

Prediction of body weight of fossil Artiodactyla

K. M. SCOTT

*Department of Biological Sciences (Zoology Unit),
Rutgers University, P.O. Box 1059
Piscataway, New Jersey 08854, U.S.A.*

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Many dimensions of the postcranial skeleton of ruminant artiodactyls scale closely with body weight and are therefore potentially useful as predictors of body weight in fossil species. Using 45 dimensions of the skeleton a series of predictive equations was generated based on the scaling relationships of the family Bovidae. As a test of their usefulness these equations were used to predict body weights of a number of living ruminant artiodactyls, and six genera of fossil artiodactyls. For most species body weight estimates within 25% of actual weight were given by the mean of the predicted weights from all measurements except lengths of long bones. While femur length was a reasonable predictor of body weight, lengths of distal long bones were unreliable and should not be used as indicators of relative or absolute body weights. Some non-length measurements are biased in certain taxonomic groups; the possibility of erroneous estimates from such measurements can be reduced by using as many estimators of body weight as are available. No species of artiodactyl tested is so highly modified in all dimensions that all results were erroneous. Subsets of measurements which might be available from a typical fossil fragment also gave reliable results.

KEY WORDS:— Artiodactyla – allometry – postcranial skeleton – weight prediction.

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INTRODUCTION

Many recent studies have called attention to the number of life-history parameters that are correlated with body weight in a variety of mammals (see for example McNab, 1963; Fleagle, 1978; Martin, 1980; Western, 1980). Estimates of the body weight of fossil species can thus play a role in many kinds of paleobiological studies, including allometric studies. Body weight estimates have been used in a variety of allometric studies of fossil lineages, especially of brain size (Jerison, 1971; Radinsky, 1978). However, more emphasis has been placed on the uses of this datum than on the calculation of it. Both allometric studies and paleoecological studies have dealt with various groups of the ungulate mammals. This study presents relationships that can be used to predict body weights in fossil pecorans, especially Bovidae, using postcranial elements.

Most attempts to estimate body weight in fossil mammals have depended on known scaling relationships between body dimensions and weight in extant mammals to extrapolate to extinct species, but little attempt has been made to evaluate potential distortions. Dental measurements of various types have been commonly used (Gould, 1975; Fleagle, 1978; Creighton, 1980) as has femur length (e.g. Martin, 1980). For ungulate body weights both Radinsky (1978) and Jerison (1971) used body length and Jerison (1971) also used limb lengths to predict body length. Gould (1974) used radius length as an indicator of relative body size in Cervidae, although he did not calculate body weights from this bone. A number of problems are associated with the use of such regressions to predict body weight. Any attempt to base predictions on a single character will occasionally give grossly inaccurate results: head and body length would be a much poorer predictor of body weight in a giraffe than in a more normally proportioned animal. This is an obvious and exaggerated example and most people are too familiar with the physical peculiarities of the giraffe to be misled. However, for most skeletal characteristics little attempt has been made to evaluate such potential distortions. Errors of this kind can be avoided by using more than a single characteristic to predict body weight. A species which shows an extreme adaptation in one body part will not necessarily be so extremely modified in other dimensions. If a number of estimates are made from various characters such aberrant estimates can be recognized and discarded.

Selection of the living taxon used to calculate the regressions from which predictions are made is an important issue. Clearly it would be ideal if all fossil species belonged to living families with a large size range. If a species has no or only a few close living relatives, the question of appropriate analogs becomes more difficult. One technique is to use more general relationships; for example femur length for a large size range of assorted mammals (Martin, 1980) or body length for all living carnivores and ungulates (Radinsky, 1978). Another possibility would be to choose morphologically similar species, perhaps those which at least belong to the same order. The choice of technique will in part be dictated by the use to which the body weights are to be put. If only gross estimates or size classes are desired more general relationships would give perfectly suitable results. However, in order to make detailed comparisons within a taxon more accurate methods would be desirable. In any case, if more exact determinations can be made for a taxon these should be useful in a variety of studies.

There are good biomechanical reasons for believing that skeletal dimensions should show a high correlation with body weights. Bones must be of sufficient

thickness to withstand the increasing compressive and bending forces which are generated with increasing body weights. Gould (1966) has pointed out that in general limb cross-section area, and thus compressive strength, does not scale directly with body weight. McMahon (1973) proposed that compressive strength is not limiting but that elastic resistance to bending is critical in determining bone dimensions and presented evidence that this is the case in ungulates as a group (McMahon, 1975). Alexander (1977) presented evidence that Bovidae scale elastically. Although neither ungulates (Scott, 1979) nor mammals generally (Alexander *et al.*, 1979) scale so as to maintain elastic similarity, as originally proposed by McMahon (1973, 1975), elastic factors may play an important role in determining skeletal structure, since many fractures are initiated by bending (Wainwright *et al.*, 1976).

MATERIALS AND METHODS

Body weight determinations

Prediction of body weight by any technique which uses regressions of body weight and some physical measurement of any kind depends on the availability of accurate data on body weight. For most small mammals and for thoroughly studied groups (such as primates) these data are readily available. The calculation of predictive equations for body weight in large herbivores has been hampered by lack of good body weight data for living species. Data taken in the field for museum specimens rarely includes body weight: the problems involved in taking this datum are obvious. Additionally, there are a number of problems involved with using one-time weights of wild ungulates. There are hourly and daily variations in body weights due to the amounts of food and water in the digestive tract (Talbot & McCulloch, 1965); this variation in live weight may be as great as 10%, depending on the contents of the stomach (Van Zyl, 1968). For domestic ungulates such variation is controlled by weighing animals after a fast but this method is not possible for wild ungulates. Individual weights thus do not necessarily provide an accurate estimate when they are available.

Many authors (for example Jerison, 1971; Radinsky, 1978) have relied on the body weights reported in Walker (1968). However, there are a number of problems associated with these data. First, weight ranges are given for a genus. While these ranges can sometimes be useful for monotypic genera, the species in many genera vary widely in size. For example, the size difference between the smallest and the largest species of *Cephalophus* is tenfold. Second, many of the ungulate records are taken from the various editions of *Rowland Ward's Records of Big Game* (Best, Edmond-Blanc & Witting, 1962) and are in fact weight records for the largest measured male. Although such records are potentially useful (see below) they must be applied with caution. Last, weight data are simply not given for a number of genera. However, weight data are available in the literature for many species of Bovidae, especially the African species. For many species mean body weights and adult ranges have been determined for collections of a number of animals (for example Meinertzen, 1938; Sachs, 1967; and other papers summarized in Von la Chevallerie, 1970). Using these sources a reasonable estimate of an average body weight of an adult animal can be determined for a

number of species. Weight estimates given by Dorst & Dandelot (1969), Bere (1970), and Jarman (1974) also appear to be relatively free of the problems mentioned for Walker (1968). Comparable weight data are generally available for North American bovids. For Asian Bovidae there are fewer body weights available and many available weights are from the reports of big game hunters. These weight data give overestimates of average male weights, since only the largest males taken are reported and hunters almost certainly selected the largest males available (see for example, Clark, 1964). Comparisons between hunters' reports and less biased weights available for some species indicates that these reports overestimate the average weight of a male by about 10%. Where I have had to use these data I have therefore reduced them accordingly. Additionally, if many records are examined some sense of the range of body sizes emerges. In some cases body weight data from big game hunters are good estimators of the weights of museum specimens: many trophies have become part of museum collections. Where I found this to be the case I used uncorrected maximum weights.

Body weight data for other ruminants are even more problematical than for Bovidae. Records from hunters seem to be the only sources available for many species; I suspect that these data are reported in many standard works. In some cases zoo records and field data are available as well. The problem of defining body weights for cervids is further complicated by large differences in size between subspecies of some species, especially Asian species with populations on the Pacific islands. Data are rarely available for all subspecies, and in many cases cited weights (e.g. Walker, 1968) do not specify subspecies or locality. I have compiled body weight data for a number of species but most are from general sources (Whitehead, 1972; Grzimek, 1972). For this reason I have not calculated predictive equations based on non-bovid ruminants, although I feel that these data can eventually be sufficiently refined to do so. I have used these data only as a check on the predictive equations from Bovidae to test the general applicability of such equations.

Given that reasonable estimates of the body weight of an average adult individual can be obtained from the literature the question of whether these estimates can be used with measurements taken on unrelated individuals from museum collections to estimate body weights remains. It is difficult to assemble sufficient data to adequately compare results from scaling individual body weights and measurements to scaling estimates of average weights and dimensions. Martin (1980) performed these comparisons for a number of species of small mammals, and found that his results were comparable. Since, in fact, one is really interested in predicting the weight of an average individual of a fossil species, average measurements of living species are probably a reasonable basis for those predictions.

Measurements and techniques

The series of 45 measurements used for the predictive equations is illustrated in Fig. 1. The exact orientation of measurements was chosen so that the measurements could be easily repeated on all bovids. These measurements were taken on 580 adult individuals belonging to 108 species of Bovidae. The specimens used are wild-caught individuals in the collections of the American Museum of Natural History (AMNH), British Museum of Natural History (BMNH), Museum

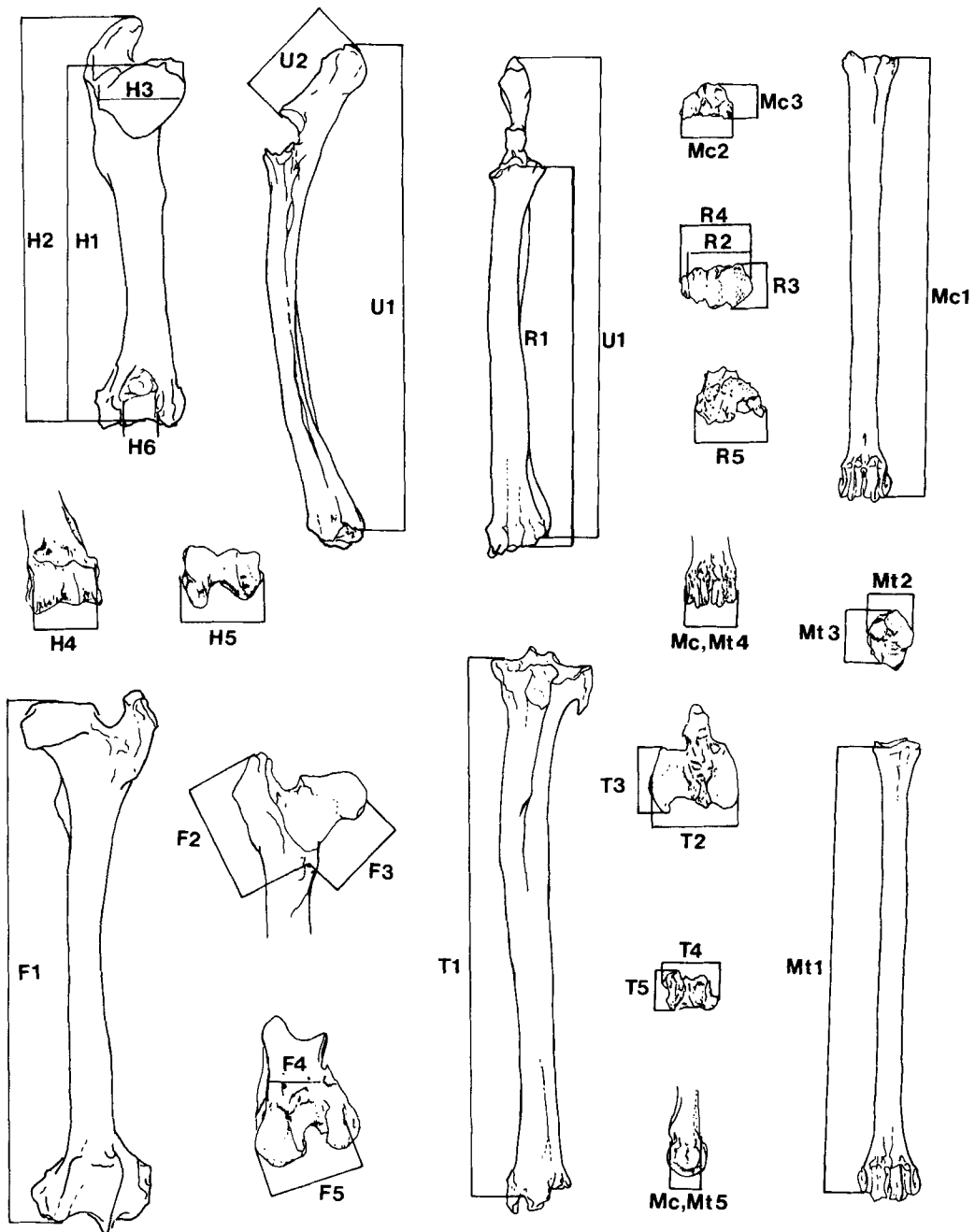


Figure 1. Definitions of the measurements used to predict body weight. H, humerus; U, ulna; R, radius; Mc, metacarpal; F, femur; T, tibia; Mt, metatarsal. All bones illustrated are from the left side of *Gazella thomsoni*.

of Comparative Zoology (MCZ), The Field Museum of Natural History (FMNH), and the United States National Museum (USNM). The museum numbers and species identifications of each specimen are given in Scott (1979). Each species was separated by sex and subspecies if there was more than a 10–15% dimorphism in weight between the sexes or subspecies. This resulted in the creation of about 175

size specific units. For each such unit the mean of each measurement was computed across all individual specimens belonging to that unit. For each unit the weight of an average individual was estimated from the literature. For each measurement I performed a least squares regression on the relationship between that measurement and body weight using log transformed data. In each case body weight was the dependent variable since it was the quantity to be predicted. This created a series of 45 equations, each of the form: $\log \text{ body weight} = b \log X + a \text{ constant}$, where b is the slope of the equation (on a log-log plot) and X is one of the measurements. To test the applicability of these equations I used them to predict body weights from each measurement of the original series of bovid measurements. In addition I calculated body weight estimates from the same series of 45 measurements taken on 190 specimens of Cervidae, Camelidae, and *Antilocapra*; specimens used are in the collections of the AMNH, FMNH, USNM, MCZ, and the Museum of Vertebrate Zoology, Berkeley (MVZ). For all of these taxa at least approximate body weights were available. I also calculated body weights for six genera of fossil artiodactyls: *Bouromeryx* (Dromomerycidae), *Aletomeryx* (Dromomerycidae), *Cosoryx* (Antilocapridae), *Capromeryx* (Antilocapridae), *Stockoceros* (Antilocapridae), and *Megaloceros* (Cervidae). Body weights of *Aletomeryx*, *Cosoryx*, and *Megaloceros* were calculated from associated bones of a single individual, respectively FAM 42883 (AMNH), FAM 57055 (AMNH), and UCMP 63524 (University of California Museum of Paleontology, Berkeley). Body weights of *Capromeryx*, *Stockoceros*, and *Bouromeryx* were calculated from the mean dimensions of four to eleven unassociated individuals from a single quarry. These specimens are in the following collections: *Bouromeryx*, AMNH (Trinity River Pit 1, Texas); *Capromeryx*, Florida State Museum (Inglis); *Stockoceros*, Los Angeles County Museum (San Josecito Cave).

For each long bone except the femur I calculated the mean weight estimated by all measurements taken on that bone except length and the standard deviation of the estimated weights. For the femur, mean predicted weight was calculated in two ways: first, using only the non-length measurements and second, using all of the femur measurements. I also calculated mean body weights from sets of measurements which might be available on a fossil fragment, for example H4–H6, the measurements on the distal end of the humerus. Multiple regressions were performed on these same series to compare predictions with those based on a single estimate or a mean estimate. The multiple regressions were performed using the maximum R -square improvement technique in the SAS procedure STEPWISE, which calculates the best one, two, and three variable models and the R -square values for each.

RESULTS

Predictive equations

The equations developed to predict body weight are given in Table 1, with the R -square values. Plots of some of the relationships are shown in Figs 2–5. Most of the dimensions except limb bone lengths scale closely with body weight. For the non-length measurements correlation coefficients between the log-transformed variables are all greater than 0.9, between raw variables greater than 0.8, and R -

Table 1. Values for use in predictive equations based on bovid data ($N=175$). For each measurement (M), the predictive equations for body weight (BW) will take the form $\text{Log } BW = b(\text{log } M) + a$. R -square values for the regressions are also given

Measurement (M)	b	a	R -square
H1	3.4556	-2.4150	0.9278
H2	3.3696	-2.4709	0.9331
H3	2.7311	0.2334	0.9434
H4	2.5499	0.4078	0.9590
H5	2.6246	0.2756	0.9604
H6	2.7630	1.3617	0.9274
H7	2.5013	1.0794	0.9529
H8	2.5424	0.8843	0.9339
U1	3.1886	-2.6320	0.8872
U2	2.6310	-0.0844	0.9436
R1	3.2052	-2.3203	0.8487
R2	2.5069	0.4311	0.9629
R3	2.5472	1.0525	0.9279
R4	2.4305	0.3756	0.9543
R5	2.4824	0.4635	0.9596
R6	2.6208	0.8854	0.9497
R7	2.5679	1.4742	0.9409
MC1	2.5109	-1.2773	0.4703
MC2	2.6495	0.6016	0.9529
MC3	2.8291	1.0620	0.9402
MC4	2.3765	0.7443	0.9203
MC5	2.6469	1.2458	0.9127
MC6	2.4354	1.2059	0.8922
MC7	2.7444	1.3815	0.9187
F1	3.5526	-2.9997	0.9326
F2	2.6934	-0.2555	0.9529
F3	2.9531	-0.0808	0.9420
F4	2.9573	0.7271	0.9415
F5	2.9053	-0.0768	0.9530
F6	2.9170	0.8627	0.9347
F7	2.7671	0.8731	0.9456
T1	3.9842	-3.8078	0.8453
T2	2.8850	-0.2758	0.9567
T3	3.2248	0.0753	0.9231
T4	2.8409	0.3222	0.9545
T5	2.9720	0.6222	0.9464
T6	2.8562	0.8318	0.9479
T7	2.9469	0.9879	0.9224
MT1	3.0701	-2.0622	0.5434
MT2	2.9220	0.6162	0.9405
MT3	3.0306	0.5755	0.9307
MT4	2.7421	0.5614	0.9418
MT5	2.9763	1.1416	0.9239
MT6	2.8710	1.1939	0.9294
MT7	2.9361	1.1375	0.9118

square values are above 0.90. Lengths of bones, especially distal bones, have lower correlation coefficients and R -square values than do non-length measurements.

Bovidae

Estimated weights for a representative sample of bovid species are given in Table 2. In general the mean body weights for each bone give the best weight

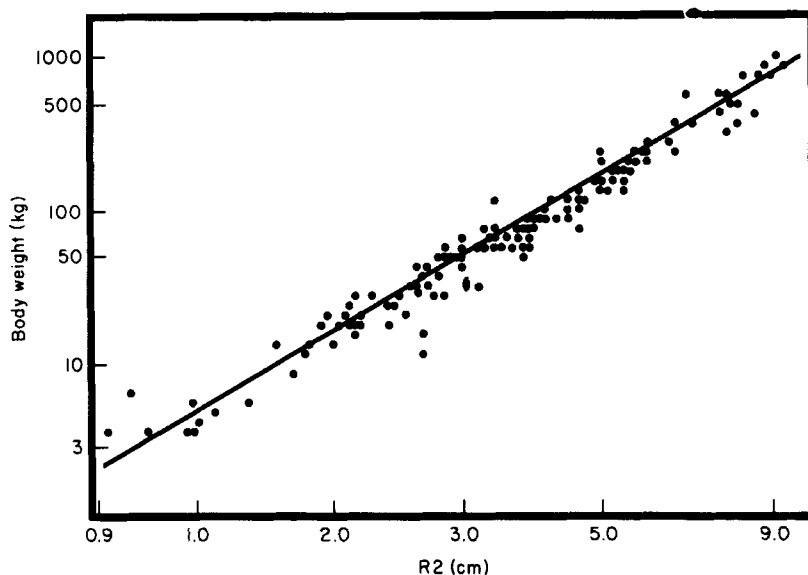


Figure 2. Log-log plot of proximal articular surface of the radius (R2) against body weight for all Bovidae.

estimates. The mean body weights give over- or underestimates for some species but these are in most cases within 15% of the body weight I used. These results show no particular taxonomic or habitat related biases with two exceptions. The body weights of large Bovini tend to be underestimated, sometimes by as much as 40%. Body weight estimates from distal bones of some of the Rupicapriini and Capriini also tend to give underestimates. Humerus and femur lengths give predictions closer to actual weight than do lengths of the distal bones for most species. Excepting *Bison*, weights predicted by humerus and femur length are less than 25% different from actual weights, while in some species metacarpal length

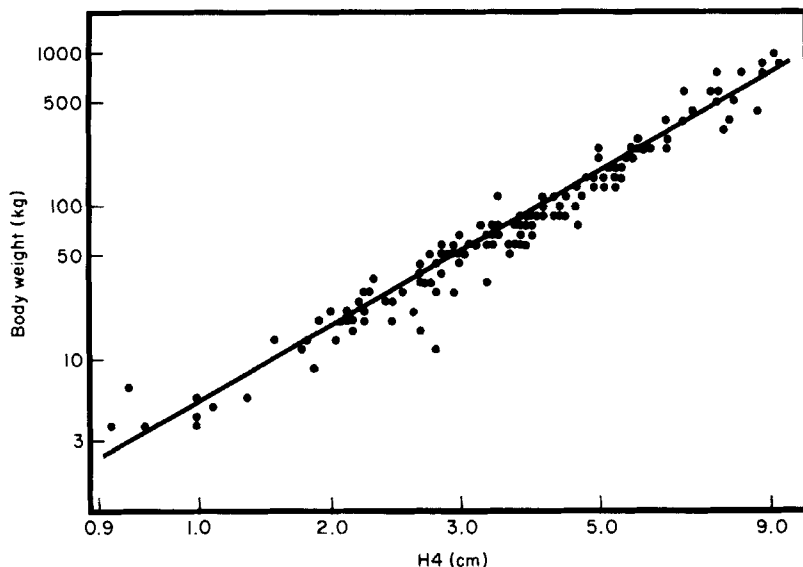


Figure 3. Log-log plot of width of distal articular surface of humerus (H4) against body weight for all Bovidae.

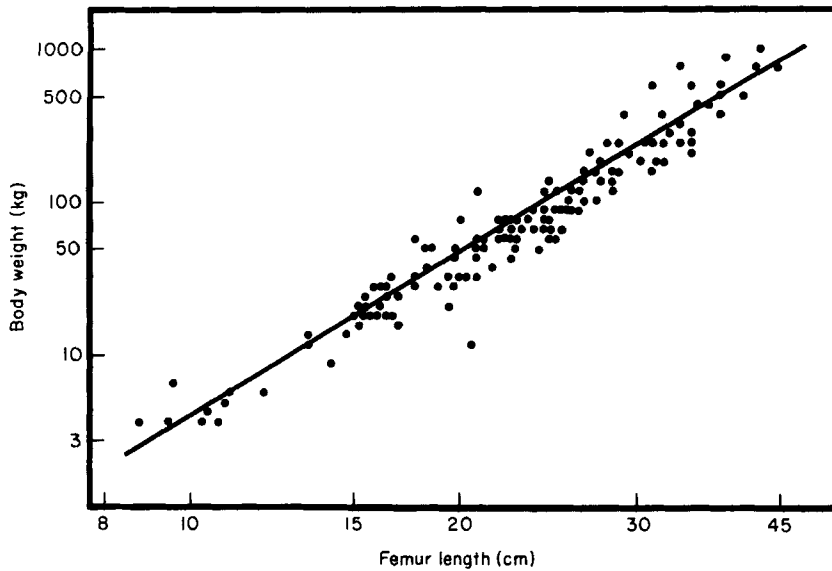


Figure 4. Log-log plot of femur length (F1) against body weight for all Bovidae.

predictions may vary by as much as 400%. Even for *Bison*, humerus and femur length underestimate less (35%, 50%) than metacarpal or metatarsal length (90%, 70%). Distal bones vary more relative to body weight than proximal bones. (Compare Figs 4 & 5 and *R*-square values in Table 2.) Weight estimates based on length of radius, tibia, metacarpal, and metatarsal show biases dependent on habitat, taxon, and body size. For example, distal bone lengths of plains living Alcelaphini and Antilopini greatly overestimate body weight, while in large Bovini and mountain-dwelling Caprini and Rupicaprini these bones give large underestimates of body weight.

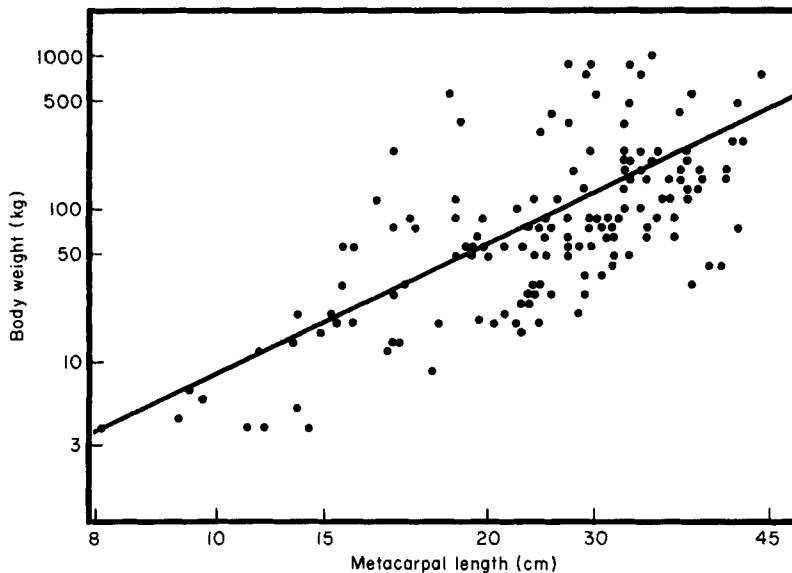


Figure 5. Log-log plot of metacarpal length (Mc1) against body weight for all Bovidae.

Table 2. Predicted body weights (kg) for sample species of living and fossil Artiodactyla. The body weight listed for each living species is for an average-sized adult male. For each long bone the top line gives the mean predicted weight of the non-length measurements \pm standard deviation (MPW \pm s.d.), and the second line gives the body weight estimated from the length of that bone (LPW). The last three columns give body weights predicted by subsets of measurements; these are distal end of the humerus (H4, H5, H6), proximal end of the radius (R2, R3, R4), and proximal end of the metatarsal (MT2 and MT3).

	Body weight	Humerus MPW \pm s.d. LPW	Radius MPW \pm s.d. LPW	Metacarpal MPW \pm s.d. LPW	Femur MPW \pm s.d. LPW	Tibia MPW \pm s.d. LPW	Metatarsal MPW \pm s.d. LPW	Distal humerus	Proximal radius	Proximal metatarsal
Bovidae										
<i>Addax nasomaculatus</i>	118	106 \pm 11 93	109 \pm 11 126	97 \pm 13 66	106 \pm 21 91	93 \pm 15 87	96 \pm 15 88	111	112	94
<i>Sylviatropa grimmera</i>	13	12.6 \pm 1.0 13.8	13 \pm .9 14.4	14 \pm 1 26.3	14.5 \pm .8 14.9	15.2 \pm 2 13.0	15.6 \pm 2 25.5	13	13.3	15.5
<i>Kobus megaceros</i>	91	101 \pm 7 100	97 \pm 10 92	95 \pm 13 110	105 \pm 10 115	100 \pm 6 131	107 \pm 3 107	101	89.9	105
<i>Madoqua kiki</i>	5	5.4 \pm .7 5.6	5.5 \pm .5 5.9	5.2 \pm .5 14.1	5.4 \pm .5 4.9	6.0 \pm .8 5.9	5.3 \pm .3 10.4	5.7	5.7	5.5
<i>Bison bison</i>	865	556 \pm 85 559	575 \pm 44 277	531 \pm 83 92	560 \pm 98 461	584 \pm 74 279	512 \pm 38 152	552	586	473
<i>Damaliscus korrigum</i>	123	131 \pm 9 132	138 \pm 4 235	140 \pm 14 173	128 \pm 14 118	136 \pm 10 150	136 \pm 13 167	135	137	142
<i>Gazella thomsoni</i>	23	28 \pm 3 19	27 \pm 3 31	28 \pm 2 63	26 \pm 2.6 24	28 \pm 3 30	31 \pm 5 52	27.3	28.2	30.8
<i>Litocranius walleri</i>	45	40 \pm 4 52	43 \pm 8 97	46 \pm 12 216	43 \pm 5 47	47 \pm 6.5 79	55 \pm 14 162	40.9	43.1	54.2
<i>Hemitragus hyalensis</i>	90	87 \pm 18 109	85 \pm 16 47	76 \pm 26 29	79 \pm 10 79	73 \pm 14 69	65 \pm 21 24	67	67	53
<i>Ovis dalli</i>	84	91 \pm 10 103	80 \pm 11 88	81 \pm 9 71	82 \pm 8 98	76 \pm 10 118	77 \pm 11 80	84	78	76
Antilocapridae										
<i>Antilocapra americana</i>	50	54 \pm 17 71	57 \pm 3 73	64 \pm 5 106	55 \pm 5 65	55 \pm 6 68	62 \pm 10 105	58	58	67

[illegible]

Cervidae and Antilocapra

As is true for Bovidae, the mean estimated weights for each bone in these taxa (using the bovid equations) give better estimates of weight than do lengths (see Table 2). Although in general they are not as close as the bovid estimates, the mean body weight estimates for most species are within 25% of actual body weights. It is difficult to judge how accurate the estimates really are since body weight data for cervids are not as good as for bovids. As for Bovidae, weight estimates calculated from cervid distal bone lengths may give gross over- or underestimates of body weights. In part the mean weight estimates from bovid equations are poorer for cervids because as a family cervids differ from bovids in some morphological features. For example, the proximal articular surface of the humerus (H3) is relatively narrower in cervids than in bovids and F2 is consistently shorter. Improved weight estimates could have been obtained by discarding these measurements. Some cervids also give somewhat higher weight estimates from hindlimb than forelimb measurements, and these tend to be closer to actual weights. The reason for this is that while length measurements vary according to habitats and habits, cervids tend to have relatively shorter forelimbs, longer humeri, and longer metatarsals than bovids of the same size (Scott, unpub. data).

Giraffidae

For both *Okapia* and *Giraffa* the femur weight estimates give reasonable approximations to body weights. The mean estimates from humerus and radius dimensions of *Giraffa* are distorted by only a single measurement. The proximal articular surface of the humerus in giraffids, as in cervids, is relatively narrower than in bovids, and the radius is more robust in the anteroposterior dimension. The metacarpals and metatarsals consistently give overestimates. Lengths obviously give large overestimates. If the weights reported in the literature for *Okapia* are accurate, only the femur and tibia give reasonable weight estimates. Estimates from other bones are consistently too high.

Camelidae

The mean estimated body weights all lie within the published weight ranges for living camelids, and are reasonably consistent between long bones. Length measurements give unsatisfactory results. Weight estimates based on length measurements gave body weights ranging from 42 to 260% of body weight, and there was no consistent pattern of variation. The standard deviations of the mean weights are higher than for the other families, again because for camelids certain measurements consistently give biased results. As in cervids, the head of the camelid humerus is consistently narrower than in bovids. The transverse distal diameters of metacarpals and metatarsals (Mc4 and Mt4) are not comparable to those of bovids or cervids. In camelids the distal articular surfaces are spread apart due to the digitigrade posture of camelids. This does not markedly distort the mean weights for these bones, however.

Fossil artiodactyls

Mean predicted weights for the six genera of fossil ungulates generally gave consistent weight estimates between bones, and standard deviations were comparable to those for cervids and *Antilocapra*. Weight predictions from forelimb bones of *Bouromeryx* consistently gave lower estimates of body weights than those from hindlimb bones. This is the only marked discrepancy in body weights. Similar differences were seen in some cervids, suggesting that cervids might serve as a better model for this genus.

Weight prediction from fragments

Although body weights predicted from only one or two measurements were in some cases less accurate, most of these predicted weights are close to those predicted from complete bones (Table 2). The weights predicted from proximal metatarsal measurements for *Hemitragus hylocrius* are erroneous because of the anteroposterior flattening of this bone. Similar errors would be generated for similarly modified taxa. Weights of large Bovini and camelids are more poorly predicted, as they are for entire bones. Body weight estimates from the multiple regressions were no more accurate than those calculated from the mean of individual predicted weights. The *R*-square values of the multiple regression are only slightly higher than those for the best single variable model. These values have therefore not been reported here.

DISCUSSION

All of the skeletal dimensions listed here can be used to predict body weight with some degree of success. It is to be expected that the mean body weight estimates for the bovid species originally used to construct the regressions would be close to actual body weights. However, the biases in the results are instructive in indicating the limitations of body weight predictions from skeletal elements and dimensions which are not reliable indicators. For bovids lengths of distal limb elements (radius, tibia, metacarpal and metatarsal) are clearly poorer predictors of body weight than are humerus and femur lengths. Excepting the large Bovini proximal bones give weight estimates within 25% of actual body weight while estimates based on distal lengths may give estimates as low as 32% or as high as 400% of body weight. Distal bones are more modified according to the habits or habitat of the species in question. Humerus and femur are not modified very much according to habitat and are therefore less likely to give biased results. It is the non-length means which are the most reliable indicators. Some of the non-length dimensions also give over- or underestimates because of habitat-related morphological changes. This is true, for example, of the anteroposteriorly flattened metacarpals and metatarsals of the rupicaprine and some caprine bovids. For most bovids and cervids no species differs from a 'normal' value in all of its dimensions; only for some species larger than about 500 kg might all estimates be wrong. It is for this reason that the mean estimates are the most reliable predictors of body weights: the effect of a single aberrant weight estimate from a highly modified dimension is minimal. Better results would be obtained by discarding obviously aberrant values. Using this approach I believe that it should be possible to obtain

weight estimates within 25%, for all but the largest species of fossil Bovidae and within 15%, for most. Modern bovids are representative of the diversity which has existed in the past in this family, and the limb morphology has been comparatively stable, so that regressions based on modern bovids should apply to all members of the family.

Extension of the results of the bovid analysis to other ungulate taxa is more problematical. Use of scaling relationships of limbs to predict body weight is possible only so long as limb bones change their dimensions with increasing body weight in a regular way, which is similar in all families. Regardless of the structural factor or factors which dictate scaling, scaling relationships should not be expected to apply over a range of different basic morphologies. Differently shaped structures transmit forces differently and may thus change in different ways as size increases. The families Equidae and Bovidae show grossly similar locomotor adaptations of the skeleton, but differ in the foot axis along which weight is distributed, number of digits, and exact shape of articular surfaces. Even if the same physical constraints governed size-related changes in the two families, scaling relationships for each dimension might differ in intercept, if not in slope. The same would be true for artiodactyl taxa such as suids (pigs) in which metapodials three and four have not fused, versus those in which they have: distribution of forces over a single cylinder may differ from that in a double cylinder. One would not expect bovid regressions generally to give accurate results for equids or suids, although they might give accurate relative weights within a family if only the intercepts of the scaling relationships varied.

Two questions are of interest with respect to generalization of these results to other Pecora. First, which taxa are structurally similar enough to the Bovidae to apply the equations given here generally? Second, are there some equations which are applicable to taxa which generally do not share the scaling relationships of bovids? Based on the results obtained here it seems that the predictive equations derived from living bovids can be used to predict body weight in the families tested, with the possible exception of the Giraffidae. For all of these families except Giraffidae the bovid equations give mean predicted weights within 25% of actual for most species. Although the risk of obtaining a grossly inaccurate estimate is always present, especially when weights are estimated from partial skeletons, if several intact long bones are available it should be possible to obtain weight estimates of this degree of accuracy for most fossil Pecora. Better weight prediction equations for Cervidae could probably be provided by calculating predictive equations from cervid dimensions. These equations may be more suitable for groups such as the Dromomerycidae, which are more deer-like postcranially. Both cervids and dromomerycids give lower weight estimates from forelimb bones in some cases, suggesting that in these taxa the forelimb may be used differently in locomotion than it is in bovids. Predictive equations based on the combined data for the living families might provide the best means for estimating the weights of fossil pecorans which do not belong to families with many living members. Although this might result in less precise estimates for taxa which would fit one or the other set of regressions it may be difficult to decide in many cases to which living group a fossil species shows greatest affinities.

Camelid weight estimates present some problems. There are so few living camelids that adequate tests are difficult. The mean weight estimates for camelids from the bovid regressions vary from 90 to 171% of actual but most of the

overestimates are for *Lama glama* which is more variable in size than the other living species, and for which a single weight estimate may be inadequate. The morphological differences between the two groups point to the desirability of separate weight estimation equations. Preliminary plots of camelid measurements against body weight for the living camelids proved to be non-linear for both arithmetic and log-transformed data. With so few living species it is difficult to decide whether this is a linear relationship with a single aberrant species or a non-linear relationship. It is therefore hard to design predictive equations based on living camelids. Further work on this problem is in progress, but I suspect that it may prove to be necessary to use the bovid and cervid estimates for camelids, although the true scaling relationships of camelids would surely be more accurate.

Some skeletal dimensions may in fact scale in similar ways in dissimilar taxa, as the results of Martin (1980) suggest is true for femur. Femur morphology is more conservative in mammals generally, and artiodactyls particularly, than is morphology of more distal bones. Hence the femur is more likely to scale in a regular way in a diverse group of mammals. Even for the highly modified Giraffidae, femoral measurements (and to a lesser degree humeral measurements) gave predictions within 25% of actual weights. Thus it seems that for groups where results between bones are inconsistent or affinities are uncertain, the femur would be the best bone to use in estimating weight.

One of the most important points brought out by this study is that long bone lengths are in many cases unreliable estimators of body weight, or even relative size. For bovids this is particularly true for the metatarsal, metacarpal and radius. Preliminary cervid data indicate that the problem may be less pronounced for cervids, but that it still exists. Distal limb segments in all the ungulate groups examined vary in length with habitat, although most other dimensions are not affected by habitat. The lengths of distal limb segments can thus be used as habitat indicators (Scott, 1979, in prep.), but they should not be relied upon to predict body weight. The would also apply to the use of limb segment lengths as estimators of relative body weights, unless it is certain that all species are found in similar habitats and share similar locomotor habits. This is certainly not the case for bovids or cervids, although cervids as a group are more uniform.

It is also important to note that there is no simple way to correct for the habitat, size, and taxonomic biases in the non-length measurements. Jerison (1973) attempted to correct for biases against heavy-bodied animals by doubling weight estimates for species he considered to be heavily built. Although weights of larger, more heavily-bodied bovids are in many cases underestimated this method would only impose a different set of errors, since it would result in gross overestimates of some species of bovids, cervids and camelids. For these larger species weight estimates would best be based on the more proximal bones that are less subject to erroneous estimates.

No one measurement is a perfect indicator of body size, and skeletal dimensions are not necessarily better predictors of body weight than body length, tooth area, or skull dimensions. All of these indicators may introduce inaccuracies because some species show adaptive modifications: for example, mustelids have long bodies, giraffes have long necks, bush dogs have short legs. However, few species deviate in all of their dimensions, and the more parameters which can be used to predict body weight the less the chance of being misled by adaptively-modified structures. In addition, the more parameters analysed in modern species the

greater the chances that one or more of them will be available in a given fossil species. It is for these reasons that I believe skeletal measurements can be reliable indicators of body weight in fossil ungulates.

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APPENDIX

Body weight (kg) of average male and female Bovidae. For non-dimorphic species only a male weight is listed and ND is listed in the female column

Species	Male	Female		
<i>Tragelaphus angasi</i>	114	68	<i>Alcelaphus buselaphus swaynei</i>	159 ND
<i>Tragelaphus buxtoni</i>	216	150	<i>Alcelaphus buselaphus caama</i>	159 ND
<i>Tragelaphus spekei</i>	91	57	<i>Alcelaphus lichtensteini</i>	136 ND
<i>Tragelaphus scriptus</i>	64	52	<i>Connochaetes gnou</i>	136 ND
<i>Tragelaphus imberbis</i>	91	64	<i>Connochaetes taurinus</i>	239 193
<i>Tragelaphus strepsiceros</i>	260	170	<i>Oreotragus oreotragus</i>	13.5 ND
<i>Tragelaphus euryceros</i>	227	182	<i>Ourebia ourebi</i>	18 ND
<i>Taurotragus oryx</i>	590	432	<i>Raphicerus campestris</i>	13.5 ND
<i>Taurotragus derbianus</i>	704	493	<i>Nesotragus moschatus</i>	4.5 ND
<i>Boselaphus tragocamelus</i>	250	170	<i>Neotragus pygmaeus</i>	3.5 ND
<i>Tetracerus quadricornis</i>	17	ND	<i>Neotragus batesi</i>	6.4 ND
<i>Bubalis bubalis</i>	725	375	<i>Madoqua phillipsi</i>	3.5 ND
<i>Anoa depressicornis</i>	56	—	<i>Madoqua saltiana</i>	3.5 ND
<i>Bos gaurus</i>	1000	510	<i>Madoqua guentheri</i>	3.5 ND
<i>Bos frontalis</i>	545	—	<i>Madoqua kirki</i>	5.0 ND
<i>Bos sauveli</i>	714	365	<i>Dorcotragus megalotis</i>	9 ND
<i>Bos grunniens</i>	525	—	<i>Antilope cervicapra</i>	45.5 29.5
<i>Syncerus caffer caffer</i>	820	420	<i>Aepyceros melampus</i>	61 45.5
<i>Syncerus caffer nanus</i>	318	—	<i>Ammodorcas clarkei</i>	31 —
<i>Bison bonasus</i>	865	—	<i>Litocranius walleri</i>	45 41
<i>Bison bison</i>	865	—	<i>Gazella subgutturosa</i>	23 —
<i>Cephalophus callipygus</i>	18	ND	<i>Gazella dorcas</i>	23 —
<i>Cephalophus dorsalis</i>	20	ND	<i>Gazella gazella</i>	27 22
<i>Cephalophus leucogaster</i>	20	ND	<i>Gazella leptoceros</i>	27 —
<i>Cephalophus natalensis</i>	16	ND	<i>Gazella pelzelni</i>	12 —
<i>Cephalophus niger</i>	11	ND	<i>Gazella spekei</i>	13 —
<i>Cephalophus nigrifrons</i>	18	ND	<i>Gazella thomsoni</i>	23 18
<i>Cephalophus rufilatus</i>	13	ND	<i>Gazella tilonura</i>	27 —
<i>Cephalophus silvicultor</i>	61	ND	<i>Gazella dama</i>	75 —
<i>Cephalophus zebra</i>	11	ND	<i>Gazella granti</i>	75 50
<i>Cephalophus monticola</i>	5.5	ND	<i>Gazella soemmerringi</i>	45.5 —
<i>Cephalophus maxwelli</i>	5.5	ND	<i>Gazella cuvieri</i>	27 —
<i>Sylvicapra grimmia</i>	13	ND	<i>Antidorcas marsupialis</i>	34 28
<i>Kobus ellipsiprymnus</i>	227	182	<i>Procapra guttorosa</i>	20 16
<i>Kobus defassa</i>	239	182	<i>Panthalops hodgsoni</i>	50 —
<i>Kobus kob kob</i>	70	45.5	<i>Saiga tatarica</i>	45 —
<i>Kobus kob leucotis</i>	82	54.5	<i>Naemohedus goral</i>	27 ND
<i>Kobus kob alurae</i>	82	54.5	<i>Capricornis sumatraensis</i>	102 ND
<i>Kobus kob thomasi</i>	91	64	<i>Capricornis crispus</i>	29.5 ND
<i>Kobus vardoni</i>	68	50	<i>Oreamnos americanus</i>	113.5 ND
<i>Kobus leche</i>	100	73	<i>Rupicapra rupicapra</i>	45 34
<i>Kobus megaceros</i>	91	73	<i>Budorcas taxicolor</i>	250 —
<i>Redunca arundinum</i>	68	57	<i>Ovibos moschatus</i>	364 —
<i>Redunca fulvorufula</i>	32	29.5	<i>Hemitragus jemlahicus</i>	91 —
<i>Redunca redunca</i>	45	38.5	<i>Capra ibex</i>	87 —
<i>Pelea capreolus</i>	23	20.5	<i>Capra caucasica</i>	87 —
<i>Hippotragus niger</i>	280	260	<i>Capra pyrenaica</i>	77 —
<i>Hippotragus equinus</i>	235	218	<i>Capra falconeri</i>	100 55
<i>Oryx gazella</i>	177	164	<i>Pseudois nayaur</i>	59 —
<i>Oryx leucoryx</i>	77	73	<i>Ammotragus lervia</i>	113 59
<i>Oryx tao</i>	205	193	<i>Ovis musimon</i>	45 —
<i>Addax nasomaculatus</i>	118	104	<i>Ovis orientalis</i>	59 —
<i>Damaliscus korrigum</i>	123	114	<i>Ovis ammon hodgsoni</i>	159 —
<i>Damaliscus dorcas</i>	73	66	<i>Ovis ammon poli</i>	136 91
<i>Damaliscus hunteri</i>	91	86	<i>Ovis ammon mongolica</i>	102 80
<i>Alcelaphus buselaphus cokii</i>	136	ND	<i>Ovis canadensis canadensis</i>	113 57
<i>Alcelaphus buselaphus letwel</i>	182	ND	<i>Ovis canadensis nelsoni</i>	73 45
<i>Alcelaphus buselaphus jacksoni</i>	182	ND	<i>Ovis dalli</i>	84 59