Functional correlates of differences in bone density among terrestrial and aquatic genera in the family Mustelidae (Mammalia)

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Summary. Increasing body density by increasing bone density has been cited as a means by which semiaquatic mammals are able to control their buoyancy in water. In order to investigate the relationship of bone density to buoyancy and the degree of morphological adaptation to a semiaquatic existence, we examined limb-bone densities in a single mammalian family. Among genera within the Mustelidae, i.e., weasels and their relatives, there is an apparent trend toward increasing limb-bone density associated with a gradation from a terrestrial to an aquatic way of life. However, the association of increasing bone density with increasing adaptation to an aquatic environment is tempered by the realization that increasing body size may also influence bone density in larger, terrestrial mammals. These results are in accordance with previous data on bone density in other mammalian orders and suggest that a new hypothesis which encompasses historical, physiological, and behavioral information would be best suited to explaining differences in this morphological relationship.

A. Introduction

The evolution from a terrestrial existence to a fully aquatic lifestyle in mammals necessitates the development of a suite of adaptations that enhance locomotor performance and stability in water (Stein 1989). Of prime importance has been the development of a streamlined body form, modification of the appendages as propulsors and stabilizers, and both internal and external structural alterations for buoyancy control. Previous investigations of aquatic adaptations in mammals have focused primarily on locomotor effects resulting from changes in body shape and in the propulsive appendages (Gray 1936; Fish 1984; Williams 1987; Fish et al. 1988). Few studies have examined adaptations which affect the buoyancy of mammals in water. Yet buoyancy control,

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i.e., the ability to dive and surface easily, is intimately associated with the ability to forage successfully and to escape predation, particularly in semiaquatic mammals.

Aquatic mammals are less dense than the water they inhabit (Aleyev 1977; Wall 1983). This positive buoyancy is due in large measure to the inclusion of air-filled spaces in their bodies (e.g., lungs) and to the high concentrations of lipids in their bodies (Howell 1930; Johansen 1962; Ling 1970; Kooyman 1973; Slijper 1976; Clarke 1979). Although these adaptations are advantageous for decreasing the effort needed either to float or to reach the surface from a great depth, low body density does present an impediment to deep diving and to foraging below the water surface. Highly derived aquatic mammals possess dynamic mechanisms such as lung collapse and thoracic compression to regulate body density (Clarke 1979; Kooyman 1989). However, such mechanisms are not found in semiaquatic or less highly derived aquatic mammals such as the sea otter which forage extensively beneath the surface.

Increasing body density by increasing the deposition of compact bone in the appendicular skeleton has been cited as a means by which many semiaquatic mammals are able to increase their specific density in order to overcome buoyancy (Wall 1983; Stein 1989). Although high bone density is also pronounced in most fully aquatic mammals, cetaceans and some pinnipeds that utilize dynamic mechanisms for buoyancy control during deep dives have secondarily reduced bone density (Wall 1983). Contrary to expectations, however, no significant differences in bone densities were found between several species of terrestrial and semiaquatic rodents and marsupials, and some semiaquatic genera were noted to have quite low bone densities (Stein 1989). This result has been viewed as a functional compromise necessitated by the need for semiaquatic mammals to locomote efficiently in two vastly different environments.

We choose to examine the relative densities of limb bones within a single mammalian family in order to test if bone density for buoyancy increases along a gradient with an increased aquatic existence. Members of the

family Mustelidae exhibit a gradation of lifestyles from terrestrial to fully aquatic. Body sizes of the species examined ranged from that of a weasel (<0.3 kg; Baker 1983) to that of a sea otter (>14kg; Kenyon 1969). By examining a single taxonomic family, we could control for differences in bone density that might result from historical constraints and allowed us to examine density differences among genera in direct relationship to the degree of aquatic adaptation exhibited by each species.

B. Materials and methods

Three pairs of species within the Mustelidae, matched according to general body size and habit, were examined. Within each pair one species was considered terrestrial, the other was an aquatic or semiaquatic counterpart. The three pairs, in turn, represent three body size classes of animals within the family. The smallest species examined are *Mustela frenata* Lichtenstein, 1831, the long-tailed weasel, and *Mustela vison* Schreber, 1777, the mink. The largest species are *Gulo gulo* Linnaeus, 1758, the wolverine, and *Enhydra lutris* Linnaeus, 1758. the sea otter. Intermediate in size between these two pairs are *Martes pennantr* Erxleben, 1777, the fisher, and *Lutra canadensis* Schreber, 1776, the river otter.

Wet weights and wet volumes were used to calculate bone densities of the femur, tibia and fibula, humerus, and radius and ulna of six adult specimens for each species as described in Stein (1989) and Wall (1983) (Table 1). Bones were soaked in water for 15min, dropped into a graduate cylinder, and the volume of water displaced was noted. Bones were weighed wet and the density was calculated as wet weight (mass) over volume. Each measurement was made three times and these values averaged for each individual. Because of the paucity of skeletal material of these taxa in museum collections, it was not possible to use bones from only left or right sides of the bodies. It also was necessary to combine sexes in order to have an appropriate sample size. Sexual dimorphism in body size is visually obvious in these taxa and it is acknowledged that the degree of variance in our results **is** exaggerated because of this factor.

Statistical analyses were performed using the SAS package of programs (**SAS** Institute, 1985) on an IBM 3090 at the University of California. Berkeley, Computing Center. Analysis of Variance (ANOVA) and t-test procedures were used to examine differences in the densities of individual limb bones among terrestrial. semiaquatic, and fully aquatic taxa prior to multivariate analyses. Principal components analysis (PCA) run on a correlation matrix was used to explore patterns of relationships among species based on differences in limb-bone densities. Broader patterns relating to ecological and locomotor specializations among species groups were examined using canonical discriminant analysis (CDA). The mustelid data were run by themselves initially (Table 1). Subsequently, however, these data were combined with density values for other mammalian taxa (Wall 1983; Stein 1989) so that more global patterns relating to bone density and buoyancy in mammals might become evident.

Combining our mustelid data with bone density values presented in other studies necessitated establishing definitions of aquatic and semiaquatic mammals that would allow us to analyze the data in a consistent manner. By our definition, aquatic taxa are those species: (1) that exhibit obvious external modifications of both the limbs and body which allow them to live successfully in water, (2) that forage primarily in water, and (3) that use water as a primary means to escape predation. Although most semiaquatic species may be characterized by these last two criteria, obvious external modifications to life in the water was the factor that generally differentiated taxa regarded as fully aquatic and those we considered to be semiaquatic in lifestyle. Fully aquatic mammals possess a fusiform body shape and specialized swimming mode with modified appendages. Therefore, sea otters are classified as aquatic because of their hydrodynamic shape and undulatory swimming mode (Williams 1989) in addition to their independence from a terrestrial habitat (Kenyon 1969). Despite the presence of webbed hind feet in the beaver or insulating blubber in the polar bear, a more terrestrial nature and generalized body form relegate these mammals to the semiaquatic category.

Wall (1983) recognized only two groups of mammals in his study, aquatic and terrestrial. Of the 22 species he designated as aquatic, seven genera were regarded as semiaquatic by our definition. These were the hippopotamus (*Hippopotamus amphibius* Linnaeus, 1758), the pigmy hippo (*Choeropsis liberiensis* Leidy, 1853), the capybara (*Hydrochoerus hydrochaeris* Brisson, 1762), the river otter (*Lutra canadensis*), the muskrat (*Ondatra zibethicus* Linnaeus, 1758), the beaver (*Castor canadensis* Kuhl, 1820), and the polar bear (*Thalarctos maritimus* Phipps, 1774). Therefore, all PCA and CDA were performed three times, first with the mustelid data alone, then with the mustelid data combined with all other bone density data as coded by Wall (1983) and, finally, with Wall's (1983) density data recorded to conform to our definitions of aquatic and semiaquatic. It was hoped that comparison of results between originally coded and recoded data would provide additional understanding of the relationship of body size and ecology to aquatic adaptations and to differences in limb-bone density in mammals.

C. Results

I. ANOVA and t-tests

For the variable femur density no significant differences existed among the terrestrial, semiaquatic, and fully aquatic taxa when the six mustelid species alone were compared. Humerus densities for semiaquatic and terrestrial species were not significantly different from one another. However, humerus density in these two groups did differ significantly ($p=0.0004$) from the humerus density in the fully aquatic sea otter. Differences among the three locomotor groups in tibia and fibula density were not significant (p 0.09). However, density mea-
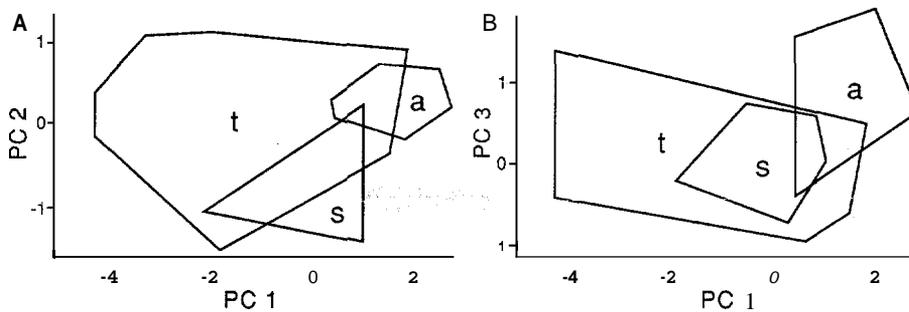
Table 1. Mean ($\pm$ SD) values for limb-bone densities in six mustelid species

Species	Group[a]	Femur	Tibia and fibula	Humerus	Radius and ulna
Mustela frenata	T	1.01 ± 0.14	1.10 ± 0.08	1.10 ± 0.11	1.13 ± 0.26
Mustela vison	S	$1.25 f 0.09$	1.31 ± 0.09	1.22 ± 0.10	1.67 ± 0.11
Martes pennanti	T	1.29 ± 0.14	1.42 ± 0.09	1.35 ± 0.11	1.55 ± 0.05
Lutra canadensis	S	1.22 ± 0.07 [b]	1.38 ± 0.10 [b]	1.30 ± 0.08	1.53 ± 0.13
Gulo gulo	**A**	1.38 ± 0.07	$1.425 0.07$	1.35 ± 0.10	1.63 ± 0.09
Enhydra lutris	**A**	1.35 ± 0.11	1.46 ± 0.06	1.54 ± 0.13	1.67 ± 0.13

[a] T, terrestrial; S semiaquatic; **A,** aquatic
[b] Sample size, 5 rather than 6

Fig. 1A, B. Plot of principle components analysis (PCA) for six species of mustelids: **A** shows a plot of PC 1 **vs** PC 2; **B** shows a plot of PC 1 vs PC 3. The letters indicate the ecological groups, *a* aquatic; *s* semiaquatic; *t* terrestrial

surements of the radius and ulna for fully aquatic and terrestrial taxa differed significantly from one another ($p<0.03$), but each group was not significantly different from the density measurements in the semiaquatic species.

When the mustelid data were combined with density measurements from Wall (1983) and Stein (1989) a somewhat different picture emerged. Femur densities for semiaquatic and terrestrial species did not differ significantly from one another, but densities for the two groups combined did differ significantly ($p=0.0001$) from fully aquatic species. The same was true of differences in humerus density. For tibia and fibula density each of the three groups was significantly different from the other ($p=0.0001$). For radius and ulna density fully aquatic and semiaquatic taxa showed similar densities but densities in these two groups combined differed significantly from those recorded for terrestrial species ($p=0.0001$).

When seven of Wall's (1983) taxa were recoded to conform to the definitions in our study (see above) results of the t-tests differed from those in the previous analysis only for femur density and humerus density. Recoding these taxa caused femur density values for the semiaquatic group to become significantly different from those of the terrestrial species so that all three groups were different from one another ($p=0.0001$). With regard to humerus density, aquatic and semiaquatic species no longer differed from one another, but densities

in these two groups were significantly different from those of the terrestrial species ($p=0.0001$).

II. Multivariate analysis – Mustelid data alone

The degree of overlap amongst individuals of each of the six mustelid species with respect to bone density was extensive (Fig. 1). In the PCA, 76% of the variation among species was explained by the first axis, a general size/density axis as all loadings were positive and approximately equal in value. The second axis, which explained 9.5% of the variation among factors, contrasted increases in femoral and humeral densities with a decrease in radius and ulna density among taxa, thus contrasting differences in densities of the proximal limb bones with those of the distal elements. Loadings for tibia and fibula were not high enough to warrant interpretation on this axis. The third PC axis explained an additional 9% of the variation among species and contrasted humeral against femoral density, or the proximal forelimb element against that of the hind limb. The fourth and final axis contributed 5.5% of the variation among species and contrasted femoral and radius and ulna densities with tibia and fibula density. Although there was only slight overlap among semiaquatic (mink, river otter) and aquatic (sea otter) individuals in this analysis, individuals belonging to large terrestrial species (fisher, wolverine) overlapped these two groups extensively. A clearer separation of aquatic individuals from terrestrial and semiaquatic species was evident when the first PC axis was contrasted against the third (Fig. 1B), suggesting that the dichotomy between differences in forelimbs and hindlimbs in aquatic mammals may be as significant an adaptation in these mammals as is the density relationship of proximal to distal elements in each of those limbs.

Differences in bone density among semiaquatic and terrestrial species of mustelids are obscured when examining the results of the CDA (Fig. 2). However, with the exception of a single sea otter specimen, these two groups are distinct from that fully aquatic taxon when differences in bone density are considered.
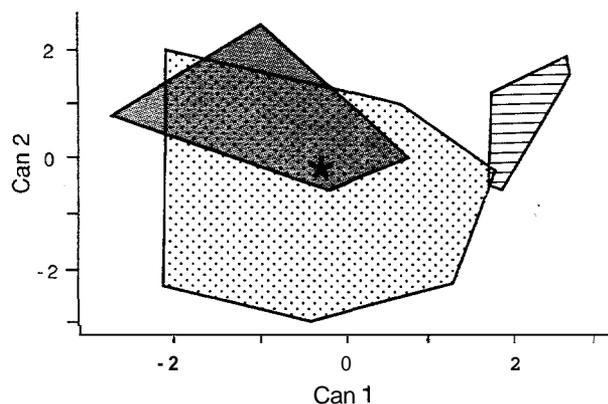

Fig. 2. Plot of canonical discriminant functions analysis for six species of mustelids. Aquatic mustelids are indicated by the *striped area,* semiaquatic mustelids are indicated by the *shaded area,* and terrestrial mustelids are indicated by the *dotted area.* The symbol ✽ represents a single individual sea otter which had lower bone densities than the other sea otters examined

III. Multivariate analyses – All density data combined

When mustelid bone density data are combined with data from Wall (1983) and Stein (1989) representing a
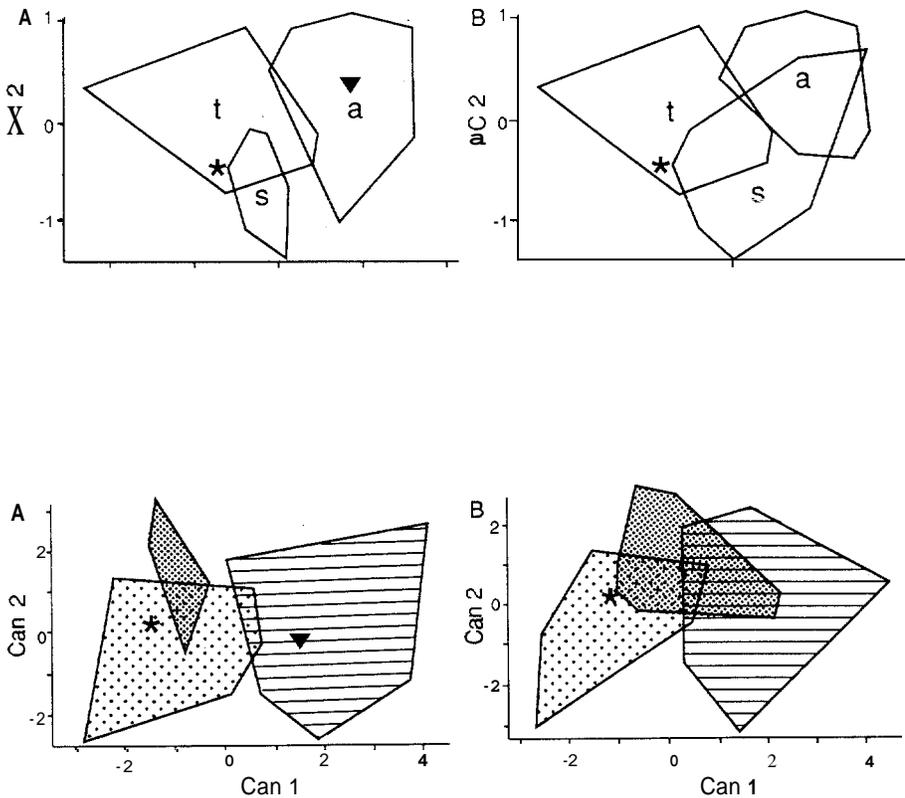
Fig. 4 A, B. Plot of canonical discriminant functions analysis utilizing all data as in Fig. 3: **A** is a plot in which all taxa retained their original group designation; **B** is a plot in which seven taxa from Wall (1983) were recoded. *Striped area* represents aquatic mammals, *shaded urea* represents semiaquatic mammals, and *dotted area* represents terrestrial mammals. Symbols ✳ and ▼ represent *Mirounga* and *Castor*, respectively

broad spectrum of mammalian taxa, a slightly different pattern emerges with regard to the relationship among terrestrial, semiaquatic, and aquatic mammals (Fig. 3). Moreover, the relationship of overall body size to bone density in mammals begins to emerge as one compares the difference between the results of PCA using originally coded and recoded data sets from Wall (1983). In Fig. 3A large mammals such as the hippopotamus and polar bear have limb-bone densities that place them well within the range of values for fully aquatic mammals. By recoding these taxa as semiaquatic (Fig. 3B), the relationship between aquatic and terrestrial mammals remains unchanged. However, semiaquatic taxa now exhibit bone densities that overlap extensively with each of the other two groups of mammals.

In each of the above plots, the first PC axis explains 85% of the variation among taxa in this analysis. This represents 9% more of the variation than that explained by the first axis when only mustelid data were considered. This is not surprising when one notes that body size of species in this larger data set ranges from small rodents, e.g., the rice rat, up through large ungulates such as the rhinoceros. However, the relationship among variables on the remaining axes is similar to the relationship observed for mustelids. The second PC axis accounted for 6.4% of the variation among species and, again, contrasted limb-bone densities of the proximal and distal elements. The third axis explained 4.8% of the variation among species and, as with the mustelid data, contrasted the densities of anterior and posterior limb bones.

Perhaps of greater interest is the way in which relationships of these three ecological/locomotor groups of

mammals change with respect to one another as the assignment of large-bodied taxa from one group to another changes. Figure 4A is a CDA plot of the three groups using Wall's (1983) data as it was originally coded. Figure 4B shows how the relationship among these groups is changed by recoding seven of the genera he examined as semiaquatic, rather than retaining their designations as aquatic (see Materials and methods). Whereas overlap between fully terrestrial and fully aquatic mammals is limited in both instances to heavy-bodied species, semiaquatic genera change from overlapping almost exclusively with terrestrial taxa of any size to overlapping to an equal degree with both terrestrial and aquatic genera. It should be noted that Wall's (1983) density values generally are based on measurements derived from a single individual and, as such, often fall some distance outside the mean value calculated for a given genus in this study, e.g., the river otter. Moreover, as stated in Wall (1983), some fully aquatic genera are known to have secondarily reduced bone density as exemplified by *Mirounga*, the elephant seal. Such low bone densities in pinnipeds and cetaceans are believe to reflect a secondary adaptation for deep diving (Wall 1983; Stein 1989).

D. Discussion

I. Aquatic and semiaquatic species

Although all six mustelid species examined in this study have been cited as proficient swimmers (Kenyon 1969;

Baker 1983; Chanin 1985), certainly they all would not be considered either aquatic or semiaquatic in nature. However, within this family, there is a definite trend toward an increase in limb-bone density that may be associated with a gradation from terrestrial to aquatic locomotor and behavioral habits. Moreover, the time that each species spends in the water and the amount that each species dives below the surface generally varies according to the density of its limb bones.

Sea otters conduct almost all of their life functions in water (Estes 1989). In contrast to most other marine mammals, sea otters have no blubber layer that can be used for buoyancy purposes (Kooyman 1973). Rather, they have a lung volume and lung weight that are greater than in the river otter and the harp seal by more than a factor of two, and it is these structures that they use to maintain a high positive buoyancy on the surface (Lenfant et al. 1970; Kooyman 1973; Tarasoff and Kooyman 1973).

Sea otters have a unique mode of feeding on the water surface (Hall and Schaller 1964), which is aided by the high buoyancy engendered by their lungs. However, this buoyancy must be offset sufficiently to allow them to dive down to 30 m for abalone and other shellfish located on the ocean floor (Kenyon 1969). Increasing limb-bone density would provide a mechanism to facilitate such diving in the absence of more dynamic strategies used to increase body density by other aquatic vertebrates.

Sperm whales change their body density with a spermaceti organ (Clarke 1979). Seals increase body density by reducing lung volume via exhalation prior to submergence, and both seals and cetaceans possess a compliant thoracic cavity to allow lung collapse at great depths (Harrison and Kooyman 1968; Ridgeway and Scronce 1969; Kooyman 1988, 1989). Many species of birds, including penguins, use gastroliths to increase their body density (Olson and Hasagawa 1979). The use of counterweights by human divers helps to speed descent and to avoid swimming efforts (Hong and Rahn 1967).

High limb-bone density in sea otters could be metabolically advantageous by reducing energy costs during submersion until buoyancy could be altered by compression of the lungs with increased depth. This effect is compounded by a 41% reduction in the metabolic cost of swimming in sea otters when submerged as compared to their surface swimming (Williams 1989). In diving ducks, 95% of the work performed during a dive is needed merely to overcome buoyancy (Stephenson et al. 1989).

The increased ballast provided by the generally denser limb bones in sea otters also could aid in stabilization when the animal is submerged. The sea otter's habit of foraging on the bottom for benthic invertebrates, especially abalone, requires it to maintain a stable attitude as abalone must be worked off the substrate by prying or bludgeoning the mollusk with a rock (Chanin 1985). The higher bone densities (Table 1) recorded for both anterior and posterior distal elements in this species would lower the position of its center of mass, thereby increasing stability. The same advantage may be accrued

by possessing a denser pelvis, which is an additional modification that has been noted in this genus (Taylor 1914).

Although Seton (1909) observed that the river otter possessed bones of great weight that enabled it to dive and swim easily underwater, neither this species nor the mink showed the degree of increased limb-bone density that was recorded for the sea otter (Figs. 1, 2). **As** semiaquatic mustelids, the mink and the river otter generally do not dive deeply, nor for extended periods of time, and they eat their food on land (Scheffer 1953; Dunstone and O'Connor 1979; Baker 1983; Chanin 1985). Indeed, the mink shows little morphological specialization for living in an aquatic environment compared to other semiaquatic mammals and it uses an energetically expensive and inefficient mode of swimming (Williams 1983). Because Stein (1989) considered that semiaquatic mammals spend most of their time on the water surface where buoyancy is an aid to aquatic locomotion, it could be argued that an increase in limb-bone density in this species actually might prove disadvantageous.

River otters predominantly prey on fish from the streams and rivers they inhabit (Erlinge 1969; Baker 1983). Moreover, they have a comparatively smaller lung volume than the more specialized sea otter (Tarasoff and Kooyman 1973). **As** such, they do not require much of an increase in bone density in order to dive and to locomote effectively in water. In addition, differences in water density between the marine environment of the sea otter and the freshwater habitat of the mink and river otter make an increase in limb-bone density much more crucial for the sea otter than for the other two species. Because freshwater is 2.5% less dense than sea water (Alexander 1990), swimming and diving by freshwater semiaquatic species does not require their body densities to be as high as densities needed by marine forms in order for these taxa to perform similar functions that require controlled buoyancy both at the water surface and when submerged.

II. *Terrestrial species*

The family Mustelidae includes 25 genera with approximately 70 species, the majority of which are terrestrial. The wolverine is the largest member of this family and can be characterized as a carrion feeder which lacks speed and agility (Walker 1975; Baker 1983). Most mustelids aggressively search for prey and they are able predators. The relatively high limb-bone density recorded for the wolverine may represent the safety factor necessary to accommodate its large body mass and, because of its ambling stride, this increase in density may not cause it to incur a large energetic cost of transport as a consequence.

In contrast, the long-tailed weasel is an active predator whose quick movements presumably require a skeleton without any osteological modifications that would increase density or decrease flexibility. Its foraging strategy lies in great measure in its agility and ferocity rather than in its strength. This species consistently showed

the lowest limb-bone density of any mustelid we examined.

The fisher is intermediate in size between the wolverine and the weasel and is more arboreal in nature than either of the other two. This species is known to live on the ground or in trees and, although not aquatic by nature, it seems to prefer areas near swamps, particularly if there are large trees (Seton 1909). The fisher has been reported to swim across lakes or rivers (Seton 1909). It also is extremely fast and agile. Thus, density values recorded for this species may represent a compromise between strength and speed, agility and stability.

III. General considerations of bone density and aquatic habits

The trends exemplified by members of the family Mustelidae are reflective of the broader trend observed when these data were analyzed together with data on limb-bone densities for other mammalian species (Wall 1983; Stein 1989). As shown in Fig. 4, terrestrial mammal species are generally distinct from fully aquatic species in limb-bone density whereas semiaquatic taxa are intermediate and overlap each of these groups extensively. The position of semiaquatic species between both terrestrial and aquatic taxa indicates that semiaquatic species do represent transitional forms between taxa from divergent environments. Substantial overlap of semiaquatic taxa with terrestrial and aquatic representatives, however, shows the difficulty of recognition of semiaquatic species as a distinct group. Although both mink and river otter are classified as semiaquatic, their capabilities for swimming, diving, and foraging underwater are quite different (Seton 1909; Erlinge 1969; Baker 1983; Williams 1983; Estes 1989). While the otter is inseparable from the aquatic habitat, association of the mink with water is not considered obligatory (Estes 1989).

In vertebrates the mechanical and physiological costs of maintaining the skeleton differ according to mode of life and activity level (Currey 1984) as well as to the constraints dictated by evolutionary history. Theoretically, the costs of maintaining an increased skeletal mass increases according to locomotor function as follows: swimmers, sedentary forms, slow runners, fast runners, and flyers. Thus, for marine mammals such as the manatee, increased bone mass is viewed as a benefit rather than as a cost by helping this animal offset the buoyancy of its lungs (Currey 1984). In contrast, limb bones in terrestrial mammals would be particularly sensitive to selective pressures influencing bone mass owing to inertial considerations. However, an increase in bone mass would not be as costly for slow runners as for fast runners, nor for burrowers as for cursors. This is supported by increased limb-bone densities in the sea otter and the wolverine compared to smaller mustelids.

The generally larger size of semiaquatic mammals when compared to their terrestrial relatives (Wolff and Guthrie 1985) implies that increased bone density in aquatic forms is simply a consequence of large body size associated with historical constraints. Large body size is useful in an aquatic environment for predator avoidance, resource use, heat conservation, and locomotor economy. The development of increased bone density for buoyancy control may have evolved as a by-product of increasing body size which is generally advantageous in amphibious mammals. Thus the advantages of increasing limb-bone density in order to overcome buoyancy would be associated with enhanced bone strength needed to support a large body on land. Increased bone strength is particularly important as body size increases in mammals (Alexander et al. 1979). Stein (1989) postulated that greater limb-bone density commensurate with increased body size in semiaquatic mammals was necessary to facilitate support and movement on land and was later useful in the evolution of aquatic mammals to increase density for diving. Once the transition to an aquatic environment had been made fully aquatic mammals subsequently evolved alternative strategies for overcoming buoyancy that enhanced physiological functions associated with deep diving as well (see above).

Data for skeletal mass in mammals support these hypotheses. They show a positive allometry with body mass (Calder 1984; Schmidt-Nielsen 1984) indicating that as body size increases the mass of the skeleton increases at an even more rapid rate. This allometry is supported by the results of our analyses wherein 76–87% of the variation among species could be attributed to differences in limb density/size alone.

The results obtained in this study indicate that mammalian limb-bone density is associated with the habits of species along a terrestrial-aquatic gradient. Increasing bone density from terrestrial to semiaquatic to fully aquatic life styles implies a structural adaptation for buoyancy control, although body size also may represent a moderating factor in the relationship between bone density and life style. Therefore any consideration of buoyancy and bone density in mammals must be coupled with an understanding of both ecology and physiological mechanisms which may or may not act in concert with bone density to facilitate buoyancy. Any conclusions must also be tempered by an understanding of the contributions which an increase in density must make to bone strength and stability and of how this increase in size and strength can effect locomotion and cost of transport.

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