

ALLOMETRY AND HABITAT-RELATED ADAPTATIONS IN THE POSTCRANIAL
SKELETON OF CERVIDAE

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ABSTRACT

Interspecific variation in the limb dimensions of Cervidae can be separated into two major categories: regular allometric changes correlated with increasing size, and deviations from regular scaling related to particular habitats or locomotor styles. Most dimensions of the skeleton are highly correlated with body weight. Lengths of radius, metacarpal, tibia, and metatarsal have the lowest R-square values. Limb lengths generally scale against body weight with negative allometry, diameters and areas with positive allometry. Exponents for most relationships of forelimb bones are higher than those of the hindlimb; that is, as body weight increases forelimb bones decrease in length more slowly and increase in thickness more rapidly than do hindlimb bones. Cervids are neither geometrically nor elastically similar: exponents for most relationships lie between elastic and geometric values. Differences in scaling between cervids and Bovidae are in part a

consequence of the difference in size range between the two families.

Departures from regular allometric trends in limb lengths were analysed by scaling the length of each limb bone against femur length, and calculating the difference between the actual and the expected length. Small cervids living in dense forest tend to have moderate length or markedly shortened limbs while Hydropotes has elongate limb segments. Most cervids weighing between 40-100 kg have elongate segments. These species are specialized for rapid, highly maneuverable locomotion and for clearing obstacles. Cervids larger than 100 kg generally have shortened limb segments. In large cervids, as in large ungulates generally, specializations for speed may not be as important as in smaller cervids.

INTRODUCTION

The species in the Family Cervidae differ markedly in general body form: some species appear to be relatively long-legged, some short-legged, some have relatively longer hind legs, while in other species the limbs appear more equal in length. Cervids also span a wide range of body sizes, live in different habitats, and display a number of different behaviors. The question can then be posed, are differences in body form a consequence solely of body size, or solely of habitat, or some combination of these and perhaps other factors. This study examines the dimensions of the postcranial skeleton of Cervidae with several objectives. First, the scaling relationships of skeletal dimensions and body weights will be determined for the complete size range of the family to identify those dimensional changes which are dictated by increasing body weight. Second, the mechanical and physical properties of the locomotor system that govern such changes will be evaluated. Third, this study will determine whether deviations from regular scaling related to habitat occur and, if so, the nature and direction of these changes.

The Family Cervidae is an excellent group in which to examine allometric changes and to test predictions which have been made about scaling in ungulates, most of which

have been based on studies of Bovidae. Cervids span a sufficiently wide size range, from approximately ten to 500 kilograms, to allow an accurate determination of scaling relationships; however, the range is narrower than it is in bovids. Although habitats vary, cervids appear to inhabit a narrower range of habitats than do Bovidae. Thus, scaling results for cervids can be contrasted to the well-studied scaling relationships of bovids to answer several interesting questions. First, can theories of scaling be generalized throughout the ungulates. Second, does the size range of the group being studied affect scaling relationships or results. Third, is the apparently wider range of habitats of bovids reflected in wider deviations from regular allometry in this group than in Cervidae?

Scaling Relationships

In any series of related animal species which span a large size range, the geometry of the skeletal system will differ among species of different sizes. As size increases, the dimensions of the supporting skeletal system must change to maintain functional equivalence as the load placed upon the skeleton changes. Such allometric changes are widespread throughout the animal kingdom; cases of isometry, or no change in shape as size increases, are rare

(Gould, 1966). Allometric changes required by increasing size can be separated from those changes related to adaptations to particular habitats or modes of locomotion (Gould, 1975). Groups of related species with similar demands of habitat would be expected to show fewer deviations from regular allometric scaling than groups in which large differences in habitat occur.

In a series of related animals of different sizes skeletal dimensions may change in one of three ways as size increases. Dimensions may maintain the same relationships to each other, so that the shape of the skeleton does not change. This is geometric similarity or isometry. Maintenance of geometric similarity indicates that the same mechanical system is adequate for the size range of the family. Skeletal dimensions may increase more rapidly than increasing body weight; such positive allometry results in larger animals with relatively longer or thicker legs than smaller species. Lastly, dimensions may increase more slowly than body weight, so that limbs become relatively shorter or more slender in larger animals. The dimensional relationships which result if a series of species maintained geometric similarity have been used to make some predictions about the kinds of scaling relationships which might be expected. In a geometrically similar series of species, limb lengths and diameters would scale as body weight to the

.33 power, and areas as body weight to the .67 power. Since the weight bearing ability of bone, or its compressive strength, depends on its cross-sectional area, this means that larger animals would have relatively less weight-bearing ability than smaller animals. Obviously, these relationships imply an upper size limit for a geometrically similar series of animals. This leads to the prediction that cross-sectional area would increase more rapidly with body weight than would geometric relationships. This is in fact seen to be the case in a variety of animal groups, although cross-sectional area never scales directly as body weight (Gould, 1966). The relationships of geometric scaling do not predict any other relationships for scaling of limb lengths and diameters.

Only a single theory of scaling relationships has been proposed which predicts all dimensional changes within the skeleton. This is the elastic similarity hypothesis (McMahon, 1973; 1975a; 1975b; 1976; 1977). McMahon proposed that in a series of animals the dimensions of the skeleton would change in such a way that the animals would maintain the same elastic resistance to bending. Bending moments are created in any tall, slender column (such as the long bones of a limb) which is loaded eccentrically, that is, in which the load is not centered directly over the column at all times. In such a column subjected to bending,

tensile stresses are created on one side of the column and compressive stresses on the other. Bone has a much higher resistance to compressive stress than to tensile stress. Thus, fracturing is often initiated on the side of a bone which is undergoing tensile stress, and compressive fractures are quite rare (Burstein et al., 1972; Curry, writing in Wainwright et al., 1976). Experimental evidence from studies on sheep indicates that long bones are subjected to bending stresses during normal locomotion (Lanyon and Baggott, 1976; Lanyon and Bourn, 1979). Lanyon (1980) also found that bending moments during growth are necessary for the attainment of normal bone size and shape in rats. Resistance to bending stresses must be an important factor in defining skeletal dimensions. If in fact it is the only factor, elastic scaling theory predicts that all long bone lengths would scale as body weight to the .25 power, all diameters as body weight to the .375 power, all areas as body weight to the .75 power, and all lengths as diameters to the .67 power.

Studies of interspecific scaling relationships in ungulates have largely been devoted to testing these predictions. McMahon (1975a) partially tested his theory by determining the length to diameter scaling relationships for a number of ungulates of the orders Artiodactyla and Perissodactyla. He found that the Family Bovidae considered

separately scaled at close to elastic predictions, and that the Artiodactyla considered together gave the next best fit. More inclusive taxonomic groups gave poorer fits to elastic predictions. His results for cervids were particularly interesting: cervids deviated farther from elastic predictions than bovids. If elastic similarity were important in determining skeletal dimensions, elastic predictions would be expected to apply equally to bovids and cervids. McMahon's study only considered length to diameter relationships and does not give full information on scaling relationships. Lister (in lit.) has scaled McMahon's data on lengths and diameters against published body weights; his results indicate that scaling relationships of cervids are closer to geometric similarity than to elastic similarity.

Studies on other ungulate groups have concentrated mainly on the Bovidae. Alexander (1977) found good agreement with elastic predictions for a small sample of seven species of bovids for relationships of length and diameters to body weight. However, Scott (ms.) found poorer agreement with elastic theory when 108 species of bovids were analysed for scaling relationships of lengths, diameters, and areas with body weights. Although resistance to bending appears to be an important factor in determining proportions of the bovid skeleton, bovids do not scale so as

to maintain elastic similarity; that is, other factors must also be important in determining bovid skeletal dimensions. Elastic scaling does not apply to mixed groups of ungulates and other mammals, either: Alexander et al. (1979) calculated scaling relationships of lengths and body weights for a "shrew to elephant" curve and found poor agreement with elastic theory.

Gaits and Adaptive Differences

The basic locomotor morphology of cervids is a type generally characterized as cursorial; the morphology of cursorial adaptations have been described by Hildebrand (1959; 1962) and Smith and Savage (1956), among others. More detailed analyses of cervid locomotor systems and locomotion are rare. Gambaryan (1974) presents the most complete analysis of gaits and skeletal proportions, but for only a few species (Cer. nippon, Cap. capreolus, Ran. tarandus). Howell (1944) presented limb ratios for several species of cervids. However, his ratios are problematical since they do not take into account the size of the animal, and also because for Artiodactyla he notes that he could not always distinguish between metacarpals and metatarsals. Muybridge (1899) published photographic sequences of several cervids, and Gambaryan (1974) includes tracings of the gallop in two species of cervids. Dagg and de Vos (1968)

included four species of cervids in their analysis of pecoran gaits. Several cervids are included in Hildebrand's gait analyses (1977) although he does not discuss cervid adaptations specifically.

Many authors (Hildebrand, 1959; 1962; Smith and Savage, 1956; Howell, 1944) have associated longer limb segments with more rapid locomotion. Specializations for high speed locomotion in the form of longer limb segments thus would be expected in ungulates which depend on speed to escape predation, especially in open country. Species which depend on the cover provided by brush, tall grass, or forest, and may only run a short distance before seeking cover would be expected to show less elongate limb segments; this group will be highly variable depending on the exact habits and habitats of the species. Species for which delivery of power at the foot is more important than speed should show the most shortened distal segments (Scott, 1979). These general factors will be modified by other considerations. Dagg and de Vos (1968) point out that substrate type will affect locomotion; animals living on yielding substrate would be expected to show fewer specializations for speed. Special feeding adaptations may also be reflected in limb morphology; the elongate limbs of the giraffe, a high level browser, is the most obvious example of this. Species depending on crypsis or those

which move in thick brush, may, on the other hand, have shorter limbs. Most of these types of modifications have been described for bovids (Scott, 1979; ms.). This paper will present a preliminary analysis of some of the types of modifications seen in cervids and speculate on the functional basis for these differences.

Many cervids live in habitats that provide at least some cover, and most species which graze in the open avoid coming out in full daylight. Most cervids do not depend on speed over distances in open places to escape predation. Cervids would therefore not be expected to show the extreme modifications of gazelles (Scott, 1979; ms.) or Antilocapra. Neither do any cervids occupy the types of cliff habitats which many bovids of the tribes Caprini and Rupicaprini do. The extremely shortened distal segments seen in these species would not be expected to find parallels among the cervids. In the Pecora, cervids would be expected to show moderate to somewhat elongate distal limb segments.

Locomotor differences in cervids may also account for some limb modifications. In ungulates generally there are a number of differences in gait which may be reflected in skeletal proportions. One which may be important for cervids is the nature of the suspended phases in the gallop.

In a galloping animal there are two phases in the stride when the animal may leave the ground completely. These phases are important since they increase the length of the stride. The two points during which suspended phases can occur are the gathered suspension which follows the step of the leading forefoot, and the extended suspension, which is pushed off by the leading hindfoot or both hindfeet more or less simultaneously. Hildebrand (1977) states that deer have only one suspended phase during the gallop, the extended suspension. Since the cervids he looked at were Hydropotes, Muntiacus, and Odo. hemionus this may be typical for many smaller cervids. However, Dagg and de Vos (1968) report a short gathered suspension for Odo. virginianus. Gambaryan (1974) also reports two suspended phases for Capreolus. Data from both Gambaryan (1974) and Dagg and de Vos (1968) indicate that the extended suspension phase is longer in small cervids than in small bovids, while the gathered phase is less important. Larger bovids, equids, and apparently larger cervids have only a single, gathered suspension phase in their stride (Gambaryan, 1974; Dagg and de Vos, 1968). These differences in use of fore- or hindlimbs to launch a phase of extension may be reflected in skeletal differences. Hildebrand (1977) also reports that mule deer use the pronk, a gait in which all four feet strike the ground simultaneously. Although many ungulates

use this gait at times, very few use it as a mode of progression over any distances. Although such gait differences may also be reflected in the skeletal system too little is known about gaits in cervids to fully analyze these possibilities.

This study will describe the general patterns of deviation from regular scaling in limb lengths and suggest probable reasons for some of the differences. These discussions will be general, rather than a species by species account, for several reasons. Good data on preferred habitat are not available for all species and for many cervid species, preferred habitats vary geographically. I did not have sufficient specimens available to compare subspecific differences, so that individuals of a species were lumped. Although this gives a general idea as to the modifications of a species, comparisons between species are premature for some cervids. Differences in morphology may not depend simply on habitat but on strategies of predator escape, and on gait and locomotor behaviors. Interpretations of morphology of introduced species, or those which may have changed habitats or behavior due to human interference are difficult. Species found in one habitat today may retain adaptations to former habitats. Lastly, cervid long bone lengths are quite variable, more so than bovids, and where sample sizes are small I cannot be

confident that some species by species differences are real.

MATERIALS AND METHODS

Measurements were taken on 183 specimens belonging to 27 species of Cervidae. The specimens used are from the collections of the American Museum of Natural History, the U. S. National Museum of Natural History, the Museum of Comparative Zoology, Harvard University, the Field Museum of Natural History, the Peabody Museum of Natural History, Yale University, and the Museum of Vertebrate Zoology, University of California (Berkeley). A list of specimens measured and the raw data are available from the author. The number of specimens measured and the species examined are listed in Appendix I. All specimens were adult individuals (as indicated by completion of epiphyseal fusion) collected in the wild which showed no sign of gross deformity. Zoo specimens were included only for Elaphurus davidianus and Dama dama, for which no other specimens were available. All measurements of long bone lengths were taken to the nearest 0.1 cm using a GPM anthropometer; all other measurements were made to the nearest 0.01 cm with a dial caliper.

Length measurements were taken on each long bone (humerus, radius, metacarpal, femur, tibia, and metatarsal). These measurements were chosen to represent the greatest

length between articular surfaces. The diameters of each bone were measured at midshaft in both the transverse and antero-posterior directions. These diameters were used to calculate the area of the bone at midshaft. Area was calculated as though the cross section of the bone were an ellipse with major and minor axes equal to the two diameters. This does not give an exact estimate since it does not take into account the size of the marrow cavity, and it should be regarded as an indication of relative amount of bone between the species studied.

Allometric equations of the form $y=mx$ were fitted to these data by performing a least squares analysis on logarithmic transformations of the data using the procedure GLM in the Statistical Analysis Systems libraries (SAS). Calculations of 95% confidence intervals of the exponents were as described in Simpson, Roe, and Lewontin (1960). The exponents (b), constants (m), and R-square values are given in Tables 1, 3, 4, and 5. Sample plots of some relationships are given in Figures 1-3, 5, and 6. Regressions of length versus diameter were calculated based on the individual specimens. For regressions involving body weight the arithmetic mean of each measurement for all specimens measured was used. Sexually dimorphic species and those in which subspecies varied by more than about 15% in body weight were separated by sex or subspecies.

For most species body weights used were weights of an average male or female individual reported in the literature. In some cases these weights were supplemented by weights recorded for museum specimens and zoo records. For each species as many weight records as possible were collected, and estimates for each species were based on these. The major sources of body weights used were Corbet and Southern (1977), Ward (1896), Allen (1940), Tate (1947), Burt and Grossenheider (1964); Medway (1969), Walker (1968), Dollman and Burlace (1935), Whitehead (1972), and Grzimek (1972). The weights given in some of these sources must be used with caution. The weights reported by big game hunters are usually weights of record males; for bovids these were found to overestimate the weight of an average male by about 10% (Scott, 1979). Where these were the only weights available they were adjusted accordingly. The same caution must be applied to body weights given in Walker (1968) since many of his weights are taken directly from sources such as Rowland Ward's Records of Big Game (Dollman and Burlace, 1935).

In order to compare deviations from regular scaling in species of different sizes limb bone lengths were transformed into dimensionless variables in the following manner. This method has been used by Emerson and Radinsky (1981) and Radinsky (1981) to study skull morphology in

carnivores, and is described in greater detail there. All long bone lengths were transformed to logarithms (base 10) and humerus, radius, metacarpal, tibia and metatarsal lengths were scaled against femur length (Figure 4). Reduced major axis equations were calculated for each of these relationships; these are of the form $\log y = b \log x + \log m$, where 'x' represents femur length. The values of b, log m, and the correlation coefficients between the variables are given in Appendix II. Femur length was chosen as a standard because, of the limb bones, it scales most closely with body weight and at about the same exponents for most Pecora, so that results between groups are comparable. Body weights are too inexact to use in this context for many ungulate species. Reduced major axis was used in these calculations because neither element could be considered dependent. The equations were used to calculate predicted bone lengths for each species. Dimensionless variables representing deviations from the regression lines were computed by dividing the actual length by the predicted length for each bone. These values are given in Table 2. Values greater than 1.00 indicate that the bone is longer than predicted; values less than 1.00 indicate that the bone is shorter than predicted. (Compare variables in Table 2 with deviations of the identified species in Figure 4.)

RESULTS AND DISCUSSION

Scaling Relationships of Limb Lengths

The scaling relationships for total limb lengths and individual limb bones with body weights are given in Table 1, and several of the relationships are illustrated in Figures 1-3. The differences in scaling relationships between the two limbs are striking. The forelimb and most of its individual elements scale with slight negative allometry at exponents close to isometry. The hindlimb and its individual elements scale with marked negative allometry, and at exponents close to the predictions of elastic theory. The exponents for humerus, total hindlimb, femur, and tibia do not differ significantly from elastic predictions. The exponents for total forelimb, ulna, and radius do not differ significantly from isometry. The exponents for metacarpal and metatarsal do not differ significantly from either elastic predictions or isometry. The confidence intervals for these two bones are larger than those for the other limb bones; metapodials vary more relative to body weight than do other long bones. This is also reflected in the lower R-square values for these bones. Within each limb the proximal bones (humerus and femur) show the highest R-square values, and these values decrease from

proximal to distal. Two questions of particular interest arise from these results: why are there differences in exponents between the fore- and hindlimbs, and does elastic scaling play a role, and why are there differences in correlation between body weight and lengths in distal versus proximal bones.

The differences in scaling between the forelimb and the hindlimb cannot be explained simply. Cervids are obviously not simply a geometrically similar series of species, nor are they an elastic series: if elastic theory were correct it should apply to both the fore- and hindlimbs equally. Hindlimb lengths increase more slowly with increasing body size than do forelimb lengths. Cervids are not unique in this respect; bovids also show the same differences, although they are less marked. I have suggested that in bovids this may be related to the shifting emphases on the two limbs during locomotion. In small bovids both the leading forefoot and the leading hindfoot push off a suspended phase, while in large bovids only the forelimb propels a suspended phase (Hildebrand, 1977; Gambaryan, 1974). In cervids the contrast in emphasis is greater with small cervids having only an extended suspension, or a long extended and short gathered suspension, while large cervids have only a gathered suspension (Hildebrand, 1977; Gambaryan, 1974; Dagg and de Vos, 1968). I believe that as

ungulates become larger the length of the forelimb is maximized to maintain the greatest possible thrust for this pushoff into the suspended phase while the hindlimb can become relatively shorter. Conversely, in small ungulates the hindlimb is relatively longer to achieve maximum thrust for the extended suspension. There is some evidence that in smaller bovids hindlimb musculature is more massive relative to body weight while in larger bovids forelimb musculature is relatively more massive (Smith and Ledger, 1965; Grand, p. comm.), but data are not available for cervids. I believe that this tendency to emphasize forelimb as size increases is a general one in ungulates, and accounts for the differences in scaling relationships of limb lengths between fore- and hindlimbs. This difference is more marked in cervids than in bovids, probably because of the greater emphasis placed on hindlimb-powered extended flight in small cervids.

All of the exponents of length to body weight relationships in cervids are higher than those of bovids. That is, limb lengths do not decrease as rapidly relative to body size in cervids as they do in bovids, so that cervids appear to be close to a geometric series in many dimensions. (Compare bovid and cervid regression lines on Figures 1-3.) These differences are in part an artifact of the size range of living species in the two families. If the length to

body weight scaling relationships of bovids are recalculated without species of body weights greater than 500 kilograms, so that the size range conforms more closely to that of cervids, the exponents are higher and closer to the cervid values. Most of the bovids larger than 500 kilograms are in the tribe Bovini, and these species differ from other bovids in a number of respects. All of their limb segments are short relative to body weight; this results in lower exponents for the entire group. Although the bovid and cervid exponents still differ when Bovini are omitted from the bovid regressions, the exponents of humerus, radius, femur, and tibia have overlapping confidence intervals. Metapodial scaling relationships still differ, with bovid exponents being much lower, and consequently total fore- and hindlimb exponents are still lower for bovids.

In cervids, as in bovids, metapodial lengths are more variable than are proximal limb elements (compare Figures 1 and 2), but the metapodials of Bovidae are more variable at any given body size than are those of cervids. Metapodial length in Bovidae is related to habitat: species which live on open plains, and which depend on speed to outrun predators, have relatively long metapodials, and species living in mountainous habitats have extremely shortened metapodials, as do the Bovini. Species living in forested areas or open hilly country show metapodials of intermediate

lengths (Scott, 1979; ms.). Although cervids do show variation in limb segment length related to habitat, the range of habitats in which cervids are found is not as varied as that of bovids. No cervid species are found in the cliff habitats utilized by many Rupicaprini and Caprini, nor are cervids found in open arid areas or living exclusively in open grasslands. Some of the more extreme modifications seen in bovid metapodials are therefore not seen in cervids. The scaling relationships of cervid metapodials are therefore different from those of bovids; the absence of species with extremely shortened metapodials probably explains the higher exponents in cervids as opposed to bovids.

In both bovids and cervids proximal bone lengths are almost entirely determined by body weight while distal limb elements vary to a greater degree at a given body weight. Much of this variation can be related to differences in habitat and locomotion in ways that will be discussed shortly. However, this difference in variability raises the question: why should proximal bones vary less? I have suggested reasons why proximal bones show less variation in bovids; these reasons apply equally to Cervidae. In any animal the bulk of the body mass will be associated with the trunk, and much of this will be locomotor musculature. This is pronounced in ungulates, since the limb musculature is

proximally placed, with very little musculature associated with distal parts of the limb. Variation in proximal bones must be constrained by the mass of musculature which originates and inserts on these bones. These constraints would not apply to more distal bones, especially the metapodials; dimensions of these bones are more free to vary.

McMahon (p. comm.) has suggested that proximal bones should conform more closely to elastic predictions because the greatest bending moments would be set up in the proximal part of a limb. However, this would only be true if limbs functioned as a single unit. Since limbs are jointed each bone must be loaded individually, and this cannot explain the closer conformity of proximal bones to elastic predictions. Alexander (1977) proposed that angulation of bones would affect the magnitude of the bending moments set up in the bone, with larger bending moments in more horizontal bones. This may in part explain the closer conformity of proximal bones with elastic scaling.

Deviations from allometric scaling: habitat differences

Small cervids. The smaller cervids can be divided into three groups: those in which limb elements are about 1.00, or only slightly elongated or shortened, those with markedly

elongate limb segments, and those with markedly shortened limb segments (Table 1 and Figure 4). The first group includes Mazama gouazoubira and Muntiacus reevsi. Mazama americana and Moschus show moderately elongate limbs. Hydropotes is the only small cervid with markedly elongate limbs. Muntiacus muntjak, Elaphodus, and Pudu show marked shortening of elements, Pudu most strongly so. All of these small cervids except Hydropotes live in areas of fairly dense thicket or bush (Whitehead, 1972; Walker, 1968). Hydropotes is found mostly in areas of tall grasses and reeds (Whitehead, 1972). Although such a habitat serves as cover for an animal the size of Hydropotes, the greater openness of the terrain probably places a greater premium on speed. Heavy undergrowth is not an environment in which speed is at a premium, nor is it even useful. Shortened limbs and a "low profile" would allow animals to move more easily through brush, and probably make them less noticeable. Interestingly, this same shortening of the limbs is seen in the duikers (Cephalophus) (Scott, 1979). The species of Mazama available to me have somewhat longer limbs than the muntjacs; the bush duiker (Sylvicapra) shows similar elongation compared to Cephalophus (Scott, 1979). However, from the information available to me at this time I am unable to say whether differences in habitat or locomotion can account for this difference.

Moschus shows a particularly interesting modification in the elongation of the tibia. This animal, along with many other small cervids gives the appearance of being higher in the rump than at the withers. Elongation of the hindlimb, especially the tibia, is characteristic of some primitive artiodactyls, tragulids, and some small forest-living bovids (Scott, 1979). I believe that this basic morphology is a primitive one for small, forest-living artiodactyls, which has been retained, in a somewhat specialized condition, in Moschus. Moschus has longer limb segments generally than tragulids and the fossil species.

It should be noted that the general impression that small cervids have hindlimbs relatively longer than forelimbs, as compared to large cervids, is correct (Figure 3). However, this difference is not indicated in these variables, which only reflect variance around regular scaling relationships. It is reflected in the scaling relationships, the more negative exponent for the hindlimb indicating that the hindlimb is relatively longer in smaller cervids, while the forelimb stays more nearly the same length in small versus large cervids.

The relatively longer hindlimb in small cervids is not unexpected in view of the fact that the extended phase of suspension forms a high percentage of the stride in small

cervids (Dagg and de Vos, 1968; Gambaryan, 1974). Gambaryan and Dagg and de Vos have also suggested that in ungulates living in areas with many obstacles a gallop with a long extended phase is ideally suited for clearing obstacles. Many small cervids may use a rapid bounding gait as a means of maneuvering in undergrowth. The elongate hindlimb in Moschus (see Figure 3) and in some primitive ungulates suggests that this may be a primitive pattern of locomotion. From this basic morphology some cervids have shortened limbs as an alternative strategy for moving through heavy undergrowth. In Hydropotes it is interesting that the most elongation occurs in the forelimb. This produces limbs more nearly equal in length in this species. Clearing obstacles (and thus emphasis on the hindlimb) may thus be less important in this species.

Medium to large cervids. Among the medium to large cervids two basic patterns emerge (Table 2). Most cervids weighing more than about 100 kg have limb segments which are about 1.00 or shorter. Alces basically fits with this group excepting that the humerus is elongate and the radius and tibia slightly so. Cervids weighing less than about 100 kg tend to have all segments elongated, with the greatest degree of elongation in the metacarpal. Rangifer shows a unique pattern with most limb elements about 1.00, but with marked elongation of the radius.

Most of the medium-sized cervids show elongate limbs and have probably specialized in the direction of a bounding gait with a long extended suspension which is suitable for clearing obstacles and highly maneuverable. This correlates well with the evidence of Dagg and de Vos (1968) and Gambaryan (1974) that the extended suspension is of long duration in smaller cervids, as opposed to small bovids and as opposed to large cervids. Many of the cervids in this grouping live in open woodland areas, and many also graze in the open. Thus it is not surprising that they should show modifications for rapid locomotion. This may be an adaptive type which is only open to smaller cervids, however. In larger species the energy required to raise the center of mass in this kind of gait may make it inefficient.

Two smaller cervids which might be expected to show elongate limbs according to my suggestions in fact have shortened limb segments. These are Blastocerus, which has limb variables about 1.00 as do larger cervids, and Axis porcinus which has quite short distal limb elements. Blastocerus lives in marshy areas. Dagg and de Vos (1968) have pointed out that species living on yielding substrate are unlikely to be specialized for rapid locomotion, since any fast gait would have phases where only one foot at a time would touch the ground and the feet would sink into the substrate. Swamp living species would thus be expected to

have shorter limb segments than similarly sized related species. C. duvauceli also has shortened distal segments, although not as markedly so for their size range.

Hog deer are found in areas of tall grass on alluvial plains, and might not be expected to show such markedly shortened limbs. This may, however, be an alternative strategy for living in tall grasses analogous to that suggested for Pudu in dense undergrowth. That is, shorter stature may decrease the chances of the animals being seen. These species may have adopted the strategy of maximizing concealment rather than speed to avoid predators.

The larger cervids do not have elongated limbs and some species show quite marked reduction in segment lengths. These species definitely place greater emphasis on the gathered suspension than on the extended suspension (Gambaryan, 1974; Dagg and de Vos, 1968), but I was unable to find much other information on gait in these species. I would expect them to use a gallop with less vertical displacement than do smaller cervids. Dagg and de Vos (1968) also state that the large cervids they studied prefer the trot to the gallop when not closely pursued. The trot is a more stable and less tiring gait than the gallop. Dagg and de Vos also point out that large cervids may not depend on speed to escape predation as much as do small cervids.

They cite Mech's (1966) study which showed that moose on Isle Royale were more successful in countering a wolf attack if they stood their ground than if they fled. This is probably true to some extent for all large as opposed to small ungulates. In this group of larger species then, limbs are not elongated for rapid locomotion.

Alces is the largest cervid and although it shares many aspects of limb segment length with the larger cervid group the humerus and radius do differ in being elongate. Elongation of proximal as opposed to distal segments mechanically results in increased power at the foot rather than increased speed. This could be related to the frequency with which moose swim and move on swampy ground. Elongation of the radius combined with only moderate elongation of the metacarpal is also characteristic of some bovids (especially Alcelaphini and Hippotragini) and camelids (Scott, 1979; unpublished data). Radius elongation may occur in place of metacarpal elongation since less stress would be placed on this bone than on the metacarpal. Even if there is selection for increased power related to swimming or moving on soft substrate in this species it cannot be to the advantage of a browser to shorten the limbs too much, and the proportions which result may be a compromise.

Rangifer also has an elongated radius and shortened metacarpal, but a slightly elongate metatarsal. The forelimb proportions are similar to those of alcelaphine bovids. I have suggested for alcelaphines that this is a mechanism for lengthening the forelimb, which pushes off the single suspended phase in these species. Again, the distal metacarpal, with less surrounding muscle, is probably more subject to increased stress, so that it is more advantageous to elongate the radius. Although Rangifer has a short extended flight it does place more emphasis on the gathered suspension phase. For this reason it may be advantageous to have one bone of the forelimb elongate, but since there is also an extended flight, the metatarsal is still slightly elongate.

Scaling of diameters and Areas with Body Weights

The scaling relationships of transverse and antero-posterior diameters vary from marked positive allometry to slightly negative allometry (Table 3, Figure 5). The exponents of forelimb bones are higher than those of hindlimb bones. Although the forelimb bones scale at exponents consistently closer to elastic predictions, and hindlimb bones at closer to geometric, most of the exponents do not differ significantly from either elastic or geometric

predictions. Only two exponents show significant differences, humerus antero-posterior diameter from geometric predictions and tibia antero-posterior diameter from elastic predictions. Since these are the only two exponents which differ significantly from either set of predictions they have little meaning in terms of the scaling relationships of these dimensions as a whole. The scaling relationships of areas follow a similar pattern to those of diameters. The forelimb bones scale with positive allometry, at close to elastic predictions, while those of the hindlimb scale with positive allometry but are closer to isometry, except the tibia, which scales with negative allometry. Cervids are thus neither geometrically nor elastically similar in these dimensions.

Areas also show lightly less variability than do diameters; transverse and antero-posterior diameters may deviate more from regular scaling in some species than do areas. Maintenance of a particular mass of bone at the midshaft appears to be more critical than whether this bone is arranged in the antero-posterior or transverse direction. This close association between area and body weight intuitively suggests that compressive strength, which is proportional to area, may be the critical factor determining midshaft areas. However, if compressive strength alone were critical, area might be expected to scale directly as body

weight, otherwise large animals would maintain a smaller margin of safety than small animals. Increasing the area of bone also increases its resistance to bending, and many of the exponents do suggest that areas scale at approximately elastic predictions. I believe that elastic factors are important in determining scaling relationships. The evidence that most fractures are initiated by bending is strong, and it is elastic resistance which counters bending forces. Long bones must maintain both sufficient resistance to bending and to compression to remain intact. Whatever the relative importance of these two factors, long bones of cervids do not increase in thickness as rapidly as would be expected. The fact that resistance to bending is important does not mean that a series of related ungulate species should be expected to scale elastically. Other factors not considered by McMahon (1973; 1975a) may be important and modify expected relationships.

There are several factors which may account for the fact that bone thicknesses do not increase as rapidly with increasing size as might be predicted. Alexander (1977) suggested for bovids that deviations from elastic scaling may result from different angulations of bones. Maximum bending moments are set up in bones which are loaded in the horizontal position; the humerus would most closely meet this requirement, and it does scale at close to elastic

predictions. Alexander also found that in larger bovids the angles between the hindlimb bones decreased as size increases. On this basis he predicted that exponents of 0.362 should be found for elastically scaling bovid hindlimb diameters, and this would give an exponent of 0.724 for areas. These values are closer to those he obtained and those given here for cervids, but they are too close to both elastic and geometric predictions to be tested.

Alexander, Langman, et al. (1977) and Alexander, Maloiy, et al. (1979) point out that large ungulates run with larger duty factors than small ones. This means that each foot remains on the ground longer and consequently that each foot is loaded with a smaller multiple of body weight. They state that stresses in the limbs of large and small animals are approximately equal. As bovids increase in size, loading during locomotion thus does not increase in direct proportion to body weight. This would mean that bones would not have to increase in area as rapidly as does body weight in order to have equal resistance to either compressive or bending forces. If these findings apply to small versus large ungulates generally this might explain why scaling relationships of areas generally are more negative than expected. Maloiy et al. (1979) have suggested that these factors negate elastic scaling theory entirely.

For bovids I have suggested that changing distribution of body mass could account for differences between fore- and hindlimb thicknesses. That is, as bovids become larger the muscle mass of the hindlimb decreases more rapidly relative to body weight than does mass of the forequarter. Cervid scaling relationships follow a similar pattern, and this suggests that distribution of mass in cervids may follow a similar pattern. However, data are not yet available to test this suggestion.

The greater amount of variation seen in diameters is interesting in several respects. McMahon (1973; 1975a) originally proposed that it is maintenance of the length to diameter relationship which is important in maintaining elastic resistance to bending. He stated that major forces in locomotion would be directed in the antero-posterior direction. However, this assumption is based on studies of animals walking or running in a straight line on a treadmill. In a galloping ungulate, especially one which is turning frequently, bending stresses must also be set up in the transverse plane, so that this dimension should scale according to elastic predictions. However, it is possible that in certain modes of locomotion greater stresses may be generated in one plane or the other. In bovids, for instance, species which live in mountainous terrain (for example, Oreamnos americanus, the Rocky Mountain goat) show

transversely expanded and flattened metapodials. I believe that these are associated with greater lateral forces generated by locomotion in these habitats by the uneven stresses created during climbing. Plains-living species tend to have very rounded metapodials. There may be other adaptive reasons for changes in the dimensions of metapodials. In some cervids the deep flexor tendon has muscular tissue associated with it. Grand (p. comm.) has observed that this musculature is well developed in Muntiacus and I have observed moderate amounts in Rangifer. The metapodials of many of the smaller cervids are flattened, perhaps to allow more surface area for this musculature to take origin. In Rangifer the metapodials are rounded but with a deep groove on the posterior surface in which the flexor tendons lie. On the other hand, the long-legged Capreolus shows the typical rounded metapodials of more speed adapted ungulates. Such adaptive differences may account for the greater variability in diameters as opposed to areas.

Scaling of Length and Diameter

The results of the scaling relationships of length with diameter provide an important test of the elastic theory since it is the relationships of these dimensions which

formed the basis for the elastic theory (McMahon, 1973). For all long bones length scales against diameter with negative allometry, that is, with exponents less than one (Table 4). However, all of the exponents are higher than those predicted by elastic theory: as diameter increases bone lengths increase less than would be predicted if cervids scale geometrically, but more than if they scaled elastically. For all bones the length to diameter relationships show high R-square values, with metapodials showing slightly lower values. These results present some interesting contrasts to those obtained for bovids, especially for distal bones. Although the scaling relationships of length to diameter for humerus and femur are similar, for all other bones the cervid exponents are much higher. In addition, the distal bones of bovids show a much greater degree of variation than do those of cervids; R-square values for length to diameter relationships of bovid metacarpals and metatarsals are 0.65 and 0.78, respectively, compared to 0.917 and 0.931, for cervids.

It is apparent that as cervids increase in size their limbs become thicker relative to length, although not as rapidly as elastic criteria predict, and not as rapidly as found in bovids. There are several reasons why diameters may scale so close to isometry in cervids. For example, if we compare metacarpals of small cervids and small bovids,

small cervids have shorter, thicker metacarpals on the average than bovids of the same size (compare regression lines on Fig. 6). Although the slope of the cervid line is steeper, for all but the smallest cervids the length of a bone for a given diameter will not differ greatly for cervids and bovids weighing from approximately 30 to 500 kg. The apparent near isometry of the length to diameter relationships of cervids is thus partly an artifact related to the relatively short, thick metacarpals of small cervids. The humerus and femur length to diameter relationships are very similar in bovids and cervids; in both families large species have relatively longer or more slender bones than would be expected. I have also suggested for bovids that in fact bending moments may be countered in other ways in proximal bones. Proximal bones are surrounded by musculature which inserts and takes origin there. Bending moments may in part be neutralized by the pull of opposing sets of muscles, although bending moments are not completely offset by the pull of musculature (Lanyon, 1980).

SUMMARY AND CONCLUSIONS

If a series of related species scales geometrically, they maintain the same relative dimensions of the locomotor system, but they are not mechanically equivalent. In order

to maintain mechanical equivalence, deviations from isometry must occur. In the locomotor system the ability to support increasing mass and load on the limbs must determine mechanical equivalence, at least in part. The smaller the range of sizes, the smaller the deviations which will be necessary to maintain equivalence as size increases. Over a wider size range scaling relationships would thus be expected to show greater deviations from isometry, than over a small size range. Species in the Family Cervidae do show deviations from geometric similarity as size increases. Lengths of hindlimb bones scale with marked negative allometry, while the bones of the forelimb scale with only slight negative allometry. Diameters and midshaft areas of forelimb bones scale with marked positive allometry while those of the hindlimb show slight positive allometry (with the exception of the tibia). All of the length to diameter scaling relationships show negative allometry, that is, bones become shorter relative to their diameter as diameter increases. Most of the scaling relationships differ from elastic predictions, bones are longer or more slender than would be predicted by elastic theory.

In smaller cervid species, then, the hindlimb is relatively longer than in larger cervids. The forelimb is also relatively longer in small cervids, but only slightly so; the forelimb is much closer to geometric similarity

than the hindlimb. Limb bones also become relatively thicker as size increases; bones of the forelimb increase in thickness more rapidly than those of the hindlimb. I believe that these scaling differences are related, at least in part, to locomotor differences between small and large cervids. In the gallop of small cervids the extended suspension phase forms a major part of the stride (Gambaryan, 1974; Dagg and de Vos, 1968) and in some species this may be the only suspended phase (Hildebrand, 1977). In the gallop of medium cervids both extended phases are present, with the extended suspension being longer in duration. In large cervids the extended suspension becomes less important and is not present in the largest species. As several authors (Gambaryan, 1974; Dagg and de Vos, 1968) have pointed out, the extended flight is well-suited for clearing obstacles, such as would be encountered in forest environments. The emphasis on the hindlimb in the cervid gallop may have arisen in small, forest-living cervids. As cervids become larger, the emphasis shifts from hindlimb to the forelimb-powered gathered suspension. This is a common trend in large ungulates and is probably related to the energetic cost of launching a heavy body into a bound off of the hindlegs. In bovids there is some evidence that the mass of musculature shifts forward. Although data are not available for cervids, if this were the case it would

explain the more rapid increase in thickness of forelimb bones as size increases.

Cervid scaling relationships differ from those of bovids in several respects. Most cervid exponents are higher than those of Bovidae, that is, cervids are closer to being geometrically similar. Cervids probably are closer to geometric similarity than are bovids in part because they span a smaller size range. The smaller the size range the greater the probability that a given mechanical design will function throughout that size range, and the smaller the deviations likely to be necessary to maintain mechanical equivalence. This is supported by the fact that regressions for bovids based on only species with body weights less than 500 kilograms are much closer to those of cervids than for the entire family Bovidae. In bovids the differential in scaling between the fore- and hindlimbs is not as extreme, although the same trends are present. In the gallop of small bovids the extended suspension is of shorter duration than in small cervids, and the two suspended phases are of more nearly equal importance. Consequently there is not as great a differential between the lengths of the two limbs.

Cervids, like bovids, do not form an elastic series but elastic resistance to bending is probably a factor in determining dimensions since fractures are usually initiated

by bending moments. As species increase in size bending moments on their limbs increase. These increased moments can be countered either by increasing the thickness of limbs or by decreasing the length of limb elements. Elastic theory maintains that so long as the appropriate relationship between the two dimensions is maintained the limb will have sufficient resistance to bending. However, while elastic scaling is possible in engineering terms, in a large ungulate it would create a very heavy distal limb element; movement of such an element would be energetically inefficient. Increasing speed is probably not important to large ungulates: their size is a defense against many predators. Thus shortening distal limb segments is probably a more mechanically efficient solution to increased bending moments in large ungulates.

Limb lengths, especially of distal elements, show the largest deviations from regular scaling relationships, and I have suggested that much of this variation is related to differences in habitat and locomotor habits. Small cervids can be divided generally into two groups, species with moderate to short limbs living in quite heavy cover, and longer legged species living in more open areas. Medium-sized cervids tend to have elongate limbs and probably have emphasized fairly rapid locomotion with a long extended suspension phase for clearing obstacles. Larger

cervids have shorter limb segments, and probably place more emphasis on gathered suspension. Speed is probably less important for large cervids. Swamp-living species also have shorter metapodials than expected for their size. As a family Cervidae show less variation in limb elements than do Bovidae. The range of habitats in cervids is narrower; this probably is responsible for the difference. Although the deviations from regular scaling and their relationships to habitat and locomotor habits have only been discussed generally the basic patterns of morphological distinction are clear. As more data on habitat, behavior, and especially gait become available, these outlines can be fleshed out into a more comprehensive picture of cervid morphology.

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Table 1. Scaling relationships of limb lengths and body weight for Cervidae. Exponents for Bovidae weighing less than 500 kg are given in parentheses. The confidence intervals of the exponent are expressed as exponent $\pm$ confidence interval. The right hand column indicates whether the elastic (E) and geometric (G) exponents, respectively, lie within the confidence interval of the experimental exponent.

	<u>EXPONENT</u>	<u>CONSTANT</u>	<u>R-SQUARE</u>	<u>E/G</u>
Forelimb	.314 $\pm$.058 (.277 $\pm$.017)	14.4	.910	no/yes
Humerus	.277 $\pm$.042 (.283 $\pm$.016)	5.7	.916	yes/no
Radius	.326 $\pm$.060 (.304 $\pm$.017)	4.9	.898	no/yes
Metacarpal	.339 $\pm$.082 (.241 $\pm$.035)	4.1	.851	yes/yes
Hindlimb	.277 $\pm$.049 (.247 $\pm$.014)	22.2	.908	yes/no
Femur	.276 $\pm$.044 (.277 $\pm$.014)	7.5	.938	yes/no
Tibia	.261 $\pm$.052 (.243 $\pm$.014)	8.9	.894	yes/no
Metatarsal	.300 $\pm$.067 (.213 $\pm$.029)	5.8	.861	yes/yes

Table 2. Mean (+ standard deviation) of transformed limb length variables.

<u>Species</u>	<u>HUMERUS</u>	<u>RADIUS</u>	<u>METACARPAL</u>	<u>TIBIA</u>	<u>METATARSAL</u>
SMALL CERVIDS, MODERATE TO ELONGATE LIMBS					
<u>Hyd. inermis</u>	0.932 $\pm$.003	1.099 $\pm$.028	1.298 $\pm$.125	1.069 $\pm$.041	1.095 $\pm$.090
<u>Moschus</u>	1.089 $\pm$.048	1.063 $\pm$.041	1.018 $\pm$.028	1.117 $\pm$.028	1.053 $\pm$.076
<u>Maz. americana</u>	1.005 $\pm$.012	1.035 $\pm$.018	1.108 $\pm$.065	1.019 $\pm$.038	1.096 $\pm$.043
<u>Maz. gouazoubira</u>	0.990 $\pm$.022	1.003 $\pm$.034	1.060 $\pm$.039	1.004 $\pm$.261	1.051 $\pm$.054
<u>M. reevsi</u>	0.999 $\pm$.016	1.000 $\pm$.028	0.985 $\pm$.053	0.975 $\pm$.018	1.017 $\pm$.032
SMALL CERVIDS, SHORT LIMBS					
<u>M. muntjak</u>	0.980 $\pm$.030	1.002 $\pm$.08	0.991 $\pm$.076	0.985 $\pm$.037	0.962 $\pm$.032
<u>E. cephalophus</u>	1.006 $\pm$.021	0.939 $\pm$.023	0.888 $\pm$.025	0.992 $\pm$.024	0.914 $\pm$.025
<u>Pudu pudu</u>	1.079	0.889	0.735	0.911	0.787
<u>P. mephistophiles</u>	1.151 $\pm$.028	0.977 $\pm$.024	0.712 $\pm$.008	0.961 $\pm$.001	0.828 $\pm$.024

MEDIUM-SIZED CERVIDS, ELONGATE LIMBS

<u>Cap. capreolus</u>	1.037 $\pm$.013	1.165 $\pm$.038	1.267 $\pm$.062	1.103 $\pm$.033	1.188 $\pm$.059
<u>C. nippon</u>	0.993 $\pm$.011	1.090 $\pm$.020	1.214 $\pm$.041	1.033 $\pm$.009	1.122 $\pm$.025
<u>O. hemionus</u>	1.030 $\pm$.026	1.082 $\pm$.039	1.104 $\pm$.043	1.048 $\pm$.027	1.147 $\pm$.038
<u>O. virginianus</u>	0.991 $\pm$.019	1.079 $\pm$.010	1.167 $\pm$.158	1.032 $\pm$.048	1.140 $\pm$.138
<u>Ozot. bezoarticus</u>	1.014 $\pm$ 0.37	1.107 $\pm$.111	1.239 $\pm$.116	1.023 $\pm$.043	1.112 $\pm$.103
<u>Axis axis</u>	0.979 $\pm$.009	1.014 $\pm$.043	1.085 $\pm$.075	0.980 $\pm$.026	1.007 $\pm$.032
<u>C. timorensis</u>	0.981 $\pm$.003	1.005 $\pm$.002	1.021 $\pm$.004	0.964 $\pm$.033	0.9.0 $\pm$.007
<u>C. eldi</u>	0.960	1.018	1.136	1.008	1.012

MEDIUM CERVIDS, MODERATE OR SHORT LIMBS

<u>Axis porcinus</u>	0.962 $\pm$.025	0.959 $\pm$.038	0.968 $\pm$.042	0.988 $\pm$.012	0.906 $\pm$.028
<u>B. dichotomus</u>	0.974 $\pm$.004	0.996 $\pm$.030	1.048 $\pm$.054	1.005 $\pm$.007	0.987 $\pm$.037

LARGE CERVIDS, SHORT LIMBS

<u>C. elephas</u>	1.030 $\pm$.015	0.998 $\pm$.039	0.922 $\pm$.062	0.998 $\pm$.013	0.948 $\pm$.043
<u>C. unicolor</u>	0.967 $\pm$.019	0.891 $\pm$.021	0.882 $\pm$.034	0.935 $\pm$.005	0.864 $\pm$.020
<u>C. duvauceli</u>	0.941 $\pm$.015	0.965 $\pm$.025	0.937 $\pm$.028	0.959 $\pm$.015	0.871 $\pm$.019
<u>Elaphurus</u>	0.964 $\pm$.009	0.960 $\pm$.017	0.966 $\pm$.032	0.966 $\pm$.015	0.928 $\pm$.022
<u>Alces alces</u>	1.112 $\pm$.024	1.040 $\pm$.032	0.862 $\pm$.025	1.000 $\pm$.020	0.950 $\pm$.023
<u>R. tarandus</u>	1.046 $\pm$.037	1.108 $\pm$.027	0.855 $\pm$.040	0.997 $\pm$.026	1.024 $\pm$.054

Table 3. Scaling relationships of antero-posterior diameter, transverse diameter, and area at midshaft to body weight, as in Table 1.

	<u>EXPONENT</u>	<u>CONSTANT</u>	<u>R-SQUARE</u>	<u>E/G</u>
ANTERO-POSTERIOR DIAMETERS				
Humerus	.3787 $\pm$.054	.480	.961	yes/no
Radius	.3589 $\pm$.056	.312	.909	yes/yes
Metacarpal	.3811 $\pm$.064	.304	.946	yes/yes
Femur	.3501 $\pm$.051	.513	.941	yes/yes
Tibia	.2934 $\pm$.063	.570	.890	no/yes
Metatarsal	.3584 $\pm$.057	.401	.935	yes/yes
TRANSVERSE DIAMETERS				
Humerus	.3849 $\pm$.053	.388	.952	yes/yes
Radius	.3801 $\pm$.054	.466	.947	yes/yes
Metacarpal	.3388 $\pm$.046	.422	.920	yes/yes
Femur	.3355 $\pm$.052	.512	.952	yes/yes
Tibia	.3526 $\pm$.054	.510	.964	yes/yes
Metatarsal	.3280 $\pm$.045	.428	.938	yes/yes
MIDSHAFT AREAS				
Humerus	.7644 $\pm$.105	.146	.960	yes/yes
Radius	.7398 $\pm$.184	.114	.941	yes/yes
Metacarpal	.7206 $\pm$.106	.101	.948	yes/yes
Femur	.6836 $\pm$.101	.206	.952	yes/yes
Tibia	.6466 $\pm$.114	.228	.952	yes/yes
Metatarsal	.6872 $\pm$.134	.134	.942	yes/yes

Table 4. Scaling relationships of length to diameter, as in Table 1.

	<u>EXPONENT</u>	<u>CONSTANT</u>	<u>R-SQUARE</u>	<u>E/G</u>
Humerus	.7375 $\pm$.002	9.8	.960	yes/no
Radius	.8662 $\pm$.004	14.4	.929	no/no
Metacarpal	.8976 $\pm$.006	11.7	.917	no/no
Femur	.7668 $\pm$.002	13.1	.962	yes/no
Tibia	.8169 $\pm$.002	15.5	.920	no/no
Metatarsal	.8366 $\pm$.004	12.4	.931	no/no

Appendix I. Species of the family Cervidae included in this study; with number of specimens measured and body weights used in the regression analyses. Species which are non-dimorphic or in which the degree of dimorphism is small are indicated by 'ND' under female weight. Specimen numbers followed by (Z) are zoo specimens; (P) indicates partial specimens.

<u>Species</u>	<u>Weight</u>		<u>Number</u>
	<u>Male</u>	<u>Female</u>	
<u>Moschus moschiferus</u>	11	ND	10
<u>Muntiacus muntjak</u>			
<u>M. m. bancanus</u>	19	ND	1
<u>M. m. grandicornis</u>	36	ND	3
<u>M. m. moschatus</u>	25	ND	2
<u>M. m. muntjak</u>	25	ND	1
<u>M. m. pleiharicus</u>	16	ND	6
<u>Muntiacus reevesi</u>	14	12	8
<u>Elaphodus cephalophus</u>	18	ND	13
<u>Dama dama</u>	67	44	1(Z)
<u>Axis axis</u>	90	60	4
<u>Axis porcinus</u>	50	35	2
<u>Cervus unicolor</u>			
<u>C. u. brookei</u>	121	91	1
<u>C. u. dejeani</u>	???	?	1
<u>C. u. equinus</u>	215	162	2
<u>C. u. francianus</u>	???	?	1
<u>C. u. niger</u>	270	?	1

<u>Cervus timorensis</u>	118	?	1
<u>Cervus duvauceli</u>	230	?	1
<u>Cervus eldi</u>	100	64	1
<u>Cervus nippon</u>	64	41	4
<u>Cervus elephas</u>			
<u>C. e. canadensis</u>	400	250	11
<u>C. e. cashmirensis</u>	200	?	1
<u>C. e. corsicanus</u>	?	?	1
<u>C. e. hispanicus</u>	250	?	1
<u>C. e. hanqlu</u>	200	?	2
<u>C. e. nannodes</u>	?	?	2
<u>C. e. scoticus</u>	180	125	1
<u>Elaphurus davidianus</u>	190	ND	7(Z)
<u>Odocoileus hemionus</u>	91	57	16
<u>Odocoileus virginianus</u>	68	45	14
<u>Mazama americana</u>	29	ND	4
<u>Mazama gouazoubira</u>	18	ND	7
<u>Hippocamelus bisulcus</u>	???	55	1(P)
<u>Blastocerus dichotomus</u>	100	?	2
<u>Ozotoceros bezoarticus</u>	40	35	2
<u>Pudu pudu</u>	13.5	ND	1
<u>Pudu mephistophiles</u>			2
<u>Alces alces</u>	450	318	14
<u>Rangifer tarandus</u>	179	110	12
<u>Hydropotes inermis</u>	12	10	2
<u>Capreolus capreolus</u>	27	21	16

Appendix II. Reduced major axis equations used to compute limb variables.

<u>Bone</u>	<u>b</u>	<u>log a</u>	<u>Correlation Coefficient</u>
Humerus	0.9966	-0.1193	.9895
Radius	1.2240	-0.4133	.9795
Metacarpal	1.3840	-0.6777	.9454
Tibia	0.9986	-0.0452	.9800
Metatarsal	1.1890	-0.3314	.9461

FIGURE LEGENDS

Figure 1. Femur length plotted against body weight on logarithmic coordinates. Solid line is the regression line for Cervidae, dashed line for Bovidae.

Figure 2. Metacarpal length plotted against body weight on logarithmic coordinates. Solid line is regression line for Cervidae, dashed line for Bovidae.

Figure 3. Hindlimb length plotted against body weight on logarithmic coordinates. Solid line is regression line for Cervidae, dashed line is regression line for Bovidae.

Certain species are identified as follows: ▼ = Moschus;
◆ = Hydropotes; ⊗ = Pudu; ★ = Antilocapra; ▲ = Axis; ■ =
C. nippon, Capreolus, Odocoileus.

Figure 4. Metacarpal length plotted against femur length on logarithmic coordinates. Certain species are identified as follows: ◆ = Hydropotes; ⊗ = Pudu; ★ = Antilocapra; ▲ = Axis; ■ = C. nippon, Capreolus, Odocoileus.

Figure 5. Area (upper curve) and antero-posterior diameter (lower curve) of metacarpal plotted against body weight on logarithmic coordinates (not to same vertical scale).

Figure 6. Metacarpal length plotted against diameter on logarithmic coordinates. Solid line is the regression for Cervidae, dashed line for Bovidae.











