)	1.06 (0.00)	38.4 (0.0)	15.0 (0.0)	0.086 (0.000)	0.037 (0.000)	130.76 (0.00)
Rattus norvegicus	T	2	0.18 (0.01)	1.65 (0.00)	24.2 (0.2)	6.1 (0.0)	0.114 (0.007)	0.022 (0.002)	95.19 (6.73)
Castor canadensis	S	1	0.69 (0.00)	6.26 (0.00)	42.7 (0.00)	24.2 (0.00)	0.106 (0.000)	0.011 (0.000)	373.07 (0.00)
Enhydra lutris	S	3	0.94 (0.06)	8.48 (0.01)	27.4 (0.9)	18.1 (0.8)	0.079 (0.01)	0.008 (0.001)	1188.77 (70.37)
Hydromys chrysogaster	S	3	0.37 (0.07)	3.33 (0.01)	18.2 (0.9)	9.5 (0.6)	0.094 (0.010)	0.008 (0.001)	454.48 (33.10)
Lutra canadensis	S	1	0.82 (0.00)	7.41 (0.00)	20.3 (0.0)	13.8 (0.0)	0.096 (0.000)	0.009 (0.000)	803.12 (0.00)
Mustela vison	S	1	0.41 (0.00)	3.73 (0.00)	24.3 (0.0)	14.4 (0.0)	0.074 (0.000)	0.009 (0.000)	338.45 (0.00)
Ondatra zibethicus	S	2	0.48 (0.13)	4.31 (0.01)	31.2 (3.4)	16.0 (4.0)	0.054 (0.004)	0.013 (0.000)	396.15 (90.39)
Ornithorhynchus anatinus	S	2*	0.78 (0.00)	7.02 (0.00)	15.2 (3.2)	9.6 (1.2)	0.130 (0.000)	0.008 (0.001)	815.38 (73.08)

*One pelage sample from *Ornithorhynchus* was too small to take buoyancy measurements.
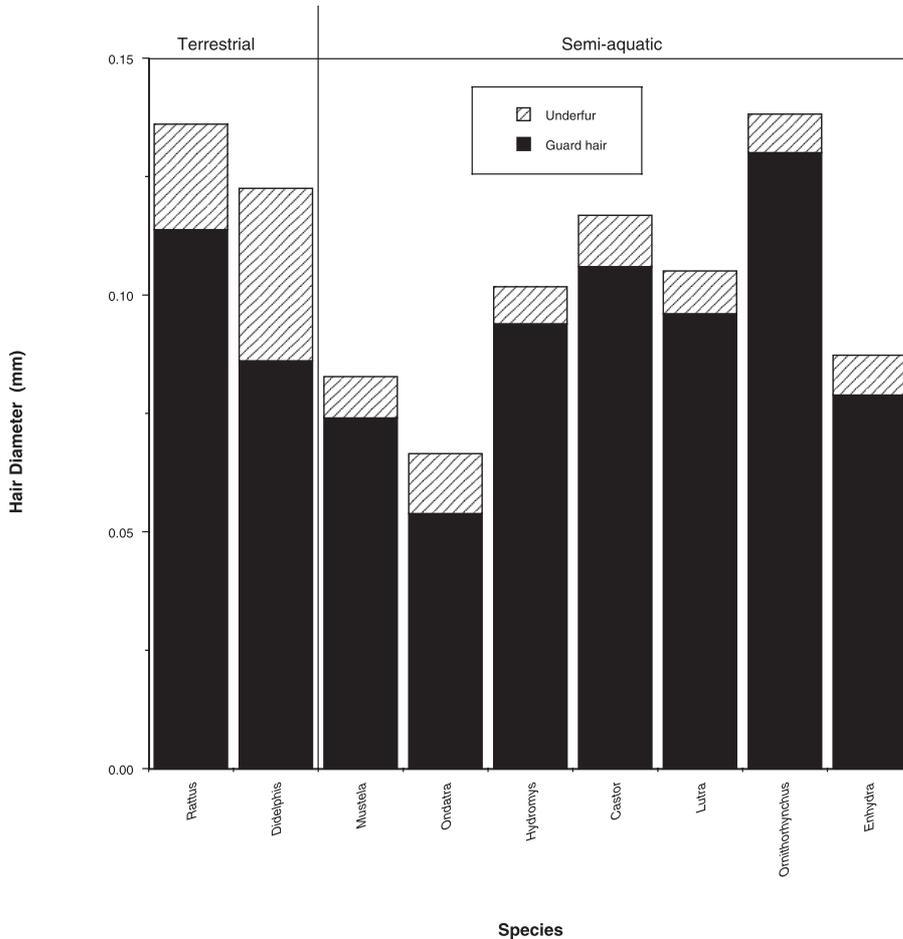
Figure 3. Comparison of guard hair diameters and underfur hair diameters among different species examined in this study.

of most other semi-aquatic mammals, although higher than the two terrestrial species in this study. Mink are not considered to have an obligatory association with water (Estes, 1989) and their swimming mode (i.e., quadrupedal paddling), bone densities and metabolic response to exercise are all indicative of greater terrestrial affinities than are the cases for other semi-aquatic species in this study (Fish & Stein, 1991; Fish, 2000). In contrast, the fur of the primarily marine sea otter was the most dense and exhibited the greatest buoyancy of all pelages tested in this study. In principle, very buoyant mammals with large volumes of air in the pelage, will be better insulated against the cold and highly thermally conductive water medium, but are expected to require more energy to dive to depth and remain submerged. However, sea otters often rest or feed while floating on their back (Kenyon, 1969, 1981), so the energy costs of submergence

may be a relatively small proportion of the energy budget.

Changes in buoyancy that are expected to occur during pelage compression during diving, and related effects on energy expenditure, are yet to be determined for semi-aquatic mammals. It is expected that pressure changes during diving will compress the pelage and allow water infiltration, thus reducing both buoyancy and insulation. Although relatively small changes in air volume have large effects on buoyancy, it has not been determined if buoyancy changes translate to a significant reduction in power costs for diving in semi-aquatic mammals. It has been estimated that a positively buoyant animal could expend 95% of total mechanical energy to work against buoyant forces to submerge (Stephenson *et al.*, 1989). In small-bodied (<1.5 kg) diving ducks, dives to 5 m decreased buoyancy by approximately 40%, but
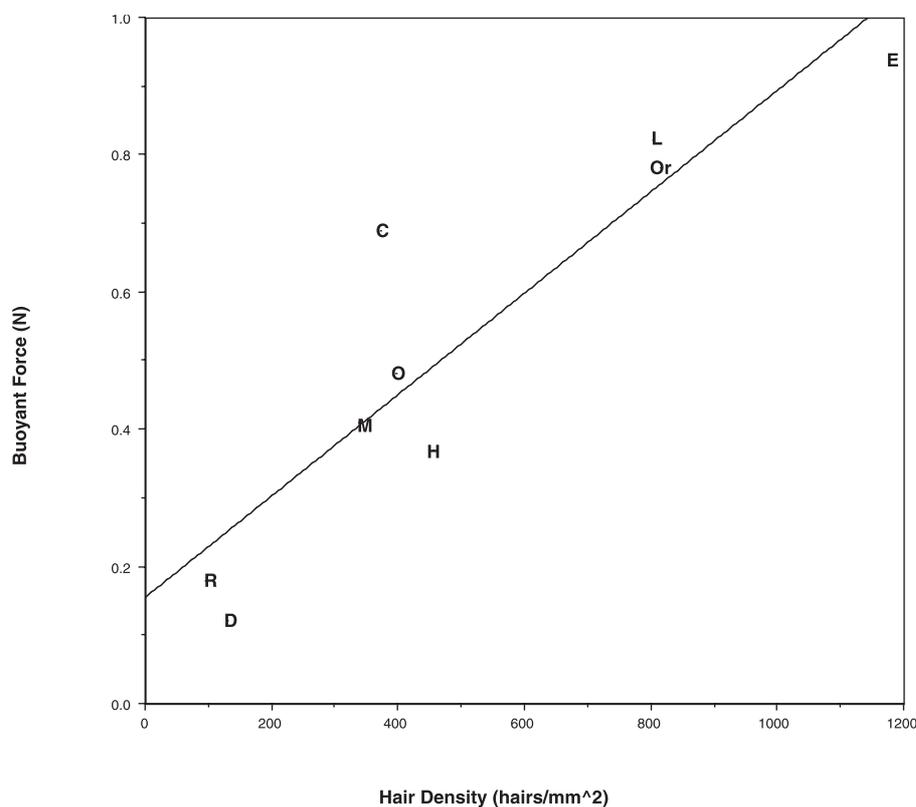
Figure 4. Relationship between means of hair density and pelage buoyant force. Symbols represent semi-aquatic species C, *Castor canadensis*; E, *Enhydra lutris*; H, *Hydromys chrysogaster*; L, *Lutra canadensis*; M, *Mustela vison*; O, *Ondatra zibethicus*; Or, *Ornithorhynchus anatinus*, and terrestrial species D, *Didelphis virginiana*, and R, *Rattus norvegicus*. The equation for the regression line is: buoyant force (N)=0.155+0.0007 hair density (hairs/mm^2).

power requirements for diving were reduced by only 4%. Furthermore, simulated buoyancy studies suggest negative buoyancy only occurs below 40 m (Lovvorn & Jones, 1991*a*). Most semi-aquatic mammals are shallow divers (Howell, 1930; Fish 2000) and even sea otter rarely dive below 55 m (Kenyon, 1969, 1981). Therefore, it is unlikely that many semi-aquatic species regularly achieve depths at which neutral buoyancy occurs. Therefore, for semi-aquatic mammals, enhanced ability to float at the water surface, and reduction in the energetic cost of maintaining trim (Fish, 1993*b*), coupled with a minimization of heat loss, could be of greater importance than reduction of locomotor costs during diving.

Fur has advantages for semi-aquatic mammals as it is a lightweight means of providing insulation on land and buoyancy in water. However, non-wettable fur is subject to water infiltration, is easily fouled, and can be compressed in water (Costa & Kooyman, 1982; Webb & King, 1984; Kruuk &

Balharry, 1990; Loughlin, 1994; Fish, 2000). Maintenance of the air layer necessitates a large fraction of the daily energy budget devoted to grooming. *Lutra lutra* was observed to groom for 18% of its time after swimming in freshwater and 33% of its time after immersion in salt water (Kruuk & Balharry, 1990). Water infiltration into the fur of *Lutra* occurred faster in salt water than in fresh water. *Enhydra* grooms its fur for 11% of the daylight hours (Kenyon, 1969). Grooming increases metabolic rate by 64% above resting level (Williams, 1989). With a shift to a fully aquatic lifestyle by various marine mammals, the fur layer was reduced or abandoned, and subsequently replaced with a thick layer of blubber. Blubber does not incur the high energy cost associated with grooming, it can not be fouled, it is highly insulative in cold water, it can be used as an energy source when food supplies are low, and it is incompressible at depth providing a stable source of buoyancy (Fish, 2000).

Table 2. Hair densities for semi-aquatic mammals from the literature.

Species	Hair Density (hairs/mm^2)	Reference
Rattus norvegicus	76.66	Sokolov, 1962
	88.46–101.92	This study
Castor fiber	309.80	Sokolov, 1962
	373.07	This study
Enhydra lutris	328.75	Sokolov, 1962
	775. 26	Williams *et al.*, 1992
	1008.00	Kenyon, 1969
	1099.99–1272.10	This study
	1253.33	Tarasoff, 1974
	1340.52	Tarasoff, 1972
Hydromys chrysogaster	169.00–193.00	Dawson & Fanning, 1981
	409.61–488.45	This study
Lutra canadensis	578.33	Tarasoff, 1974
	669.37	Tarasoff, 1972
	803.12	This study
Mustela vison	241.58	Kaszowski *et al.*, 1970
	338.45	This study
Ondatra zibethicus	106.61	Sokolov, 1962
	110.00–120.00	Hart, 1956
	305.76–486.53	This study
Ornithorhynchus anatinus	570.00	Sokolov, 1962
	600.00–900.00	Carter, 1965
	669.23 – 815.38	This study
	837.00	Grant & Dawson, 1978

Despite its limitations in water, the possession of non-wettable fur is well suited to mammals that maintain amphibious habits. Fur provides buoyancy for animals that swim at the water surface, while on land the low volume and mass of the fur helps to minimize the energy consumption of terrestrial locomotion and permits freedom of movement by the limbs.

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