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## Bovids as indicators of Plio-Pleistocene paleoenvironments in East Africa

Reconstructions of the paleoenvironments of early hominids offer a framework for understanding hominid ecological and behavioral adaptations. Habitat reconstructions typically rely upon various biological or physical habitat indicators, and here we present reconstructions of the Plio-Pleistocene paleohabitats of Koobi Fora and Olduvai Gorge as based on fossil bovids (Artiodactyla: Bovidae). Bovids are the most common faunal element at most Neogene hominid and hominoid fossil localities and have been widely studied. This study addresses the functional morphology of the bovid femur through discriminant function analysis and provides additional support for the observation that certain features of the femur demonstrate clear correlations with the amount of vegetative cover in different modern habitats. The reconstructions for both Koobi Fora and Olduvai Gorge suggest that the full range of environments inhabited by living bovids was present during the Plio-Pleistocene. Koobi Fora appears to have had a somewhat higher percentage of more closed habitats than the relatively more open habitats of Olduvai Gorge. These habitat reconstructions are in broad agreement with other reconstructions based on a purely taxonomic approach to the bovid remains. Grounding our reconstructions of paleoenvironments in studies of functional morphology can help to develop a richer idea of the habitats and resources available to early hominids.

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### Introduction

An integral element to reconstructing the course of hominid evolution includes understanding the kinds of the environments in which the hominids lived. The idea is an old one, and can be found in the description of the Taung child by Raymond Dart who argued:

“For the production of man a different apprenticeship was needed to sharpen the wits and quicken the higher manifestations of intellect—a more open veldt country where competition was keener between swiftness and stealth, and where adroitness of thinking and movement played a preponderating role in the preservation of the species.” (Dart, 1925: p. 199)

The biological and behavioral adaptations of every species are in part a consequence of the selection pressures that operate within its specific environment, and more detailed reconstructions of Pliocene and Pleistocene environments will aid our understanding of the course of hominid evolution. However, it is important to note that the hominids themselves may have been sufficiently generalized in their locomotor and foraging behaviors that they potentially could have lived in and utilized a wide variety of habitats. The most useful environmental reconstructions are probably best based on an understanding of the ecological parameters of the complete fauna as well as the physical aspects of the fossil locality.

Paleohabitat reconstructions based on bovids are very popular because these animals are usually the most common element of the fauna in most Neogene fossil localities. The radiation of this family in the Neogene has seen its members evolving to inhabit a wide range of

environments that stretch from montane forest to arid desert, and to fill a range of body masses that varies by nearly three orders of magnitude (Kingdon, 1982).

The great utility of fossil bovids as habitat indicators has been demonstrated in the past by a number of studies (e.g., Gentry, 1970; Scott, 1979, 1985; Vrba, 1980; Greenacre & Vrba, 1984; Kappelman, 1984, 1986, 1988, 1991; Shipman & Harris, 1988; Solounias & Dawson-Saunders, 1988; Plummer & Bishop, 1994). The earliest studies depended upon a simple and direct assessment of the taxonomic affinity of the fossils, followed by an extension of the habitat preferences of the living relatives back to the fossil taxa. Because fossil bovids are generally assigned to species on the basis of cranial characteristics (e.g., dental, skull, and/or horn core morphologies), this approach is somewhat limited to rather complete cranial specimens and often necessarily ignores the usually more abundant postcranial material. The approach of “taxonomic affinity” represents a type of substantive uniformitarianism and finds some support in the fact that many closely related bovids do share some of the same habitat preferences at the generic or even tribal level. This method’s obvious weakness is that the habitat preferences are simply accepted and cannot be tested. The widespread use of this approach for reconstructing paleohabitats is, in part, pragmatic, because a focus on systematics leads many field projects to almost exclusively collect cranial remains and leave postcranial remains uncollected.

A more recent approach to reconstructing habitat preferences relies on functional morphology as a means to understanding dietary and locomotor adaptations and the way that these adaptations are linked to specific ecological or habitat parameters. This method offers the opportunity to build hypotheses that can be tested among living taxa. When these hypotheses are verified with strong correlations, the results can be extended with some confidence to the fossil record. The linkage between certain morphological patterns and their functional expression in specific habitats has generated a growing literature over the past several years (e.g., Van Valkenburgh, 1987; Kappelman, 1988, 1991; Solounias & Dawson-Saunders, 1988; Plummer & Bishop, 1994; Bishop, 1994; Spencer, 1995) and is increasingly becoming known as “ecological functional morphology”, “ecomorphology”, or “eco-funk”. This approach offers several advantages over a uniformitarian or, more simply, a “nearest relative’s habitat preference” approach, the most important of which is its testability as noted above, as well as the fact that the exact taxonomic affinity of the fossil need not be known. Combining a taxon free data set with the approach of ecological functional morphology permits the incorporation of unassigned, or sometimes even unassignable, elements into the study. Caution must be exercised here because taxonomic affinity may still partly control at least a portion of the expression of certain morphological traits.

One postcranial element that has proven useful in past habitat reconstructions is the bovid femur. Gentry (1970) noted that specific morphologies of the femur (as well as many other elements of the bovid skeleton) appear to represent functional complexes that demonstrate clear linkages between locomotor patterns and habitat preferences. These patterns were explored by Westlye (1982) and given a detailed treatment by Kappelman (1988, 1991). Briefly, certain functional complexes of the bovid femur are linked to locomotor patterns displayed by bovids across the habitat spectrum. For example, bovids living in more closed canopy settings often encounter a complex nearly three-dimensional substrate of standing as well as downed tree trunks, shrubs, roots, and bushes, all of which effectively limit high-speed cursorial locomotion. Bovid from these settings are found to have a more nearly spherical femoral head shape that produces a highly mobile hip joint and provides a high degree of

maneuverability. At the other end of the habitat spectrum are those species from more open habitats that offer only occasional ground-level obstacles. These bovids have a femoral head that is more cylindrical in shape and acts to limit movements to the parasagittal plane, and a distal femur with a larger moment arm for the extensors. These morphologies facilitate more rapid cursorial locomotion across what is essentially a two-dimensional substrate. Bovid living in the wide variety of broken-cover habitats that fall between the extremes of forest and plains demonstrate intermediate femoral morphologies (Kappelman, 1988). Discriminant function analysis has been used to test the strength with which these different features of the femur can be used to sort extant species among these three habitat categories, and these features were shown to have a high discriminating power. The approach was extended to include an analysis of the Miocene hominoid localities of Fort Ternan, Kenya, and the Chinji Formation in Pakistan (Kappelman, 1991). This methodology is here extended to the Plio-Pleistocene record from Olduvai Gorge, Tanzania, and Koobi Fora, Kenya.

### Materials and methods

The sample of extant bovids is given in Appendix I and in general incorporates the sample from Kappelman (1988, 1991) with the addition of arid and open habitat taxa (*Oryx gazella*, *Oryx tao*, *Addax nasomasculatus*) and the buffalo (*Syncerus caffer*), and the exclusion of non-African taxa and other rare taxa (e.g., *Litocranius walleri*) (compare Appendix I with Kappelman, 1991: Appendix I). Several individuals whose measurements were shown to be several standard deviations beyond the mean values for their species were deleted from the sample ( $n=7$ ). The final sample consists of 188 specimens from eight tribes and 38 species and is composed of adult, wild animals with males and females pooled for each species. Extant specimens are housed in the Museum of Comparative Zoology (MCZ, Cambridge, MA, U.S.A.) and the American Museum of Natural History (AMNH, New York, NY, U.S.A.).

The sample of fossil bovids is given in Appendix II. These specimens are from the Plio-Pleistocene levels of Olduvai Gorge, Tanzania and Koobi Fora, Kenya and are housed in the Kenyan National Museum (KNM) with a few additional specimens in the British Museum (Natural History) (BMNH, London, U.K.).

Previous reconstructions of hominoid and hominid paleoenvironments based on bovids as ecological indicators relied on a simple three part division of modern habitats into open, intermediate, and closed habitats as based on the relative degree of vegetative cover (Kappelman, 1988, 1991; Plummer & Bishop, 1994). Although this simple division has the advantage of producing a higher percentage of correct assignments, the utility of this approach can be questioned because so many diverse habitats are subsumed into the intermediate category. Attempting more detailed habitat categorizations for each species may provide more useful information for paleohabitat reconstruction. The ideal categorization for a study of this kind would be based on field observation that exactly characterized the specific habitat preferences of each individual bovid that was to be included in the sample prior to collection, and pooled all such individuals of a species. However, it is not possible today to either collect a sample of this type, or generally even reconstruct this level of detail from museum records because in most cases there was not enough information recorded for each specimen at the time that it was collected to permit a determination of exactly where the specific individual lived, or the specific parts of the environment that it inhabited. Habitat categories for each species must then be drawn from the literature.

The present study attempts to address the issue of habitat structure by offering a slightly more detailed breakdown of habitat subtypes. Four general categories of habitat, forest, heavy cover (bush, woodland, swamp, close to water), light cover (light bush, tall grass, hilly areas), and plains (edge or ecotone, open country, arid country), are used, with the gradient of the degree of canopy cover running from closed to open conditions. The assignments of each species to a particular habitat category generally follows Scott (1979, 1985), Kingdon (1982), and Kappelman (1988), but also takes into consideration the kinds of selection pressures on locomotion and body mass that are specific to each species in its particular habitat (see Kappelman, 1991; Plummer & Bishop, 1994). For example, even though *Kobus kob* is generally thought of as an open habitat species, it also relies on woodlands and must be able to maneuver through and across this more complex substrate. This species is here classified as “light cover”. Most edge and ecotone species (*Aepyceros melampus*, *Hippotragus equinus*, *Hippotragus niger*, *Alcelaphus lichtensteini*) spend time within the more open end of this habitat spectrum and are subject to predation by highly cursorial predators. There is then some considerable selective advantage placed on more cursorial locomotion for these “edge and ecotone” species and they are here classified as “open country”. The habitat categories for each species included in this study are given in Appendix I. It should be noted that this is a somewhat subjective and provisional classification, and is open to revision as more information about the behaviors of various bovid species becomes available.

Habitat structure appears to exert some general selection constraints on body mass with regard to predator avoidance strategies and diet (see Estes, 1974; Jarman, 1974). For example, large bovids are commonly found in more open habitats and usually rely on either their large size and/or herd behavior and vigilance as the first line of predator avoidance. Small bovids are usually found in more closed habitats, are more often solitary, and rely upon crypsis and stealth to avoid predators. The relationship between body mass, habitat structure, morphology, and diet has just begun to be explored (see Spencer, 1995) and there are some interesting correlations. For example, bovids living in forests or more closed habitats are often browsers or frugivores, are commonly territorial, and are intimately acquainted with the location of their patchily distributed but high energy food sources (Estes, 1974; Jarman, 1974). Bovid living in open habitats generally subsist on widely available grass blades that are often of lower nutritional quality than browse or fruit, and often must migrate long distances in “pursuit” of this food (Jarman & Sinclair, 1979). This coarse separation between high and low food quality along a gradient from small to large body mass reflects the fact that smaller animals have relatively higher metabolic rates than larger animals and require a relatively higher intake of energy (Jarman, 1974; Bell, 1971; Schmidt-Nielson, 1979) that is more easily satisfied with rich fruit or browse. Large bovids have relatively lower metabolic rates as a consequence of large body mass and are able to subsist on more commonly available but generally lower quality foods such as grass but must have larger home ranges to satisfy their absolutely larger energy requirements (McNab, 1963). Although there are many exceptions to these general relationships, the role of body mass deserves some investigation with regard to habitat structure. Joint surface area is often a strong predictor of body mass (Jungers, 1988; Ruff, 1988), and a calculation of femoral head area (see below) has been used to test this relationship in bovids and estimate body mass for the fossil bovids as based on a regression equation from extant species.

The features of the bovid femur used in this study are the same as those used previously (Kappelman, 1988, 1991: Figure 1) and the reader is referred to these earlier studies for a more detailed description and discussion. The variables used are:

*Femoral head shape score (FHSS).* Femoral head shape was scored on the distribution of articular area in the cranial projection and measured the taper of the femoral head along the mediolateral axis.

*Femoral head area (FHA).* Area ( $\text{cm}^2$ ) was calculated from a simple geometric construction of the superior view of the femoral head articular surface (see Kappelman, 1987, 1988).

*Lesser trochanter anteroposterior:mediolateral (AP:ML) ratio (LTR).* The anteroposterior and mediolateral dimensions at the lesser trochanter were measured with dial calipers. This AP:ML ratio describes the morphology of the proximal femur at the distal margin of the intertrochanteric fossa.

*Proximal AP:ML shaft ratio (PSR).* The anteroposterior and mediolateral dimensions of the proximal shaft at the base of the lesser trochanter were measured with dial calipers. The AP:ML ratio provides an estimate of the loading forces that operate through the proximal shaft.

*Patellar lip height ratio (PHR).* The anteroposterior heights of the medial and lateral patellar lips to the respective femoral condyles were measured perpendicular to the shaft with an osteometric board. The ratio of the medial:lateral dimension describes the relative symmetry of the distal femur.

*Patellar groove ratio (PGR).* The arc length of the medial and lateral margins of the patellar groove were measured with a flexible tape from the proximal margin of each lip to its distal end. The ratio of the medial:lateral arc length describes the symmetry of the patellar groove shape.

*Medial patellar lip height:arc length ratio (PMR).* The anteroposterior height from the medial patellar lip to the femoral condyle was measured with an osteometric board while the medial arc length was measured from the distal to proximal margins with a flexible tape. The ratio of the AP height:arc length describes the relationship between the length of the path tracked by the patella relative to the distance of the medial lip from the condyles.

*Medial patellar lip ratio (MPLR).* The distance from the medial patellar lip to the femoral condyle in the anteroposterior plane, and the distance from the center of the patellar groove to the intercondylar notch were measured perpendicular to the shaft with an osteometric board and a dial calipers, respectively. The ratio of the medial patellar lip height to the distal AP shaft diameter estimates the relative moment arm of the extensor muscles that cross the knee.

Discriminant function analysis is used to assess the reliability of these features of the femur for distinguishing among extant bovids from different habitats. The features of the femur are entered as variables and used to predict habitat membership for the extant individuals, with these results next used to classify the extinct forms according to the most likely habitat grouping. This study used the discriminant function analysis routine in the Statistical Package for the Social Sciences (SPSS 4.0 for Macintosh, SPSS Inc., 1990). SPSS calculates several probabilities that describe the likelihood that an individual case belongs to a specific habitat group. The extant bovid sample included values for each of the 188 individuals rather than

species means in order to take into consideration the individual variation that certainly also existed among the fossils.

## Results

### *Statistics, morphology, and function*

The summary statistics for each feature of the femur for every extant habitat group are given in [Table 1](#). Most of these femoral variables show either a clear increase (FHSS, LTR, PSR) or decrease (PHR, MPLR) in magnitude with increasingly closed conditions, while the remaining variables show only a general (FHA, PGR) or no discernible pattern (PMR). As was demonstrated in the earlier study based on three habitat categories only, there is support for a morphological trend across the habitat spectrum from closed to open country ([Kappelman, 1991](#)). The extremes of this trend can be expressed in functional terms as one of greater maneuverability in the hindlimb of more closed canopy taxa as marked by a more spherical femoral head shape (high FHSS score), a greater moment arm for the external rotators of the hip (high LTR), a shaft cross-sectional shape that in part reflects greater AP-directed loading forces transmitted through the femoral head to the proximal shaft (high PSR), and a lower moment for extension at the knee (low MPLR, PHR, and PGR). Open habitat taxa are marked by a more cylindrical femoral head shape (low FHSS score), a lower moment arm for the external rotators of the hip (low LTR), a shaft cross-sectional shape that in part reflects higher ML-directed loading forces transmitted through the femoral head to the proximal shaft (low PSR), and a greater moment for extension at the knee (high MPLR, PHR, and PGR).

### *Body mass*

It was suggested earlier that the relationship between body mass and habitat structure might show correlations with certain predator avoidance behaviors and perhaps diet. Various measurements of the femoral head have proven to be accurate predictors of body mass in other mammalian groups (e.g., [Jungers, 1988](#); [Ruff, 1988](#)), and its utility for bovids can be investigated by regressing FHA against body mass for the extant sample of bovids. In only very rare cases does there exist any record of the actual weight for a bovid museum specimen, probably because of the great difficulty involved in weighing such large specimens in the field. The regression instead relies on mean body masses for those extant taxa that have fairly accurately known values, and these have been averaged for males and females from the same species (see Appendix I: data from [Kingdon, 1982](#)). A least squares regression (LSR) of FHA against body mass shows that

$$\log_{10} \text{ body mass (kg)} = 0.5705 + 1.4425 \times \log_{10} \text{FHA (cm}^2\text{)}$$

and the results are plotted in [Figure 1](#). The statistics for LSR and reduced major axis (RMA) along with the traditional regression statistics are reported in [Table 2](#) (see [Smith 1993a,b](#) and [Kappelman, 1995](#)). The correlation coefficient of  $r=0.988$  and the low mean percentage prediction error (MPE) of 13.2% provide strong support for the use of FHA to estimate body mass for fossil bovids. The corrected detransformed body mass values for the fossil bovids are given in Appendix II. Body mass and FHA measurements for the extant bovids are given in Appendix I and those for the FHA measurements by habitat group are listed in [Table 1](#). These data suggest a general trend of increasing body mass from more closed to more open habitats, with the exception being that several bovid species from heavy cover (*Tragelaphus strepsiceros*,

**Table 1** Statistics of the femoral features of extant bovids by habitat group

Habitat group	<i>n</i>	X	S.D.	OR	CI
Femoral head shape score (FHSS)					
Forest	29	9.15	2.89	3.73–14.30	8.622–9.675
Heavy cover	32	7.09	3.20	– 0.06–6.51	6.533–7.642
Light cover	40	3.35	2.49	– 3.43–8.06	2.967–3.737
Open	87	– 1.41	1.90	– 7.19–2.62	– 1.605– – 1.206
Femoral head area (FHA)					
Forest	29	4.55	2.24	1.12–8.26	4.146–4.962
Heavy cover	32	13.70	6.30	6.51–29.81	12.607–14.790
Light cover	40	8.40	9.15	2.05–36.76	6.982–9.816
Open	87	10.89	4.76	3.83–26.99	10.393–11.393
Lesser trochanter AP:ML ratio (LTR)					
Forest	29	1.04	0.08	0.91–1.25	1.020–1.049
Heavy cover	32	0.94	0.07	0.74–1.10	0.928–0.953
Light cover	40	0.93	0.08	0.79–1.11	0.915–0.938
Open	87	0.88	0.06	0.74–1.03	0.878–0.890
Proximal AP:ML shaft ratio (PSR)					
Forest	29	1.08	0.09	0.94–1.30	1.061–1.093
Heavy cover	32	1.06	0.10	0.87–1.24	1.047–1.080
Light cover	40	0.99	0.07	0.79–1.13	0.975–0.998
Open	87	0.97	0.05	0.81–1.09	0.960–0.971
Patellar lip height ratio (PHR)					
Forest	29	1.07	0.02	1.04–1.11	1.065–1.072
Heavy cover	32	1.14	0.04	1.06–1.24	1.129–1.143
Light cover	40	1.15	0.06	1.06–1.33	1.136–1.155
Open	87	1.17	0.03	1.10–1.25	1.163–1.170
Patellar groove ratio (PGR)					
Forest	29	0.10	0.05	0.90–1.08	0.987–1.005
Heavy cover	32	1.06	0.06	0.91–1.23	1.049–1.069
Light cover	40	1.05	0.10	0.71–1.39	1.030–1.062
Open	87	1.14	0.09	0.92–1.35	1.126–1.146
Medial patellar lip height:arc length ratio (PMR)					
Forest	29	1.11	0.08	1.00–1.38	1.098–1.125
Heavy cover	32	1.06	0.05	0.95–1.20	1.046–1.065
Light cover	40	1.11	0.11	0.98–1.64	1.091–1.124
Open	87	1.05	0.06	0.86–1.19	1.040–1.052
Medial patellar lip ratio (MPLR)					
Forest	29	1.38	0.04	1.32–1.45	1.375–1.388
Heavy cover	32	1.47	0.07	1.34–1.65	1.455–1.479
Light cover	40	1.50	0.12	1.39–1.81	1.484–1.521
Open	87	1.54	0.05	1.39–1.64	1.533–1.544

*n*, Sample size; X, mean; S.D., standard deviation; OR, overall range; CI, 95% confidence interval.

*Tragelaphus euryceros*, *Kobus ellipsipyrmnus*) show body masses that are on average larger than those from either forest or light cover. Estimates of body mass for fossil bovids may serve to provide a rough sorting of specimens by habitat structure.

### Discriminant function analysis

#### *Extant bovids*

Two discriminant function analyses were conducted using the eight femoral variables discussed above and the entire sample of 188 extant bovid specimens. Data were not ordered, and a

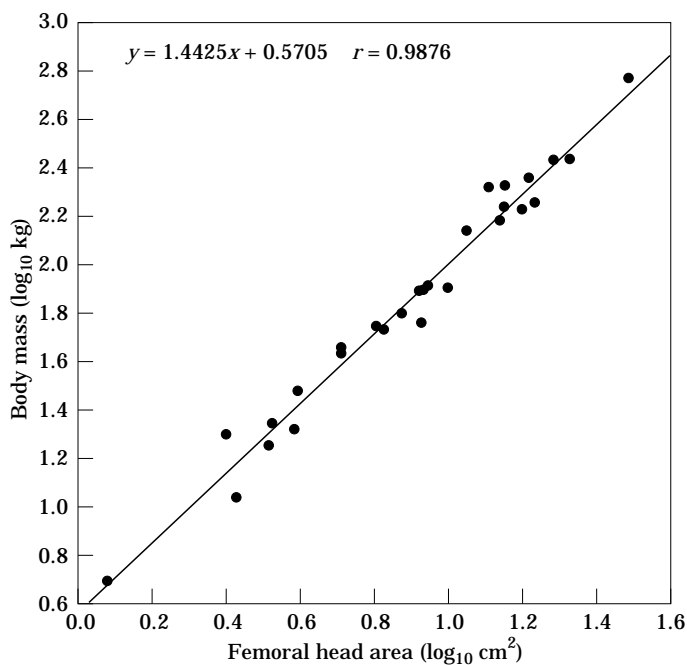


Figure 1. A plot of the regression of femoral head area ( $\log_{10}$ ,  $\text{cm}^2$ ) by body mass ( $\log_{10}$ , kg) based on the sample of extant bovids by species means (see Appendix I) shows a high correlation of  $r=0.988$  between these variables for the bovids included in this study. The equation,  $\log_{10}$  body mass (kg) =  $0.5531 + 1.4582 \times \log_{10}$  femoral head area ( $\text{cm}^2$ ), can be used to predict the body mass of fossil bovids. Regression statistics are given in Table 2.

stepwise discriminant function analysis was conducted with the MAHAL method with Statistical Package for the Social Sciences (SPSS Inc., 1990). This SPSS routine produces the largest Mahalanobis distance ( $D^2$ ) for the two closest groups. A partial F-ratio exceeding a value of 1.0 was used as the minimum criterion for the stepwise entry of a variable into the analysis. The statistical analysis reported above showed that the variances and means were positively correlated and a  $\log_{10}$  transformation was carried out to produce variances independent of the means (Sokal & Rohlf, 1981: p. 419). Box's M test was calculated to assess the equality of the group covariance matrices of the  $\log_{10}$  transformed data. A varimax rotation subroutine in SPSS (ROTATION-COEF) was used to rotate the pattern matrix in order to aid the interpretation of the results. Separate scatter plots of the discriminant functions for each individual and every habitat group are included to permit the visual inspection of the data.

The first analysis (Table 3) calculated three discriminant functions using all eight variables with an increase in the F-ratio with the addition of each new variable. The three functions accounted for 85, 11 and 4% (or 76, 15, and 9% for the varimax rotation) of the variance. A matrix of the pooled within-group correlations showed the predictor variables FHSS, LTR, and PGR to be most strongly correlated with function 1, FHA with function 2, and PHR, MPLR, PMR, and PSR with function 3 [Table 3(a)]. Box's M test calculated  $P < 0.001$  which does not exceed the value of 0.001 suggested by Tabachnick & Fidel (1983: p. 233) in order to guarantee robustness of the significance tests.



**Table 2 Regression statistics for estimating body mass by femoral head area (FHA)**

Variable	<i>n</i>	<i>r</i>	Least squares regression (LSR) Slope	Intercept	S.E.E.	F-test	SE	RE	CF	MPE	± 20% OBM	Reduced major axis regression (RMA) Slope	Intercept
FHA	28	0.988	1.4425	0.5705	0.076	$P < 0.0001$ ( $F_{1,126} = 1055$ )	1.015	1.022	1.018	13.2	75.0	1.460	0.555

Sample includes all species from Appendix I with body masses from Kingdon (1982). *n* is the sample size.

Regression statistics include slope and intercept for both the least squares regression (LSR) and reduced major axis (RMA), with  $\log_{10}$  transformations. Example:  
 $y = 1.4425x + 0.5705$ , where  $y = \log_{10}$  body mass (kg),  $x = \log_{10}$  femoral head area ( $\text{cm}^2$ ).

For LSR: *r* is the correlation coefficient; S.E.E. is the standard error of the estimate.

SE is the smearing estimate; RE is the ratio estimator; CF is the correction factor and equals  $(SE + RE)/2$ .

MPE is the mean percentage prediction error, listed as a percentage.

± 20% OBM is the percentage of predicted body masses that fall within ± 20% of observed body mass.

**Table 3 Discriminant function analysis for extant bovids using eight predictor variables**

(a) Pooled within-group correlations between functions and variables

Variable	Function 1	Function 2	Function 3
FHSS	0.85508*	0.21850	-0.16741
LTR	0.36060*	-0.28141	0.32128
PGR	-0.31271*	0.21224	0.28077
FHA	-0.20354	0.80771*	0.14771
PHR	-0.41373	0.41397	-0.56615*
MLDR	-0.39520	0.21371	-0.45330*
PMR	0.15695	-0.35049	-0.37959*
PSR	0.31461	0.20249	0.37660*
% Variance	85.18	10.61	4.21
Significance	$P < 0.001$	$P < 0.001$	$P < 0.001$

(b) Classification results (total correct=85.11%)

Actual group	<i>n</i>	<i>Predicted group membership</i>				% Correct
		Forest	Heavy cover	Light cover	Open	
Forest	29	27	1	1	0	93
Heavy cover	32	2	23	6	1	72
Light cover	40	4	2	31	3	78
Open	87	0	0	8	79	91

(c) F-test between groups (DF=8, 177)

	Forest	Heavy cover	Light cover
Heavy cover	13.4 $P < 0.001$	—	—
Light cover	18.9 $P < 0.001$	11.6 $P < 0.001$	—
Open	69.3 $P < 0.001$	42.5 $P < 0.001$	21.6 $P < 0.001$

The first analysis produced correct habitat classifications for 85% of the extant bovids. The four habitats varied from a low of 72% correct for heavy cover to a high of 93% for forest, with light cover at 78% correct and open country at 91% correct [Table 3(b)]. An F-test of the between group separations was significant for each pair of groups at  $P < 0.0001$  [Table 3(c)]. Figures 2(a) and (b) provide plots of the first two discriminant functions from the varimax rotation that account for 91% of the variance.

The second discriminant function analysis was conducted using the four features of the proximal femur only (Table 4). Limiting the variables to only those of the proximal femur makes it possible to include a larger sample of fragmentary femora from Olduvai Gorge and Koobi Fora in the later analysis that includes the fossils. A stepwise discriminant analysis using the MAHAL subroutine that included all four variables and calculated three discriminant functions that account for about 89, 10, and 1% (or 74, 15, and 11% in the varimax rotation) of the variance. A matrix of the pooled within-group correlations showed

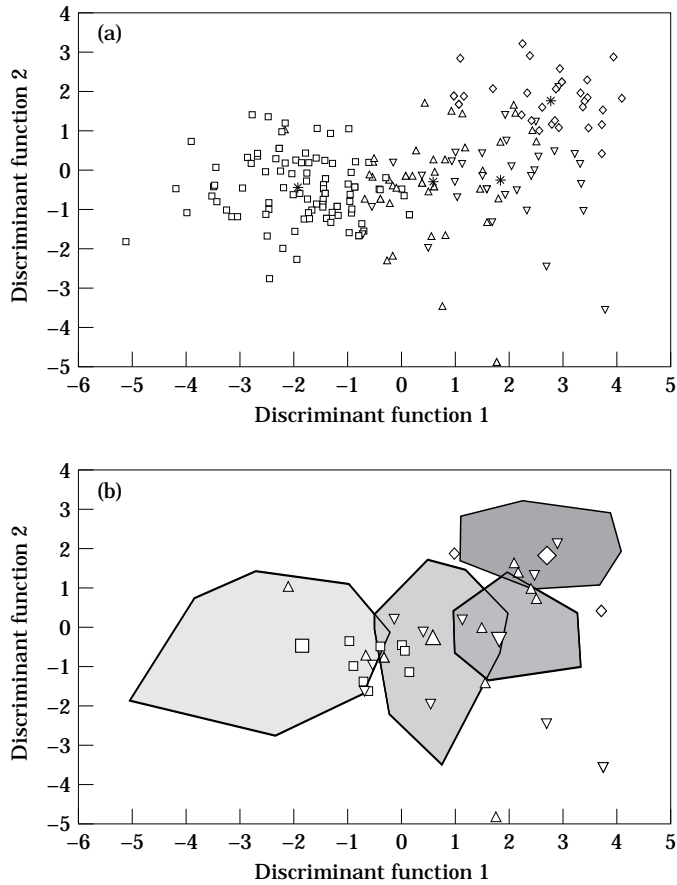


Figure 2. The results from the discriminant function analysis for the eight variables of the bovid femur correctly assigns 85% of the individuals to their original habitat (see Table 3). (a) A plot of the first two varimax rotated discriminant functions that account for 91% of the variance is shown for the entire sample of 188 individuals by their original classification and illustrates the dispersion of the data. Symbols: diamonds, forest; downward triangles, light cover; upward triangles, heavy cover; squares, open country; stars, group centroids. (b) Data and symbols as in (a) with the correctly classified bovids from each of the four habitat groups enclosed in boxes. These boxed areas are stippled along a gradient from dark to light that represents the spectrum of closed to open cover, with group centroids given as the symbols in (a). The 28 extant bovid individuals that are reclassified into a different habitat are shown as separate symbols. Most of these individuals fall close to the edge of their original habitat.

the predictor variable FHSS to be most strongly correlated with function 1, FHA with function 2, and LTR, and PSR with function 3 [Table 4(a)]. Box's M test of the covariance matrix calculated a  $P < 0.001$  which again does not meet the criterion suggested by Tabachnick & Fidel (1983: p. 233).

The restricted discriminant function analysis correctly classified 81% of the extant bovid individuals [Table 4(b)] with a high of 91% correct for open country, to a low of 68% for light cover. The separation between the group means is significant at  $P < 0.001$  [Table 4(c)]. Figure 3 provides a plot of the first and second discriminant functions from the varimax rotation that accounts for 89% of the variance.

**Table 4** Discriminant function analysis for extant bovids using four predictor variables

(a) Pooled within-group correlations between functions and variables

Variable	Function 1	Function 2	Function 3
FHSS	0.89771*	0.28978	-0.32839
LTR	0.38010	-0.23964	0.86958*
FHA	-0.22197	0.86873*	-0.13390
PSR	0.32712	0.28374	0.73184*
% Variance	88.65	10.26	1.09
Significance	$P < 0.001$	$P < 0.001$	$P < 0.05$

(b) Classification results (total correct=81.38%)

Actual group	<i>n</i>	<i>Predicted group membership</i>				Correct (%)
		Forest	Heavy cover	Light cover	Open	
Forest	29	24	4	1	0	83
Heavy cover	32	1	23	6	2	72
Light cover	40	5	4	27	4	68
Open	87	0	0	8	79	91

(c) F-test between groups (DF=4, 181)

	Forest	Heavy cover	Light cover
Heavy cover	22.1 $P < 0.001$	—	—
Light cover	27.9 $P < 0.001$	19.2 $P < 0.001$	—
Open	128.0 $P < 0.001$	74.3 $P < 0.001$	39.7 $P < 0.001$

*Reclassification of extant bovids*

The reclassification of extant individuals into other than their actual habitats included 28 individuals from 16 species for the analysis that used eight variables, and 35 individuals from 17 species for the restricted analysis that used four variables. The vast majority of the reclassifications from the full data set consisted of one or two individuals from a species (19 individuals from 13 species), with only three species (nine individuals) demonstrating the reclassification of one-half or more of the individuals from a species. The restricted analysis showed six species (21 individuals) with one-half or more of the individuals reclassified into another habitat, with the remaining 14 individuals belonging to 11 species (Table 5).

In most cases the reclassification assigned individuals to the next closest habitat, and the majority of mistaken sortings were between heavy and light cover (Table 5). Several of these species (e.g., *Kobus megaceros* and *K. ellipsiprymnus*) are represented by small sample sizes, and in the case of *K. megaceros*, the Nile lechwe, the original characterization of its riparian grassy swamp habitat as heavy cover might be in error. Only the reclassification of *Sylvicapra grimmia* from light cover to forest displayed a jump that completely spanned an intervening habitat type, but this reclassification results from the fact that this species plots near the boundary

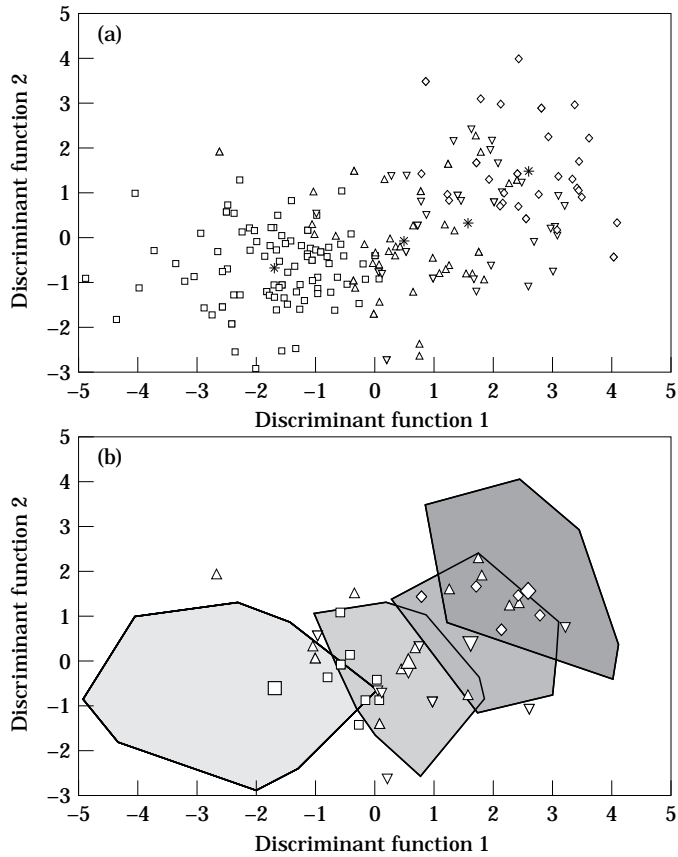


Figure 3. The results from the discriminant function analysis that uses four variables of the proximal bovid femur correctly assigns 81% of the individuals to their original habitat (see Table 4). (a) A plot of the first two varimax rotated discriminant functions that account for 89% of the variance is shown for the entire sample of 188 individuals by their original classification and illustrates the dispersion of the data. Symbols as in Figure 2(a). (b) Data and symbols as in Figure 2(b) with boxed areas depicted for the correctly classified bovids from each of the four habitat groups and stippled along a gradient from dark to light that represents the spectrum of closed to open cover. Group centroids given as the symbols in (a). The 35 extant bovid individuals that are reclassified into a different habitat are shown as separate symbols. Most of these individuals fall close to the edge of their original habitat or plot in the area of overlap.

between light cover and forest and its completely outside of the range for heavy cover. The reclassification of this species was noted in the earlier study of the femur that used a simple three habitat division (Kappelman, 1991: p. 108) as well as in a study of metapodials (Plummer & Bishop, 1994). It raises the interesting issue of the role that taxonomic affinity plays in these reclassifications. Even though *S. grimmea*, the bush duiker, is known to inhabit tall grass, it is also known to frequent bushland thickets (K. Reed, pers. comm.), and this variety of habitat use suggests that the original classification should have been heavy rather than light cover. This species is reclassified into forest habitat where all of the other cephalophines are found. Cephalophine femora are remarkably similar in overall morphology and this similarity may reflect some genetic canalization of the expression of these traits. However, *S. grimmea* demonstrates some of the most extreme “open habitat” values of any cephalophine (see

**Table 5** Habitat reclassifications of one half or greater of the individuals from a species by each of the two discriminant function analyses

Species	Number reclassified/total number*	Original habitat	Most likely reclassification†
<i>Cephalophus silvicultor</i>	4/6 [4]	Forest	Heavy cover
<i>Sylvicapra grimmia</i>	4/5 [8]	Light cover	Forest
	5/5 [4]	Light cover	Forest
<i>Kobus kob</i>	3/6 [4]	Light cover	Open country (1) Heavy cover (2)
<i>Kobus megaceros</i>	3/4 [8]	Heavy cover	Light cover
	4/4 [4]	Heavy cover	Light cover
<i>Kobus ellipsiprymnus</i>	2/2 [8]	Heavy cover	Light cover
	2/2 [4]	Heavy cover	Open country (1) Light cover (1)
<i>Syncerus caffer</i>	3/5 [4]	Light cover	Heavy cover (2) Open country (1)

\*[4] is the four variable analysis, [8] is the eight variable analysis.

†(#) is the number of individuals reclassified to that habitat.

Appendix I) which seems to underscore the selection pressures exerted by more open habitats on cursorial locomotion.

As noted above, the analysis that is limited to features of the proximal femur resulted in additional reclassifications. A second cephalophine, *Cephalophus silvicultor*, the yellow-backed duiker, is the largest of the duikers, and its reclassification from forest into heavy cover may, with the inclusion of the FHA predictor variable in the analysis, reflect the influence of its larger body size. A split reclassification is seen in *K. kob*, where two of the six specimens sorted from light to heavy cover, and the third into open country, while the other three specimens remain in the original category of light cover. The classification of *K. kob* across three types of habitats probably reflects its truly intermediate morphology. *S. caffer*, the buffalo, also demonstrates a similar split reclassification from light cover to heavy cover (two individuals) and open country (one individual) which may reflect its well-known diversity of habitat use, large body size, or some combination of the two (Sinclair, 1977).

The reclassifications of from three to six species by the two discriminant function analyses should offer some caution in interpreting the habitat assignments of fossil specimens. In most cases the assignment of a given species to either end of the habitat spectrum can be done with a high degree of confidence, whereas exact sortings into the middle range of habitats (bush, swamp, close to water, hilly areas, tall grass) are more problematic. As discussed earlier, at least part of this difficulty lies in the original categorization of the vegetatively complex environments into four simple habitat categories. There does, however, appear to be some improvement in assessing the ecological "grain" of the habitats by moving from three to four habitat subdivisions. However, the robustness of these classifications could possibly be improved by equalizing the sample sizes of the four habitat groups. The failure of Box's M test of the equality of the covariance matrices for both analyses suggests that there is potentially an over-classification of individuals into habitat groups having a greater dispersion. The habitat reclassifications of individuals falling near the boundaries that separate groups should be treated with caution, but this difficulty can in part be addressed by examining the probability at which an individual case is assigned to a particular group.

*Fossil bovids from Koobi Fora and Olduvai Gorge*

The eight and four variable analyses were repeated with the extant bovids and the sample of Plio-Pleistocene bovids listed in Appendix II. There are nine complete femora for the eight variable analysis, with two of these from Olduvai belonging to the same individual [Table 6(a)]. There are an additional 18 fragmentary femora [Table 6(b)], which when added to the nine complete femora, provide a sample of 27 proximal femora for the four variable analysis. These specimens were entered into the analysis as “habitat unknown”. The habitat classifications of each specimen and the probabilities for its assignment to that group are given in Table 6. The specimens are plotted in Figures 4(a) and (b).

The fossil bovids from Koobi Fora and Olduvai Gorge demonstrate femoral morphologies similar to those of modern bovids living in a range of open through heavy cover habitats, with only one specimen showing an assignment to forest habitat. In the case of the left and right femora from the same individual, BMNH M 22453 (SHK II, *Antidorcas recki*), the habitat classifications are identical and demonstrate very similar probabilities. In only two of the nine cases (eight individuals total) for the complete femora are the habitat classifications based on four variables in disagreement with the classifications for the same specimens based on the full set of variables. In the case of the first exception, DK I 5385 (an antelope) is assigned essentially equal probabilities for belonging to either the light cover or open country groups for the eight variable analysis, and a somewhat higher probability for light cover than open country in the four variable analysis. This specimen plots near the boundary between open country and light cover and is quite distant from the other two habitat groups. The second specimen, BK II 268 (*Pelorovis*) has a heavy cover assignment in the four variable run, and an open country assignment in the eight variable run. This specimen has the largest FHA of any of the fossil bovids and this feature causes it to plot high along function 2 with low probabilities of falling that far away from the centroids of both of these groups. Its assignment to open country has a somewhat higher probability than its assignment to heavy cover.

## Discussion

The discriminant function analyses presented here lend support to the idea that the bovids from the Plio-Pleistocene habitats of Koobi Fora and Olduvai Gorge display a set of morphologies that are similar to those found in modern bovids that inhabit the entire range of modern environments. These results suggest the presence of a variety of habitats ranging from primarily more open conditions (light cover and open country) to more closed conditions (heavy cover) with limited evidence for forest. Although the sample of bovid femora from Koobi Fora is much smaller than that from Olduvai (five *vs.* 22 specimens), the results tentatively suggest the presence of more closed conditions at Koobi Fora and more open conditions at Olduvai Gorge. The conclusion that a range of open to closed habitats existed during the Plio-Pleistocene of East Africa is in general agreement with other paleoenvironmental reconstructions of Olduvai Gorge and Koobi Fora as based upon functional interpretations of fossil bovid metapodials (Plummer & Bishop, 1994), calculations of bovid tribal frequencies (Kappelman, 1984, 1986; Shipman & Harris, 1988), and reconstructions based upon other elements of the fauna (Jaeger, 1976; Kappelman, 1984, 1986; Harris, 1983, 1991), flora (Bonnefille, 1985), geology (Hay, 1976) and geochemistry (Hay, 1976; Cerling *et al.*, 1977; Sikes, 1994) (and see Peters & Blumenshine, 1995). Unfortunately, the present sample of bovid femora from any particular locality or stratigraphic level is not large enough to attempt an assessment of habitat change through time. Earlier studies that used either the

**Table 6** Habitat classification of fossil bovid specimens

(a) Eight variable discriminant function analysis

Specimen No.	Taxon	Most likely group	$P(X/G)^*$	$P(G/X)^\dagger$	Second most likely group	$P(G/X)^\dagger$
KNM ER 1377A	Tragelaphine	Light cover	0.5204	0.6100	Forest	0.3306
BMNH M 22453 (SHK II)	<i>Antidorcas recki</i>	Light cover	0.1181	0.9865	Open	0.0077
BMNH M 22453 (SHK II)	<i>Antidorcas recki</i>	Light cover	0.0978	0.9838	Open	0.0121
FLK W 95	Alcelaphini	Open	0.9204	0.9814	Light cover	0.0186
DK I 5385	Antilopini	Open	0.6258	0.4996	Light cover	0.4917
BK II 067/5364	Alcelaphini	Open	0.5488	0.9935	Light cover	0.0063
FLK N II 067/4885	<i>Antidorcas recki</i>	Open	0.5144	0.7025	Light cover	0.2959
BK II 268	<i>Pelorovis</i>	Open	0.1971	0.8862	Light cover	0.0677
DK I 3330	Antilopini	Open	0.1793	0.9624	Light cover	0.0370

\* $P(X/G)$  is the probability of an individual being that far from the group centroid.† $P(G/X)$  is the probability of an individual belonging to the assigned group.



**Table 6 (continued)**  
 (b) Four variable discriminant function analysis

Specimen No.	Taxon	Most likely group	P(X/G)*	P(G/X)†	Second most likely group	P(G/X)†
MINK II 101	<i>Kobus cf. K. kob</i>	Forest	0.7220	0.6126	Heavy cover	0.3117
BK II 802	Tragelaphini	Heavy cover	0.9125	0.8682	Light cover	0.0819
BMNH 16 BR 1	"Bovini"	Heavy cover	0.8280	0.7086	Forest	0.2405
KNM ER 2277A	<i>Kobus</i> sp.	Heavy cover	0.4027	0.4743	Light cover	0.4484
KNM ER 1317	Bovidae	Heavy cover	0.3302	0.6534	Open	0.1924
BMNH 16 CR 13	Bovidae	Heavy cover	0.2205	0.6988	Light cover	0.1765
BK II 268	<i>Pelonomis</i>	Heavy cover	0.0675	0.7846	Open	0.1599
KNM ER 1377A	Tragelaphine	Light cover	0.8126	0.7127	Forest	0.2063
BMNH M 22453 (SHK II)	<i>Antidorcas recki</i>	Light cover	0.3442	0.6230	Forest	0.3607
DK1 5385	Antilopini	Light cover	0.2996	0.6182	Open	0.3338
BMNH M 22348 16 CR 9	"Antilopini"	Light cover	0.2549	0.8097	Forest	0.1565
BMNH M 22316	Antilopini	Light cover	0.2226	0.5845	Forest	0.4054
BMNH M 22453 (SHK II)	<i>Antidorcas recki</i>	Light cover	0.2009	0.5555	Forest	0.4324
BMNH M 47695	<i>Gazella capricornis</i>	Light cover	0.0251	0.9399	Forest	0.0566
FLKW 95	Alcelaphini	Open	0.9735	0.9346	Light cover	0.0630
DK I 3051	Hippotragini	Open	0.8730	0.9623	Light cover	0.0834
FLK NII 067/4885	<i>Antidorcas recki</i>	Open	0.8331	0.7451	Light cover	0.2498
FLKNI 800	Hippotragini	Open	0.6510	0.9951	Light cover	0.0046
KNM ER 5551G	? <i>Kobus sigmoidalis</i>	Open	0.6253	0.9975	Light cover	0.0025
BMNH 16 CL 10	Alcelaphini	Open	0.5341	0.9948	Light cover	0.0050
BKII 067/5364	Alcelaphini	Open	0.4555	0.9848	Light cover	0.0114
FLK NI 1027	<i>Antidorcas recki</i>	Open	0.3551	0.9992	Light cover	0.0008
KNM ER 1615E	Bovidae	Open	0.2569	0.6459	Light cover	0.3535
DK1 3330	Antilopini	Open	0.1905	0.9053	Light cover	0.0945
BKII 7	Alcelaphini	Open	0.0530	0.9999	Light cover	0.0001
BMNH VI 1586 16 DL 9	Bovidae	Open	0.0463	0.9999	Light cover	0.0001
BK II 308	Alcelaphini	Open	0.0005	1.0000	Light cover	0.0000

\*P(X/G) is the probability of an individual being that far from the group centroid.

†P(G/X) is the probability of an individual belonging to the assigned group.

KNM ER specimens are from East Lake Turkana and housed in the Kenya National Museum. BMNH specimens are from Olduvai Gorge and housed in the British Museum (Natural History). All other specimens are from Olduvai Gorge and housed in the Kenya National Museum.

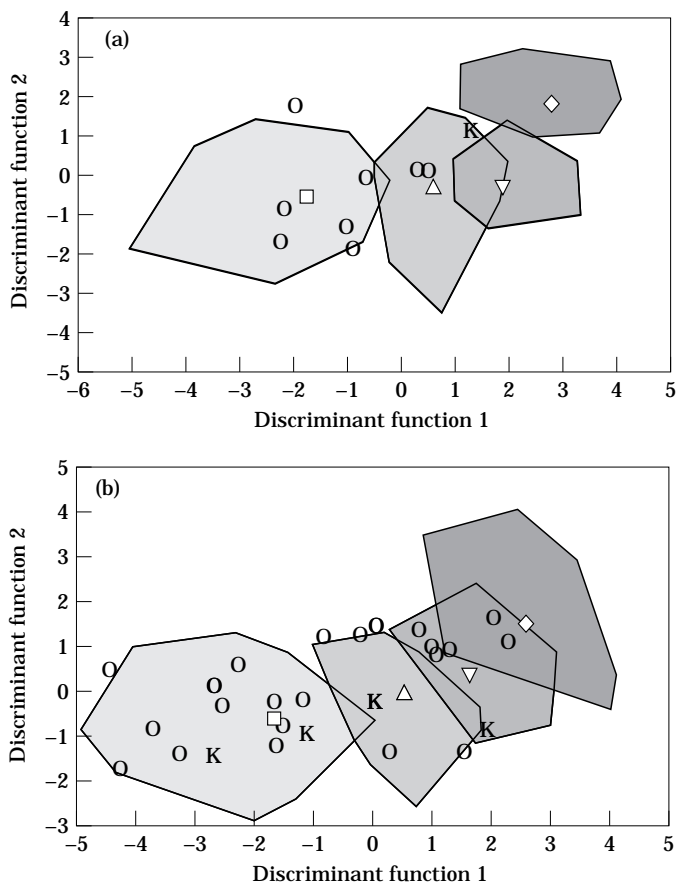


Figure 4. The classification results for the discriminant function analyses that include fossil bovids from Koobi Fora and Olduvai. (a) Extant bovids plotted as in Figure 2(b) (eight predictor variables) with the fossil bovids shown as letters. The single complete bovid specimen from Koobi Fora (K) is assigned to either light cover ( $P=0.61$ ) or forest ( $P=0.33$ ). The bovids from Olduvai Gorge (O) plot within or near the open country and light cover groups. The two specimens near the centroid for light cover are left and right femora from the same individual of *Antidorcas recki*. The *Pelorovis* specimen plots above and outside the range of open habitat. (b) Data plotted as in Figure 3(b) (four predictor variables) with the fossil bovids shown as letters. The bovid specimens from Koobi Fora (K) are scattered within the center of the plot and suggest the presence of a gradient from heavy cover to open country. The bovids from Olduvai Gorge (O) suggest the full range of modern habitats, with the densest concentration of bovids found along the open country to light cover gradient.

femur (Kappelman, 1988, 1991) or metapodials (Plummer & Bishop, 1994) and relied on a simple threefold habitat division demonstrated generally clear separations between specimens from the extremes of open and closed habitat, with intermediate habitat animals showing the largest number of reclassifications. The present study attempted to address some of the variation within the intermediate category by sorting extant bovids into two subhabitats, light and heavy cover, and taking into consideration some of the particular habitat-specific traits of each species for its habitat assignment. The four general habitat categories (open, light cover, heavy cover, and forest) reflect a gradient of increasing vegetative cover and ground level obstacles. If future studies could actually quantify habitat complexity and percent cover for

each of the various extant species, the somewhat subjective nature of the present assignments could be tested.

A difference in collection methods at Koobi Fora and Olduvai is probably largely responsible for the difference in the number of femora known from these two sites. For example, specimens from Olduvai were largely collected during archaeological excavations while specimens from Koobi Fora were largely surface collected, and the bias at the latter site was in favor of cranial over postcranial specimens. Future work at especially Koobi Fora should pay particular attention to collecting all identifiable material. As in the previous study of Miocene bovid femora (Kappelman, 1991), this study provides support for the utility of the femur in sorting among extant bovids that inhabit the full range of modern environments. The femur is a useful skeletal element for such studies because the functional aspects of its morphology appear to be clearly correlated with different styles of locomotion (Kappelman, 1988).

Other interesting differences in the bovid samples remain. The sample of bovid femora from Olduvai is small relative to, for example, the sample of metapodials (see Plummer & Bishop, 1994). It seems likely that the small sample size of femora reflects a taphonomic bias present at the time of site formation and perhaps points to differences in the pattern of carcass disarticulation, transport, and/or processing (see Hill, 1975, 1984). Prey size and availability are commonly thought to be the factors that most strongly influence the predation patterns of large carnivores (see Vrba, 1980). Kappelman (1984) investigated percent representation of bovids with different body masses through the section at Olduvai and concluded that the most commonly represented bovids were of size class C (100–300 kg) and size class A (<25 kg), with a variable representation of classes B (25–100 kg) and D (<300 kg). Extant bovids of size classes A and C live in a variety of habitats and it does not seem likely that a size-related accumulator bias was responsible for the pattern of habitat difference and change through time at Olduvai as reported by Kappelman (1984). Body mass estimates calculated by LSR for the sample of bovid femora from Olduvai suggest a fairly even representation of the four size classes (see Appendix II) and the absence of any clear size-related predator bias. It is likely that there are other taphonomic biases present in each of the two sites, with perhaps either stream channel or lake margin habitats being originally more common, differentially preserved, or selectively sampled (see Behrensmeyer, 1975; White, 1988; Peters & Blumenshine, 1995).

This study demonstrates a strong correlation between the area of the femoral head (FHA) and body mass in living bovids which in turn can be used to predict body mass in fossil bovids. As discussed earlier, there is a general relationship between body mass and habitat in that the largest bovids are most commonly found in open country while the smallest bovids are known to inhabit closed environments. The general interplay between predator avoidance strategies, food quality, habitat structure, and body mass suggests that this relationship probably held in the past as well, but this idea is testable by combining the approach of ecological functional morphology outlined here along with other independent indicators of habitat structure. The inclusion of femoral head area as a predictor of body mass demonstrated an increase in the power of the discriminant function analyses. It is interesting to note that some of the smallest bovids from forest and light cover habitats have discriminant function scores that are very similar to one another, with many individuals plotting right at the edge of the distribution between these two groups. This observation appears to support the idea that a truly meaningful characterization of habitat must be examined from the perspective of each individual species. For example, a lightly wooded area may present many more ground-level obstacles to a small bovid than a large bovid, and such obstacles could limit cursorial

locomotion in the small species. In addition, small bovids are probably able to rely upon crypsis and stealth in a lightly wooded setting while a large bovid would not be able to blend in with such limited cover. A truly-quantified characterization of habitat complexity should somehow be measured from the perspective of a given body mass in order to accurately assess the “grain” of the individual species’ niche. Future work should attempt to address this issue.

The analysis that includes only features from the proximal femur is slightly less successful in correctly classifying extant bovids to their correct habitat, and this result suggests that the classifications from the full analysis should be given somewhat greater weight in assessing the habitat assignments of the fossil bovids. For example, in the case of the complete right and left femora from the single individual of *A. recki* (BMNH 22453), the partial analysis calculates similar probabilities for assignments to either light cover (0.58) or forest (0.40) while the full analysis calculates a much greater probability (>0.98) for an assignment to light cover. Similar results are seen in the other complete and partial femora for the two additional *A. recki* specimens and the other antilopines (see Table 6). These results suggest that *A. recki* probably inhabited the lightly covered to more open parts of the environment at Olduvai Gorge. The analysis of the metapodials by Plummer & Bishop (1994) used a three rather than four part division of habitat. Their results for complete metapodials of *A. recki* demonstrated a mixed sorting between open and intermediate habitats with intriguing differences between the fore- and hindlimb [metacarpals ( $n=16$ ): four open, 12 intermediate, none closed; metatarsals ( $n=10$ ): seven open, two intermediate, one closed] and they assigned this species to “intermediate” habitat. When these results are taken in combination with the results reported here, it appears that *A. recki* lived in the more open part of the “intermediate” habitat reported by Plummer & Bishop (1994), probably in conditions that bordered on open rather than closed country. Body mass may play a role in the way that *A. recki* and many of the other small bovids plot close to the edge of the light cover habitat group and near the boundary with forest [see Figures 4(a) and (b)]. As discussed above, the locomotor and predator avoidance strategies of the small bovids like *A. recki* (19–31 kg, see Appendix II) in even a light cover habitat might have been more similar to those of larger bovids from more closed habitats. These results again underscore the importance of better assessing the exact habitat attributes of living taxa with regard to their body mass.

This study demonstrates that quantitative assessments of functional morphology can offer important insights into the interplay between an organism and its environment and provide an additional tool for paleoenvironmental reconstruction. When samples are large enough, this approach can be used to assess how this interplay may have changed through time. Unfortunately, many efforts in fossil collecting continue to ignore postcranial elements largely because of the difficulty in establishing attributions for these specimens at the species level. The results of this and other studies demonstrate the great utility of a functional approach for paleoenvironmental reconstruction and provide strong support for the position that all fossils identifiable to element should be collected. Although ecological functional morphology is often said to be “taxon free”, its only taxon free aspect lies in the fact fossils not identified to taxon can be included in the study. It is important to note that ecological functional morphology depends upon a solid database that integrates the behaviors, ecology, and morphology of well-characterized living taxa, and such data are anything but “taxon free”. Many aspects of the morphology of the femur (as well as many other aspects of the cranium, dentition, and skeleton) are correlated at the level of the genus or tribe, and these features together may represent some of the basic adaptations that underlie the expansion or radiation of certain groups within or across their specific habitats (Kappelman, 1991). The critical question of

whether the morphological features that appear to have strong ecological correlates are in fact adaptations with a clear functional role, or are traits shared with other closely related forms without a clear functional role, is one that can only be tested from the perspective of the modern world. The approach of ecological functional morphology for reconstructing paleoenvironments is preferred over the alternative method that depends on a strictly taxonomically-based sorting of close relatives by habitat and extends these correlations to the fossil record (e.g., Vrba, 1980; Kappelman, 1984; Shipman & Harris, 1988). The former methodology permits one to formulate and test hypotheses as based on correlations in living taxa, and extend these predictions to the fossil record. However, it is critical to note the convergence of these two approaches: as ancient taxa and faunas become increasingly modernized through time, the two approaches should merge. For example, the paleohabitat reconstructions for Olduvai reported here along with those of Plummer & Bishop (1994) that are based on ecological functional morphology are in close agreement with those from an earlier study by Kappelman (1984) that was based on correlations between habitat and bovid tribal affinity.

In many ways bovids offer one of the best elements of the fauna for reconstructing the paleohabitats of fossil hominids. Unlike small mammals that also have small day and home ranges, and whose remains may be concentrated by unknown carnivores, or isotopic sampling that may necessarily be quite restricted in lateral extent (e.g., Sikes, 1994), bovids generally have large day and home ranges. Although taphonomic or collector biases may select against the incorporation of the very smallest bovids into the fossil record (Hill, 1975, 1984; Behrensmeyer *et al.*, 1979) or the museum collection, bovid remains should "sample" the full range of habitats that existed within many square kilometres of the area around the fossil locality rather than a much more tightly focused microhabitat. All of these different approaches to habitat reconstruction should be combined to offer tests of alternative methodologies. The reconstruction for Olduvai Gorge suggests that the area in the immediate vicinity of the paleolake was more heavily vegetated, but that more open country conditions existed in the immediate area surrounding the lake (Hay, 1976; Jaeger, 1976; Cerling *et al.*, 1977; Bonnefille, 1985; Kappelman, 1984, 1986; Shipman & Harris, 1988; Plummer & Bishop, 1994; Sikes, 1994; Peters & Blumenschine, 1995). Plio-Pleistocene hominids had moderately large body masses (McHenry, 1994; Kappelman, 1995) and, with inferred large day and home ranges, probably moved through all of these habitats (see Oliver *et al.*, 1994 and articles within).

## Conclusion

An earlier study of the bovid femur demonstrated strong correlations between morphology and function that are linked to locomotor patterns and appear to be dictated by habitat complexity and methods of predator avoidance (Kappelman, 1988, 1991). The present study expands these observations to include a more detailed breakdown of the category of intermediate habitats into light and heavy cover, and provide some consideration of the role that body mass plays in the overall adaptive response to habitat structure. A discriminant function analysis that uses eight predictor variables from the femur demonstrates an 85% correct classification of extant bovids to their known habitats with misclassifications of half or more of the individuals from three out of 38 species. A second analysis that includes only features of the proximal femur was 81% successful with misclassifications of six out of 38 species.

The discriminant function analyses were repeated to include Plio-Pleistocene fossil bovids from Koobi Fora and Olduvai Gorge. The results from the two analyses that included all eight predictor variables for the complete femur and a restricted set of four variables from the proximal femur are in very close agreement and suggest that both localities had varying combinations of the full range of environments inhabited by modern bovids with perhaps somewhat more closed conditions at Koobi Fora, and more open conditions at Olduvai Gorge. The smallest bovids attributed to the Antilopini are assigned by both the full and restricted analyses to either open country or light cover but not heavy cover or forest. These results provide broad support for other reconstructions of the paleohabitats at both Olduvai Gorge and Koobi Fora as based on the bovid faunas (Kappelman, 1984, 1986; Shipman & Harris, 1988; Harris, 1991; Plummer & Bishop, 1994) and reconstructions based upon many other paleoenvironmental indicators (Hay, 1976; Jaeger, 1976; Cerling *et al.*, 1977; Harris, 1983; Bonnefille, 1985; Sikes, 1994; Peters & Blumenschine, 1995).

We now have the tools at our disposal for producing detailed reconstructions of the paleoenvironments where hominids lived and evolved. Methods anchored in the testable foundation offered by functional morphology provide a release from more conventional and largely untestable purely taxon-based approaches. Although it is now possible to produce detailed reconstructions of ancient environments, the challenge that remains is to how to decide where within these complex settings the early hominids were living and what, exactly, they were doing in order to ensure their survival and success.

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## Appendix I

## Bovid species by habitat and femoral characters

SUBFAMILY		Species	(n)	Habitat group	Body mass (kg)	FHSS (S.D.)	FHA (S.D.)	LTR (S.D.)	PSR (S.D.)	PHR (S.D.)	PGR (S.D.)	PMR (S.D.)	MPLR (S.D.)
Tribe	Genus												
BOVINAE													
Tragelaphini													
<i>Tragelaphus</i>													
		<i>scriptus</i>	12	F	43	10.62 (2.76)	5.114 (1.037)	1.006 (0.063)	1.062 (0.086)	1.071 (0.022)	0.995 (0.053)	1.091 (0.054)	1.391 (0.037)
		<i>imberbis</i>	5	HC	82	7.45 (1.12)	8.592 (0.954)	1.001 (0.033)	1.180 (0.066)	1.129 (0.013)	1.180 (0.039)	1.037 (0.044)	1.426 (0.034)
		<i>strepsiceros</i>	5	HC	214	7.29 (2.61)	14.124 (4.492)	0.869 (0.011)	0.987 (0.048)	1.163 (0.047)	1.060 (0.039)	1.043 (0.046)	1.510 (0.026)
		<i>spokei</i>	5	HC	78	9.28 (2.08)	8.199 (1.678)	0.958 (0.058)	1.102 (0.073)	1.085 (0.025)	1.007 (0.058)	1.089 (0.071)	1.429 (0.077)
		<i>eunyceros</i>	9	HC	270	8.47 (3.39)	21.067 (3.799)	0.986 (0.052)	1.095 (0.059)	1.128 (0.020)	1.048 (0.047)	1.047 (0.056)	1.432 (0.044)
Bovini													
<i>Syncerus</i>													
		<i>caffer</i>	5	LC	580	4.78 (1.43)	30.623 (6.121)	0.883 (0.060)	0.889 (0.073)	1.287 (0.028)	1.133 (0.254)	1.226 (0.235)	1.793 (0.014)
CEPHALOPHINI													
Cephalophini													
<i>Cephalophus</i>													
		<i>callipygus</i>	2	F	18	11.42 (0.10)	3.227 (0.864)	1.043 (0.011)	1.040 (0.040)	1.077 (0.006)	1.041 (0.057)	1.240 (0.197)	1.375 (0.019)
		<i>caenulus</i>	2	F	—	7.28 (5.02)	1.262 (0.000)	1.052 (0.133)	1.233 (0.089)	1.063 (0.029)	1.023 (0.032)	1.065 (0.092)	1.405 (0.034)
		<i>dorsalis</i>	1	F	22	11.73	3.297	1.160	1.115	1.053	1.000	1.026	1.333
		<i>niger</i>	2	F	—	8.16 (1.26)	4.484 (1.133)	1.203 (0.066)	1.178 (0.010)	1.070 (0.042)	0.985 (0.049)	1.099 (0.083)	1.351 (0.029)
		<i>silvicultor</i>	6	F	63	8.37 (1.11)	7.448 (0.424)	1.029 (0.071)	1.095 (0.035)	1.069 (0.007)	1.002 (0.040)	1.111 (0.027)	1.372 (0.033)
		<i>grimmia</i>	5	LC	20	6.55 (1.35)	2.493 (0.500)	1.047 (0.038)	1.071 (0.029)	1.096 (0.020)	0.993 (0.044)	1.160 (0.057)	1.418 (0.022)

## Appendix I (Continued)

## Bovoid species by habitat and femoral characters

SUBFAMILY		Species	(n)	Habitat group	Body mass (kg)	FHSS (S.D.)	FHA (S.D.)	LTR (S.D.)	PSR (S.D.)	PHR (S.D.)	PGR (S.D.)	PMR (S.D.)	MPLR (S.D.)
Tribe	Genus												
HIPPOTRAGINAE													
Reduncini													
<i>Kobus</i>													
		<i>kob</i>	6	LC	79	2.38 (1.48)	8.4.19 (1.000)	0.924 (0.060)	1.014 (0.067)	1.161 (0.019)	1.089 (0.060)	1.038 (0.045)	1.531 (0.019)
		<i>megaceros</i>	4	HC	—	4.92 (2.87)	8.0.20 (0.833)	0.887 (0.043)	0.964 (0.068)	1.164 (0.057)	1.023 (0.033)	1.081 (0.066)	1.515 (0.099)
		<i>ellipsopygmus</i>	2	HC	210	1.39 (2.04)	12.698 (7.816)	0.922 (0.057)	0.981 (0.057)	1.161 (0.030)	1.092 (0.033)	1.029 (0.027)	1.536 (0.014)
		<i>defassa</i>	2	HC	—	4.01 (1.51)	18.354 (3.369)	0.843 (0.142)	1.003 (0.103)	1.173 (0.019)	1.150 (0.110)	1.060 (0.011)	1.548 (0.004)
		<i>arundinum</i>	6	LC	58	2.99 (1.81)	8.393 (3.798)	0.856 (0.044)	0.951 (0.057)	1.137 (0.032)	1.055 (0.079)	1.073 (0.036)	1.480 (0.026)
		<i>fulvovirgata</i>	5	LC	30	2.91 (2.49)	3.832 (0.241)	0.912 (0.018)	0.963 (0.050)	1.109 (0.020)	0.995 (0.032)	1.086 (0.043)	1.420 (0.016)
		<i>redunca</i>	6	LC	45	3.21 (2.40)	5.117 (0.367)	0.908 (0.050)	1.013 (0.054)	1.131 (0.012)	1.030 (0.026)	1.046 (0.039)	1.428 (0.021)
Hippotragini													
<i>Hippotragus</i>													
		<i>equinus</i>	3	OC	270	— 1.13 (1.36)	18.996 (7.571)	0.892 (0.026)	1.025 (0.031)	1.164 (0.037)	1.186 (0.008)	0.998 (0.031)	1.519 (0.063)
		<i>niger</i>	5	OC	228	0.24 (2.14)	16.439 (1.155)	0.858 (0.023)	0.932 (0.032)	1.160 (0.015)	1.168 (0.043)	1.013 (0.046)	1.521 (0.045)
		<i>gazella</i>	6	OC	169	— 2.18 (1.51)	15.651 (2.039)	0.892 (0.036)	0.982 (0.031)	1.190 (0.027)	1.180 (0.051)	0.962 (0.065)	1.561 (0.045)
		<i>tao</i>	3	OC	—	— 2.35 (2.94)	11.091 (1.413)	0.872 (0.036)	0.945 (0.060)	1.186 (0.018)	1.160 (0.017)	1.028 (0.014)	1.610 (0.022)
		<i>nasomaculatus</i>	3	OC	—	— 1.92 (0.43)	9.519 (0.780)	0.903 (0.103)	0.8688 (0.056)	1.188 (0.013)	1.129 (0.024)	1.000 (0.026)	1.579 (0.029)

## Appendix I (Continued)

SUBFAMILY		Species	(n)	Habitat group	Body mass (kg)	FHSS (S.D.)	FHA (S.D.)	LTR (S.D.)	PSR (S.D.)	PHR (S.D.)	PGR (S.D.)	PMR (S.D.)	MPLR (S.D.)
Tribe	Genus												
Alcelaphini													
<i>Damaliscus</i>		<i>lanatus</i>	5	OC	136	-0.33 (1.21)	11.289 (0.637)	0.865 (0.035)	1.010 (0.036)	1.172 (0.025)	1.170 (0.032)	1.046 (0.037)	1.567 (0.036)
		<i>dorcus</i>	6	OC	—	0.37 (0.82)	6.749 (0.992)	0.849 (0.014)	0.967 (0.024)	1.148 (0.029)	1.147 (0.025)	1.075 (0.021)	1.530 (0.031)
		<i>hunteri</i>	2	OC	80	-0.18 (0.50)	9.770 (0.751)	0.908 (0.002)	0.992 (0.033)	1.138 (0.026)	1.165 (0.054)	1.049 (0.010)	1.517 (0.058)
<i>Alcelaphus</i>		<i>baselaphus</i>	12	OC	155	-1.63 (1.61)	13.606 (1.351)	0.877 (0.046)	0.992 (0.038)	1.152 (0.029)	1.146 (0.044)	1.048 (0.035)	1.537 (0.040)
		<i>lichensteini</i>	3	OC	171	0.22 (1.94)	13.924 (1.618)	0.851 (0.086)	0.989 (0.059)	1.165 (0.018)	1.153 (0.039)	1.074 (0.042)	1.566 (0.018)
<i>Connochaetes</i>		<i>gnou</i>	2	OC	—	-1.38 (0.57)	12.173 (1.817)	0.841 (0.008)	0.937 (0.018)	1.236 (0.021)	1.336 (0.011)	1.000 (0.000)	1.611 (0.014)
		<i>taurinus</i>	8	OC	180	-2.23 (2.12)	16.908 (1.117)	0.797 (0.033)	0.927 (0.038)	1.202 (0.026)	1.280 (0.083)	0.997 (0.021)	1.597 (0.035)
ANTILOPINAE													
Neotragini													
<i>Ourebia</i>		<i>montana</i>	3	LC	—	2.53 (2.11)	3.035 (0.280)	0.942 (0.074)	0.985 (0.082)	1.115 (0.029)	1.019 (0.016)	1.167 (0.030)	1.472 (0.010)
<i>Raphicerus</i>		<i>campstris</i>	4	LC	11	0.97 (3.74)	2.640 (0.751)	0.975 (0.081)	1.010 (0.056)	1.112 (0.017)	1.030 (0.042)	1.125 (0.051)	1.471 (0.017)
<i>Madoqua</i>		<i>guntheri</i>	4	F	5	5.54 (1.81)	1.191 (0.085)	1.000 (0.015)	0.979 (0.035)	1.064 (0.025)	0.958 (0.063)	1.164 (0.036)	1.383 (0.037)
Antilopini													
<i>Aepyceros</i>		<i>melampus</i>	10	OC	53	-1.25 (2.09)	6.653 (0.599)	0.945 (0.052)	0.992 (0.037)	1.152 (0.019)	1.037 (0.060)	1.052 (0.037)	1.501 (0.045)
<i>Gazella</i>		<i>thomsoni</i>	1	OC	21	-3.19	3.833	0.979	0.971	1.146	1.075	1.093	1.469
		<i>granti</i>	11	OC	55	-2.43 (1.92)	6.313 (0.514)	0.891 (0.032)	0.931 (0.039)	1.151 (0.021)	1.012 (0.043)	1.108 (0.048)	1.493 (0.049)
<i>Antidorcas</i>		<i>marusipialis</i>	7	OC	—	-1.78 (2.14)	4.547 (0.457)	0.954 (0.051)	0.973 (0.041)	1.168 (0.026)	1.103 (0.048)	1.109 (0.028)	1.520 (0.018)

Habitat groups: H, forest; HC, heavy cover; LC, light cover; OC, open country. Body mass from Kingdon (1982).

**Appendix II**  
**Measurement of femoral characters of fossil bovids from East Lake Turkana and Olduvai**

Specimen No.	Taxon	Estimated body mass (kg)	FHSS	FHA	LTR	PSR	PHR	PGR	PMR	MPLR
KNM ER 1377A	Tragelaphine	85	4.62	8.67	1.023	0.899	1.136	1.028	1.027	1.572
KNM ER 1317	Bovidae	386	2.90	24.54	0.914	1.011	—	—	—	—
KNM ER 1615E	Bovidae	26	- 1.26	3.81	0.879	0.910	—	—	—	—
KNM ER 5551G	? <i>Kobus signoidalis</i>	113	- 3.49	10.58	0.823	0.970	—	—	—	—
KNM ER 2277A	<i>Kobus</i> sp.	121	7.44	11.07	0.879	0.933	1.130	—	0.975	1.477
BMNH 16 BR 1	"Bovini"	194	8.75	15.31	1.018	1.018	—	—	—	—
BMNH 16 GL 10	Aleclaphini	138	- 3.21	12.09	0.928	1.022	—	—	—	—
BMNH 16 CR 13	Bovidae	408	2.61	25.45	1.041	1.013	—	—	—	—
BMNH VI 1586 16 DL 9	Bovidae	145	- 6.06	12.51	0.815	0.916	—	—	—	—
BMNH M 22453 (SHK II)	<i>Antidorcas recki</i> (right)	18	3.60	3.04	1.062	0.960	1.206	1.152	1.126	1.659
BMNH M 22453 (SHK II)	<i>Antidorcas recki</i> (left)	18	4.15	3.03	1.016	0.960	1.211	1.218	1.103	1.686
BMNH M 22348 16 CR 9	"Antilopini"	39	2.07	5.12	1.092	0.930	—	—	—	—
BMNH M 22316	Antilopini	20	4.11	3.27	1.041	0.927	—	—	—	—
BMNH M 47695	<i>Gazella capricornis</i>	15	4.93	2.59	0.874	0.833	—	—	—	—
FLK NN I 800	Hippotragini	195	- 2.91	15.36	0.903	0.989	—	—	—	—
DK I 3051	Hippotragini	205	- 0.94	15.91	0.866	0.967	1.205	1.356	0.998	—
BK II 067/5364	Aleclaphini	344	- 1.06	22.64	0.837	0.978	1.219	1.203	1.099	1.646
BK II 308	Aleclaphini	89	- 5.91	8.97	0.861	1.344	—	—	—	—
FLK W 95	Aleclaphini	76	- 1.54	8.04	0.905	1.003	1.206	1.218	1.108	1.569
BK II 7	Aleclaphini	416	- 4.73	25.81	0.859	0.996	—	—	—	—
DK I 3330	Antilopini	28	- 3.06	4.04	0.990	0.964	1.088	1.000	1.176	1.265
DK I 5385	Antilopini	28	0.09	4.01	1.003	1.089	1.163	1.105	1.124	1.437
FLK N II 067/4885	<i>Antidorcas recki</i>	26	- 0.93	3.81	0.886	1.053	1.165	1.071	1.113	1.487
FLK N I 1027	<i>Antidorcas recki</i>	30	- 4.82	4.25	0.783	1.082	—	—	—	—
BK II 802	Tragelaphini	285	6.28	19.90	1.009	1.017	1.117	—	—	1.460
BK II 268	<i>Pelorovis</i>	732	3.66	38.02	0.825	1.000	1.257	1.380	1.063	1.714
MNK II 101	<i>Kobus</i> cf. <i>K. kob</i>	91	7.72	9.10	1.061	1.040	1.135	—	—	1.513

KNM ER specimens are from East Lake Turkana and housed in the Kenya National Museum. BMNH specimens are from Olduvai Gorge and housed in the British Museum (Natural History). All other specimens are from Olduvai Gorge and housed in the Kenya National Museum. Estimated body mass is the detransformed predicted body mass times the correction factor calculated from the LSR equation in Table 1.