

Morphology and Locomotor Adaptations of the Bovid Femur in Relation to Habitat

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ABSTRACT Extant bovids inhabit a wide diversity of environments that range from forest to savanna and display locomotor patterns that are habitat specific. I report here on an investigation of the linkage between these locomotor patterns and habitat based on a study of the morphology of the bovid femur. Femoral head shape, shaft dimensions, and knee structure are examined and support a statistically significant separation of the different morphological complexes present in bovids from forest, broken cover, and savanna habitats. Morphological differences are primarily related to locomotor patterns as reflected in the degree of cursoriality displayed by bovids in different habitats. Cursorial bovids from savanna environments have laterally expanded femoral heads that act to limit the degree of abduction and axial rotation at the hip, and elliptically shaped distal femora that increase the moment arm of the extensor muscles that cross the knee. Forest bovids have spherically shaped femoral heads. This morphology permits a much higher degree of abduction and axial rotation at the hip and appears to provide greater maneuverability in a vegetationally complex habitat. Bovid living in broken cover environments that fall between the extremes of closed canopy forest and savanna display an intermediate set of femoral characters. This approach to the relationship between habitat and locomotion offers a potentially powerful means with which to examine the interplay between structural form and function in bovid evolution.

Studies of the relationship between morphological structure and function provide important insights about the interactions between living species and their environment. One area of functional morphology that has been especially successful in delimiting such relationships is the study of locomotor systems. Cursorial mammals all display various adaptations to rapid locomotion in terrestrial settings. Extant species of the family Bovidae (Mammalia, Artiodactyla) provide an excellent natural group of cursorial mammals with which to examine finer-scale relationships between morphology and function within a limited locomotor category and across a variety of habitats ranging from the extremes of tropical forest to desert.

I report here the results of an investigation of the structure of the femur as an approach to the study of bovid locomotion. This investigation pays special attention to the way that substrates differ across the habitat spec-

trum from forest to savanna and how these habitat differences are related to different patterns of locomotion. Femoral morphology is shown to be related to the degree of cursoriality displayed by bovids from across the habitat spectrum.

MATERIALS AND METHODS

A series of measurements of the bovid femur was designed to investigate the relationship between functional morphology and habitat. The femur was selected for several reasons. First, the highest degree of potential rotation in the hindlimb is found at the hip joint. Any differences in abduction and axial rotation existing between bovids from different habitats will be obvious in the hip. Second, the knee joint is the site over which the

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TABLE 1. Bovid species by habitat, predator avoidance strategy, and femoral characters¹

Subfamily Tribe Genus	Species	Habitat—predator avoidance strategy (subhabitat)	(N)	FHSS (SD)	PSR (SD)	PGR (SD)	MPLR (SD)	FL (SD)
Bovinae Tragelaphini <i>Tragelaphus</i>	<i>spekei</i>	Broken cover—run to cover (swamp)	5	9.28 (2.08)	1.102 (0.073)	1.007 (0.058)	1.429 (0.077)	28.0 (3.48)
	<i>scriptus</i>	Forest—cryptic	12	10.62 (2.76)	1.062 (0.086)	0.995 (0.053)	1.392 (0.037)	22.6 (2.03)
	<i>imberbis</i>	Broken cover—run to cover (bush)	5	7.45 (1.12)	1.180 (0.066)	1.108 (0.039)	1.426 (0.034)	27.0 (1.87)
	<i>strepsiceros</i>	Broken cover—run to cover (bush)	5	7.29 (2.61)	0.987 (0.048)	1.060 (0.039)	1.510 (0.026)	33.1 (3.32)
	<i>euryceros</i>	Forest—cryptic	10	7.88 (3.70)	1.093 (0.056)	1.057 (0.052)	1.428 (0.044)	35.9 (3.10)
Boselaphini <i>Boselaphus</i>	<i>tragocamelus</i>	Forest—cryptic (1)	4	7.38 (1.12)	1.006 (0.048)	1.182 (0.096)	1.548 (0.044)	33.5 (1.11)
	<i>quadricornis</i>	Forest—cryptic (2)	4	13.18 (1.97)	0.921 (0.049)	1.072 (0.055)	1.449 (0.037)	16.6 (0.48)
<i>Tetracerus</i>								
Cephalophinae Cephalophini <i>Cephalophus</i>	<i>caerulus</i>	Forest—cryptic	2	7.28 (5.02)	1.233 (0.089)	1.022 (0.032)	1.405 (0.034)	10.8 (0.07)
	<i>callipygus</i>	Forest—cryptic	2	11.42 (0.10)	1.040 (0.040)	1.040 (0.057)	1.374 (0.019)	16.0 (0.64)
	<i>dorsalis</i>	Forest—cryptic	1	11.73	1.115	1.000	1.333	16.5
	<i>niger</i>	Forest—cryptic	2	8.16 (1.26)	1.178 (0.010)	0.985 (0.050)	1.350 (0.029)	18.4 (3.25)
	<i>silvicultor</i>	Forest—cryptic	6	8.37 (1.11)	1.095 (0.035)	1.002 (0.040)	1.372 (0.033)	24.1 (0.88)
<i>grimmea</i>	Broken cover—run to cover (tall grass, lie in forms)	5	6.55 (1.35)	1.071 (0.029)	0.993 (0.044)	1.418 (0.022)	14.6 (1.00)	
Hippotraginae Reduncini <i>Kobus</i>	<i>ellipsiprymnus</i>	Broken cover—run to cover (close to water)	2	3.95 (1.58)	1.008 (0.096)	1.094 (0.030)	1.548 (0.003)	33.4 (0.57)
	<i>defassa</i>	Broken cover—run to cover (close to water)	2	2.70 (0.346)	0.960 (0.043)	1.218 (0.014)	1.524 (0.030)	32.4 (1.27)
	<i>kob</i>	Plains—flight	6	2.38 (1.48)	1.014 (0.067)	1.089 (0.060)	1.531 (0.020)	26.1 (1.31)
	<i>megaceros</i>	Broken cover—run to cover (swamp)	5	3.92 (3.33)	0.975 (0.064)	1.032 (0.035)	1.517 (0.086)	25.8 (1.62)
	<i>arundinum</i>	Broken cover—run to cover (tall grass, lie in forms)	5	3.09 (2.01)	0.943 (0.060)	1.024 (0.026)	1.475 (0.026)	25.1 (0.92)
<i>Redunca</i>	<i>fulvorufula</i>	Broken cover—run to cover (hilly areas)	5	2.91 (2.49)	0.963 (0.050)	0.995 (0.032)	1.420 (0.016)	19.9 (0.25)
	<i>redunca</i>	Broken cover—run to cover (tall grass, lie in forms)	6	3.20 (2.40)	1.013 (0.054)	1.030 (0.026)	1.428 (0.021)	22.6 (0.82)

<i>redunca</i>	(hilly areas) Broken cover—run to cover (tall grass, lie in forms)	6	(2.49) 3.20 (2.40)	(0.050) 1.013 (0.054)	(0.032) 1.030 (0.026)	(0.016) 1.428 (0.021)	(0.25) 22.6 (0.82)
<i>Hippotragus</i>							
<i>equinus</i>	Broken cover—run to cover (edge or ecotone)	3	-1.13 (1.36)	1.025 (0.031)	1.186 (0.008)	1.518 (0.063)	32.9 (3.19)
<i>niger</i>	Broken cover—run to cover (edge or ecotone)	5	0.24 (2.14)	0.932 (0.032)	1.168 (0.043)	1.521 (0.045)	31.1 (0.71)
<i>Damaliscus</i>							
<i>lunatus</i>	Plains—flight	5	-0.33 (1.22)	1.010 (0.036)	1.170 (0.032)	1.567 (0.036)	27.1 (1.26)
<i>dorcas</i>	Plains—flight	7	0.75 (1.25)	0.963 (0.024)	1.148 (0.024)	1.528 (0.029)	22.3 (0.40)
<i>hunteri</i>	Plains—flight	2	-0.18 (0.50)	0.992 (0.033)	1.165 (0.054)	1.517 (0.058)	24.8 (0.21)
<i>Aelclaphus</i>							
<i>buseclaphus</i>	Plains—flight	12	-1.63 (1.61)	0.992 (0.038)	1.146 (0.044)	1.537 (0.040)	28.4 (1.33)
<i>lichtensteini</i>	Broken cover—run to cover (edge or ecotone)	3	0.22 (1.94)	0.989 (0.059)	1.153 (0.039)	1.566 (0.018)	28.8 (0.57)
<i>gnou</i>	Plains—flight	2	-1.38 (0.57)	0.936 (0.018)	1.336 (0.011)	1.611 (0.014)	24.4 (0.92)
<i>taurinus</i>	Plains—flight	10	-2.02 (3.23)	0.927 (0.034)	1.263 (0.082)	1.588 (0.038)	28.3 (1.71)
<i>Antilopinae</i>							
<i>Neotragini</i>							
<i>Ourebia</i>							
<i>montana</i>	Broken cover—run to cover (tall grass, lie in forms)	3	2.53 (2.11)	0.985 (0.082)	1.019 (0.016)	1.472 (0.010)	15.4 (1.14)
<i>Raphicerus</i>							
<i>campestris</i>	Broken cover—run to cover (tall grass, lie in forms)	4	0.96 (3.74)	1.010 (0.056)	1.030 (0.042)	1.471 (0.018)	14.8 (1.30)
<i>Madoqua</i>	Forest—cryptic	4	5.54 (1.81)	0.979 (0.035)	0.958 (0.063)	1.383 (0.037)	10.7 (0.36)
<i>Antilopini</i>							
<i>Antilope</i>							
<i>cervicapra</i>	Plains—flight	3	-0.71 (1.14)	0.926 (0.048)	1.099 (0.050)	1.523 (0.026)	19.0 (0.91)
<i>Aepyceros</i>							
<i>melampus</i>	Broken cover—run to cover (edge or ecotone)	10	-1.25 (2.09)	0.992 (0.037)	1.037 (0.060)	1.501 (0.044)	22.6 (0.91)
<i>Litocranius</i>							
<i>walleri</i>	Broken cover—run to cover (specialized feeder)	2	-2.74 (2.20)	1.033 (0.040)	1.032 (0.016)	1.470 (0.013)	20.2 (0.78)
<i>Gazella</i>							
<i>subgutturosa</i>	Plains—flight	1	-1.38	0.898	1.143	1.541	14.7
<i>gazella</i>	Plains—flight	2	4.28	0.931	1.098	1.463	16.1
<i>thomsoni</i>	Plains—flight	2	0.84 (5.70)	0.952 (0.027)	1.058 (0.023)	1.437 (0.045)	18.4 (2.62)
<i>granti</i>	Plains—flight	12	-2.14 (2.09)	0.938 (0.044)	1.008 (0.045)	1.492 (0.046)	22.4 (0.83)
<i>soemmeringi</i>	Plains—flight	1	-3.45	0.926	0.964	1.545	21.1
<i>Antidorcas</i>							
<i>marsupialis</i>	Plains—flight	8	-1.36 (2.31)	0.961 (0.051)	1.105 (0.045)	1.526 (0.023)	18.3 (1.11)

¹Habitat and predator avoidance strategy after Scott ('79).

(1), (2): habitat from Schaller ('67) and Walker ('75).
FL in cm; all other femoral characters dimensionless.

quadriceps femoris muscle group passes. An increase in the potential moment of this muscle group should be expressed as a relatively larger moment arm.

A total of 195 specimens from eight bovid tribes and 41 species was measured (Table 1). Measurements were taken from adult, wild animals; only rarely were zoo animals included. The number of individuals per species varied from 1 to 12 (mean of 5). Both males and females were included in the sample of specimens from each species. Specimens are housed in the Museum of Comparative Zoology (Cambridge, MA) and the American Museum of Natural History (New York, NY). Original measurements for each specimen are in Kappelman ('86).

This study concentrated on bovids living in forest, broken cover, and savanna habitats and excluded those living on cliffs, mountains, and high mountain plateaus (excluding primarily members of the tribes Saigini, Rudicaprini, Ovibovini, and Caprini). Also excluded were the very largest bovids (> 250 kg: tribe Bovini and large *Taurotragus*).

The body weights of bovids included in this study range from 4 to 250 kg. Given a size range of two orders of magnitude, there exists a distinct possibility that some of the differences in femoral morphology may result simply from allometrically related scaling differences. All characters investigated were examined against both habitat and body size in order to test for size independence. Femoral length is significantly correlated with body size across the weight range investigated here (Scott, '85) and is used as an approximation of body size. Femoral length (FL) was measured from the medial condyle to the cranial portion of the femoral head (Table 1).

The typical habitat for each species is taken from the compilation in Kappelman ('86; as modified from Scott, '79) (Table 1). "Closed" habitat has a generally continuous tree canopy and includes forest. "Open" habitats are those without tree cover and include savannas and grasslands. Bovids assigned to the category of "intermediate" habitats live in broken cover environments falling between the extremes of forest and savanna. This category includes such diverse environments as bush, tall grass, swamp or close to water, and edge or ecotone. Although this category includes a mix of ecological settings, it proves useful in distinguishing these environments from those at the ends of the habitat spectrum.

The femoral characters used here were chosen because of their previously demonstrated utility in locomotor studies of other mammalian groups. These various characters are situated near the two ends of the femoral shaft. Proximal and distal femoral fragments are common in the fossil record, and it should be possible to use these characters in studies of fossil bovids.

The characters measured are detailed in Figure 1 and include:

Femoral head shape score (FHSS) (Fig. 1A)

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. The score is dimensionless and represents the difference between the areas of the medial half (Fig. 1A: back hatch area) and lateral half (Fig. 1A: forward hatch area) of the femoral head divided by the total area (Fig. 1A: sum of back and forward hatch areas) multiplied by 100. Areas were measured from color transparencies. The mediolateral (ML) length of the femoral head (Fig. 1A:1) was measured and divided into eighths, and the widths in the anteroposterior dimension perpendicular to the ML dimension were measured at these 7 points (Fig. 1A:2-8). The area of each half of the femoral head was calculated by multiplying the ML length by the sum of the three medial (Fig. 1A:3-5) or lateral (Fig. 1A:6-8) anteroposterior (AP) widths plus one-half of the middle AP width (Fig. 1A:2). The 7 construction lines provide a close approximation of the total area of the femoral head as confirmed by subsequent digitized measurements.

Proximal AP/ML shaft ratio (PSR) (Fig. 1B)

The anteroposterior and mediolateral shaft dimensions at the distal base of the lesser trochanter were measured with dial calipers. The AP/ML ratio provides an estimate of the various loading forces that operate through the proximal femur.

Medial patellar lip ratio (MPLR) (Fig. 1C)

The distance from the medial patellar lip to the femoral condyle in the anteroposterior plane (Fig. 1C:1), and the distance from the center of the patellar groove to the intercondylar notch (Fig. 1C:2) were measured perpendicular to the shaft of the femur with an osteometric board and dial caliper, respectively. The ratio of the medial patellar lip

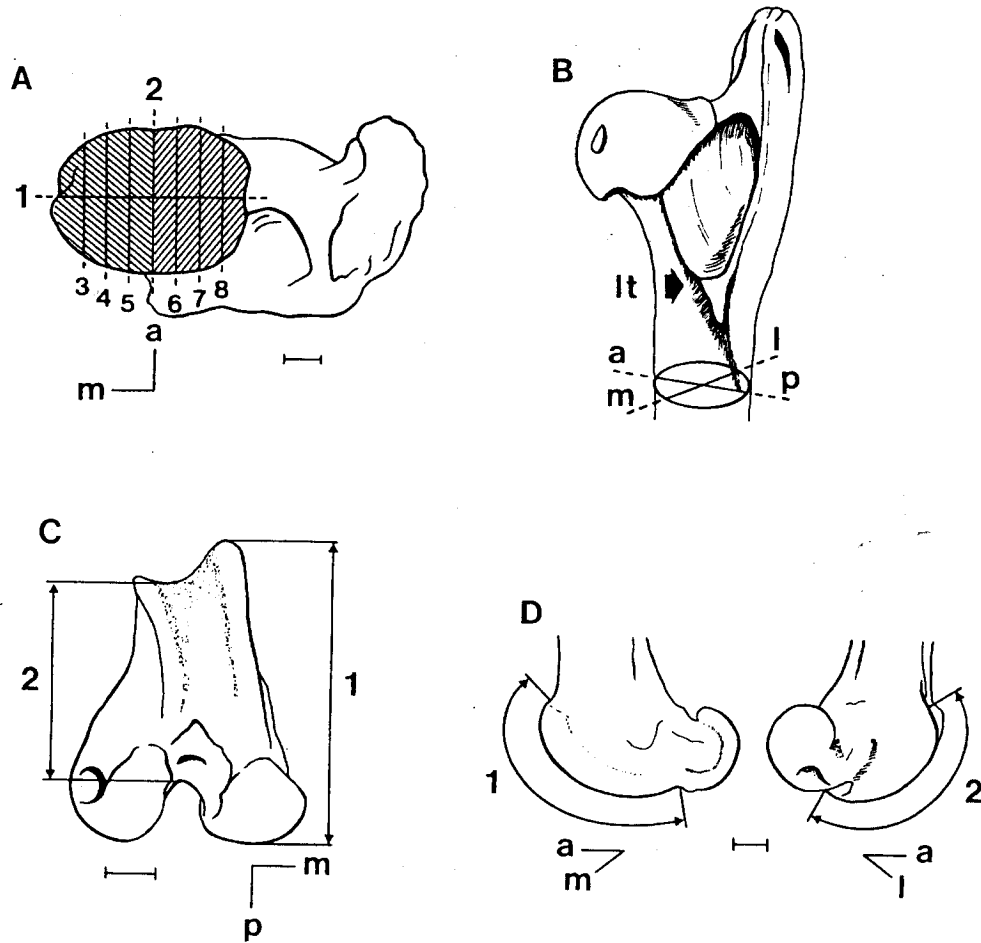


Fig. 1. Measurements of femoral characters. See Materials and Methods for explanation. A: Femoral head shape score, FHSS (cranial view). B: Proximal AP/ML shaft ratio, PSR. C: Medial patellar lip ratio, MPLR

(distal view). D: Patellar groove ratio, PGR (1, medial view; 2, lateral view). a, anterior; l, lateral; lt, lesser trochanter; m, medial; p, posterior. Scale bar equals 1 cm.

height to the distal AP shaft thickness (Fig. 1C:1/2) estimated the relative moment arm of the extensor muscles that cross the knee.

Patellar groove ratio (PGR) (Fig. 1D)

The arc length of the medial (Fig. 1D:1) and lateral (Fig. 1D:2) margins of the patellar groove were measured with a flexible tape from the proximal margin of the lip to its distal end. The ratio of the medial to the lateral arc lengths (Fig. 1D:1/2) served to estimate the relative symmetry of the patellar groove morphology.

RESULTS

Statistics for the various morphological characters measured in this study were calculated for each bovid species and the three

habitat groups (Tables 1, 2; Sokal and Rohlf, '81). The means and 95% confidence intervals for each character by habitat group are presented in Figure 2. These data support a relationship between bovid femoral morphology and habitat type.

The proximal femur

Femoral head shape score (FHSS)

Femoral heads demonstrating a high degree of lateral taper are more spherically shaped and score higher FHSS values than heads with less lateral taper that are more rectangularly shaped. Bovids with the highest values are found in closed or forested habitats while bovids with intermediate values frequent broken cover habitats. The lowest scores are found in bovids living in open

TABLE 2. Sample sizes (N), group means (X), standard deviations (SD), observed ranges (OR), and 95% confidence intervals (CI) of the four morphological characters of the bovid femur by habitat group

Habitat group	N	X	SD	OR	CI
FHSS					
Open	73	-0.80	2.58	-7.19-7.38	-1.40-0.20
Intermediate	75	3.03	3.91	-5.30-11.34	2.13-3.93
Closed	47	9.07	3.18	2.56-15.51	8.14-10.00
PSR					
Open	73	0.962	0.049	0.863-1.134	0.950-0.974
Intermediate	75	1.011	0.079	0.855-1.243	0.993-1.029
Closed	47	1.061	0.090	0.848-1.296	1.035-1.087
MPLR					
Open	73	1.532	0.049	1.393-1.643	1.520-1.544
Intermediate	75	1.477	0.058	1.338-1.652	1.463-1.491
Closed	47	1.411	0.061	1.323-1.598	1.393-1.429
PGR					
Open	73	1.129	0.096	0.953-1.352	1.107-1.151
Intermediate	75	1.058	0.072	0.910-1.228	1.042-1.074
Closed	47	1.031	0.077	0.900-1.321	1.009-1.053

savanna settings. Femoral head shape is independent of body size ($r = .01$, $P \geq .05$, $n = 195$). Although there is overlap in the total range of femoral head scores, each of the three habitat groups is separated from the others at the 95% confidence intervals (Fig. 2A).

The differences in bovid femoral head shape documented here are functionally related to different patterns of cursoriality displayed by bovids in different habitats. Bovids with more rectangularly shaped femoral heads (low FHSS) are found in open environments (Fig. 3A). These habitats present few structural obstacles at ground level and bovids living here are highly cursorial. The distinctive femoral head morphology of open country bovids appears to increase the effectiveness of cursorial locomotion by anatomically limiting the range of abduction and axial rotation and thereby restricting hindlimb movements to the parasagittal plane. This decrease in hip mobility contributes to hindlimb propulsion by preventing unnecessary axial rotation and lateral excursions of the limb.

Bovids with more spherically shaped femoral heads (high FHSS) are found in closed environments at the other end of the habitat spectrum (Fig. 3B). This environment, with its almost three-dimensional network of bush, shrubs, tree trunks, and the occasional downed tree, presents a complex and uneven substrate for a large terrestrial mammal. Closed habitats effectively limit high-speed cursorial locomotion; instead, forest bovids

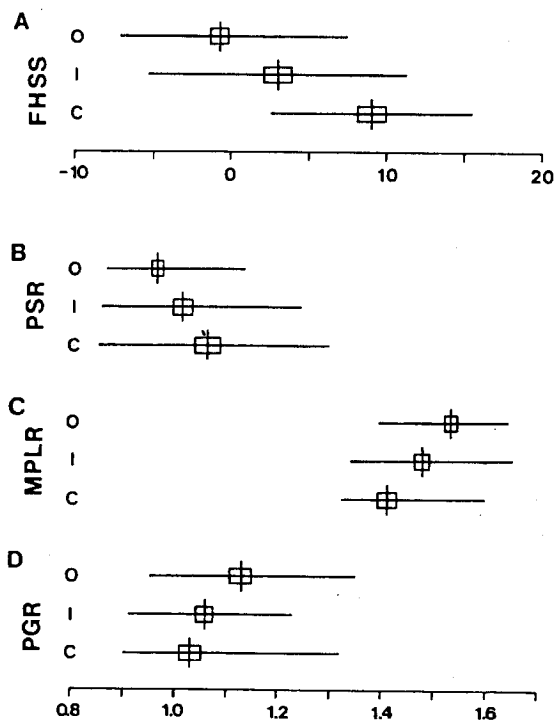


Fig. 2. Statistics for the femoral characters. See Table 2 and Results for explanation. Vertical line, range; horizontal line, range; open box, 95% confidence interval. Habitat groups: C, closed; I, intermediate; O, open.

generally follow a series of well-known paths or runways that wind through the dense vegetation. This pattern of locomotion requires maneuverability and places emphasis on a greater degree of abduction and axial rota-

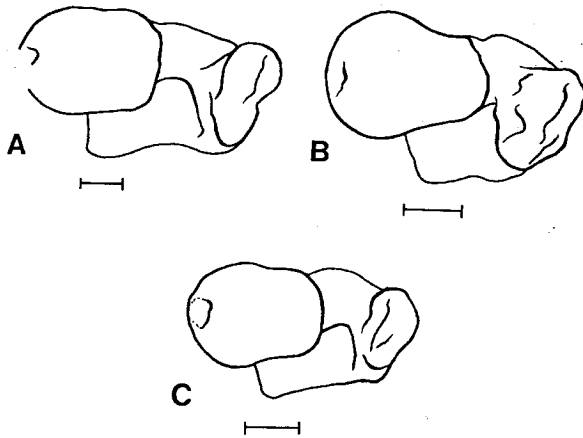


Fig. 3. Cranial view (medial to left) of right-side femoral heads from (A) savanna, (B) forest, and (C) broken-cover habitat bovids. Compare (A) the inflated lateral margin of the articular surface (*Gazella granti*, FHSS = -2.58, AMNH 82056) with (B) the reduced lateral and more spherically shaped medial margins (*Tragelaphus scriptus*, FHSS = 10.32, AMNH 53245). The bovid in C has an intermediate morphology (*Redunca fulvorufula*, FHSS = 2.11, AMNH 82066). See Results, Proximal Femur, for explanation.

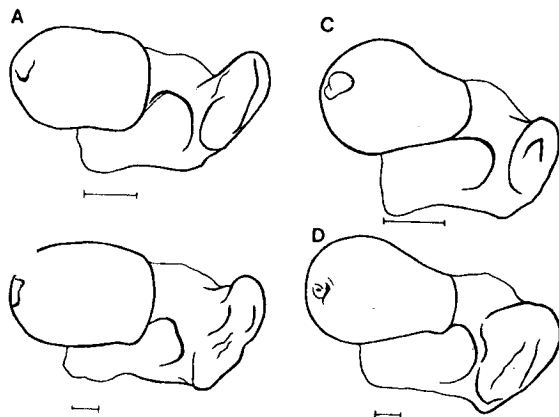


Fig. 4. Cranial view (medial to left) of femoral heads from bovids living in savanna (A, *Gazella thomsoni*, MCZ 13244; B, *Connochaetes taurinus*, MCZ 83503) and forest (C, *Cephalophus dorsalis*, MCZ 43048; D, *Taurotragus euryceros*, AMNH 88414). Note the similarity in the shape of the articular surfaces between A and B, and C and D. See Results, Proximal Femur, for explanation. Scale bar equals 1 cm.

tion at the hip. The distinctive spherically shaped femoral head morphology of closed-habitat bovids facilitates increased hip mobility.

Bovids living in broken cover environments demonstrate intermediate femoral head morphologies (intermediate FHSS) (Fig. 3C). These substrates have a varying amount of ground cover, which somewhat limits

highly cursorial locomotion. The intermediate femoral head shape probably represents a compromise between the competing demands of restricting limb movements to the parasagittal plane while still retaining some moderate degree of hip mobility.

It is instructive to compare the femoral head morphologies from bovids of different body sizes inhabiting the same environment. Figure 4 shows cranial views of two open country bovid femora from an antelope (Fig. 4A) and an alcelaphine (Fig. 4B), and two closed-habitat femora from a cephalophine (Fig. 4C) and a tragelaphine (Fig. 4D). Although the members of each pair of species from the open and closed habitats differ in body weight by a factor of 10, they still demonstrate the same basic femoral head shape. Each species is from a different subfamily (Table 1). The distinctive morphologies are then either homoplastic or retained from a distant common ancestor within the pairs of species living in similar habitats. The great morphological similarity witnessed between unrelated species of such different body sizes argues for the strength of the selection pressure for hip joint movements associated with habitat specific patterns of locomotion.

Proximal AP/ML shaft ratio (PSR)

Bovids from open habitats demonstrate smaller PSR values than bovids from closed habitats (Fig. 2B). There is separation between the habitat groups at the 95% confidence intervals. There is no correlation between PSR and femoral length ($r = .06$, $P \geq .05$, $n = 195$).

Measurements of cross-sectional shaft geometry have been used to study the various loading forces that are generated during locomotion (Burr et al., '81; Currey and Alexander, '85; Lanyon and Rubin, '84; Ruff and Hayes, '83). Although a precise calculation of the cross-sectional second moments of inertia requires the total area and the distribution of the area around the centroid of the shaft, the major and minor axes of bending rigidity generally approximate the greatest and least diameters of the shaft cross section. The AP/ML ratio of the femoral shaft at the lesser trochanter serves to approximate the loading forces generated during locomotion that pass through the proximal femur along these planes.

The most cursorial bovids from open habitats have larger ML than AP diameters in the proximal femur (ratio < 1) than bovids

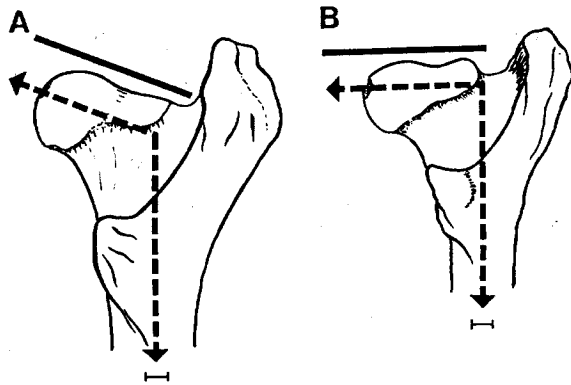


Fig. 5. Posterior view (right side, medial to left) illustrating the orientation of the cranial articular surface of the femoral head with respect to the vertical axis of the shaft. Compare (A) the more vertical inclination of forest bovids (*Boselaphus tragocamelus*, AMNH 16216) with (B) the more horizontal inclination of savanna bovids (*C. taurinus*, MCZ 13677). See Results, Proximal Femur, for explanation.

from closed habitats (ratio > 1) (Fig. 2B). The morphology of the proximal femur of open habitat bovids then appears to provide greater bending rigidity in the mediolateral plane. This feature is related to the differences in femoral head morphology discussed above, which not only either limit or enhance the degree of rotation at the hip but also determine the manner in which forces are translated through the hip joint and femoral shaft.

The cranial surface of the femoral head of closed habitat bovids is more vertically oriented (Fig. 5A) than that of open country bovids, which is approximately perpendicular to the long axis of the femoral shaft (Fig. 5B). This horizontal aspect of the femoral head imparts more horizontally and laterally directed forces through the proximal femur. A larger mediolateral proximal shaft diameter in open-country bovids resists the bending that such forces generate. The more cranially oriented femoral head of closed habitat bovids imparts more vertically oriented forces through the proximal femur and generates less bending along the mediolateral axis. It appears that the larger ML forces generated through the proximal femur in open habitat bovids are one consequence of a femoral head morphology that is designed to restrict movement at the hip to the parasagittal plane. Femoral head architecture then in part accounts for the differences in proximal shaft morphology observed among bovids from different habitats.

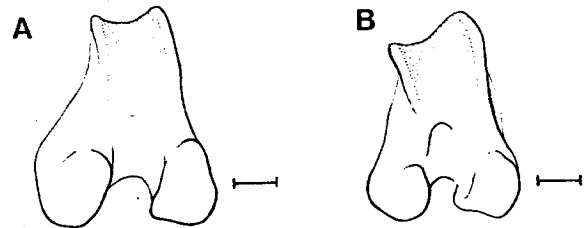


Fig. 6. Distal view of the patellar morphology of right femora (medial to right) of (A) forest (*Cephalophus niger*, MCZ 39758) and (B) savanna (*G. thomsoni*, MCZ 13244) bovids. Note (A) the equal size and overall symmetry of the patellar lips and (B) the asymmetry and taller medial patellar lip. See Results, Distal Femur, for explanation.

The distal femur Medial patellar lip ratio (MPLR)

Bovids from more open habitats demonstrate a much larger MPLR than bovids from closed habitats, with no overlap at the 95% confidence intervals (Fig. 2C). MPLR is significantly correlated with femoral length ($r = .31$, $P < .01$, $n = 195$). Larger bovids have larger medial patellar lips relative to the AP dimension of the distal shaft than smaller bovids.

Patellar groove ratio (PGR)

Bovids from closed habitats generally have symmetrical patellar grooves (Fig. 6A), with the medial and lateral patellar lips approximating each other in both shape and length ($PGR \sim 1$). Bovids from increasingly more open habitats demonstrate more asymmetry in shape. Their femora have a taller medial than lateral patellar lip (Fig. 6B) and a longer medial than lateral patellar lip arc ($PGR > 1$). As seen in Figure 2D, while there is separation at the 95% confidence intervals between bovids from open and closed, and open and intermediate habitats, there is wide overlap between the closed- and intermediate-habitat bovids. This character is significantly correlated with femoral length ($r = .39$, $P < .01$, $n = 195$).

Hindlimb extension provides the majority of propulsive force in most bovids. The morphological contrasts witnessed in the distal femora of bovids from different habitats can be understood in relation to the moment arm for the extensor muscles that cross the knee. These muscles are of the m. quadriceps femoris group and arise from origins near the proximal femur (m. vastus lateralis), pelvis (m. rectus femoris), and the proximal three-fourths of the femoral shaft (m. vastus medi-

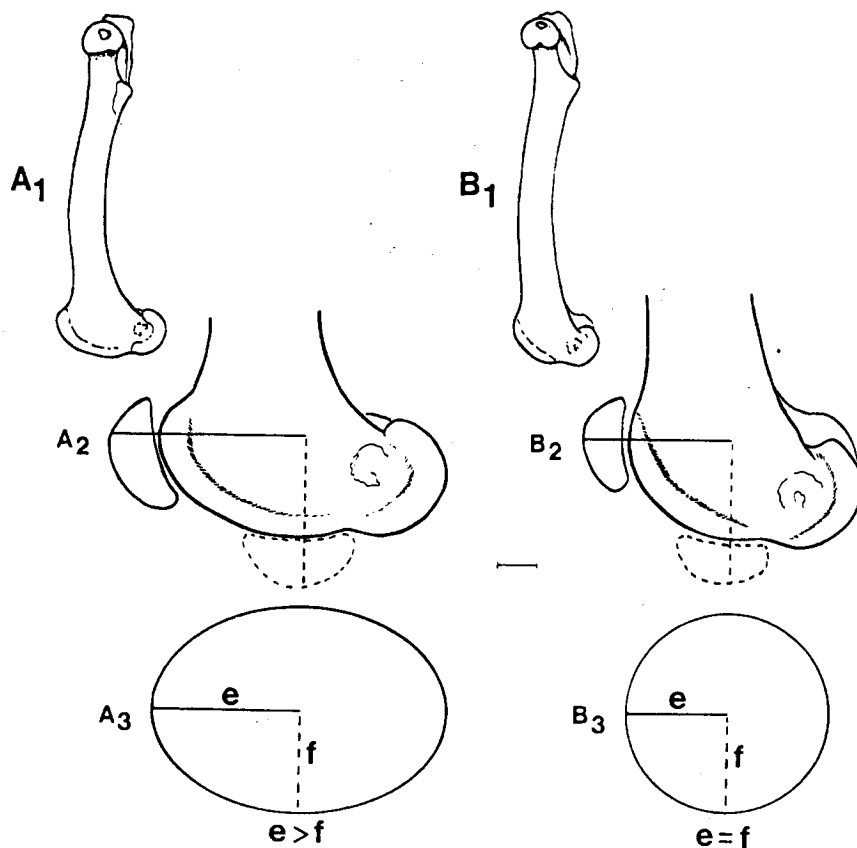


Fig. 7. Medial view of bovid femora (anterior to left) from (A₁) savanna (*Damaliscus dorcas*, AMNH 81729) and (B₁) forest (*T. scriptus*, AMNH 53221). A₂, B₂: The path tracked by the patella from flexion (dotted lines) through extension (solid lines). A₃, B₃: Models emphasizing the elliptical shape of the distal femur in savanna

bovids vs. the circular shape in forest bovids. The point of intersection between the solid and dotted lines approximates the center of rotation of the knee joint. The length of the lines is the estimated extent of the lever arm in e, extension; f, flexion. See Results, Distal Femur, for explanation. Scale bar equals 1 cm.

alis and lateralis) (Richter, '70) and pass into the ligamentum patellae which inserts on the tibial tuberosity. The primary movements imparted by these muscles are translational within the parasagittal plane (Currey, '84). The patella (which lies behind the ligamentum patellae) is an unusually large sesamoid bone that acts to increase the moment arm of the extensors around the center of rotation of the knee joint. The greater the distance the patella is from the center of rotation, the greater the moment arm of the quadriceps group.

The two characters of the distal femur discussed here serve to estimate the relative extent of the moment arm. The presence of a relatively large moment arm in open country bovids is suggested by the large ratio of the medial patellar lip to the distal shaft in the AP dimension (large MPLR). In addition, not only is the arc of the medial patellar lip

longer than that of the lateral patellar lip in open than in closed habitat bovids (large PGR), but the shapes of the arcs inscribed by the medial lips also differ. Closed-habitat bovids have patellar lip arcs that are both roughly circular in shape. In contrast, the lateral lip arc of open country bovids is usually more circular while the medial lip arc resembles an ellipse (cf. Fig. 7A₁, B₁).

The highly eccentric elliptically shaped medial aspect of the distal femur of open country bovids also guarantees a progressive increase in the moment arm of the extensors as the patella tracks through its groove while the limb moves into extension (cf. Fig. 7A₂, B₂). This large increase in the distance of the ligamentum patellae away from the center of rotation may serve to maintain a large turning moment through extension (cf. Fig. 7A₃; $e > f$; B₃; $e = f$). However, the larger moment arm of savanna bovids need not nec-

essarily translate into an absolutely larger moment. Various other factors (e.g., muscle fiber angulation and length, muscle mass, degree of limb excursion, the contribution of two limb muscles, etc.) must be considered when calculating the moment (Gans and de Vree, '87).

Unlike the characters of the proximal femur, the characters of the distal femur are significantly correlated with body size. However, the r^2 values are low and account for only 10% (MPLR) and 15% (PGR) of the variability. Even though the r^2 s are low, it may prove to be the case that large bovids also benefit from having a larger moment arm for the extensor muscles that cross the knee. In addition, a large medial patellar lip may confine the movement of the patella as it tracks through its groove during extension and help to prevent its medial dislocation. It should, however, be noted that of the 4 characters discussed here, PGR demonstrates the weakest correlation with habitat type ($r = .43$) and has a slightly weaker correlation with femoral length ($r = .39$). The correlation between MPLR and habitat ($r = .64$) is stronger than that of MPLR and femoral length ($r = .31$). In sum, this stronger correlation with habitat argues for the relatively greater importance of the relationship between femoral morphology and habitat structure.

DISCUSSION

Differences in habitat structure encountered from closed canopy forest to open savanna appear to be primary determinants of bovid locomotion. Bovids living in open habitats depend upon speed and are highly cursorial (Sinclair, '83). Their increase in locomotor performance is aided by a distinctive femoral head morphology which largely restricts movement at the hip to the parasagittal plane and by a more elliptically shaped knee which produces a large moment arm for the extensor muscles. Forest bovids have an equally distinctive femoral head morphology that is spherically shaped and permits a high degree of rotation and abduction at the hip. The greater maneuverability that this morphology facilitates is related to the demands of movement through, around, and over the often-dense forest-floor vegetation.

Other workers have commented on these contrasts in bovid femoral morphology (Gentry, '70; Westlye, '82; Hildebrand, '85) and linked the morphological differences to functional restrictions in hindlimb movement.

Gentry ('70) appears to have been the first worker to suggest that the distinctive femoral head shape of open habitat bovids acts to limit rotation and abduction. Femoral head shape also exerts important constraints on the degree of abduction and lateral rotation in cursorial carnivores and restricts their limb movements to the parasagittal plane (Jenkins and Camazine, '77). It is interesting to note that "pursuit" carnivores and highly cursorial bovids are homoplastic for general femoral head shape, especially when one considers that both groups evolved in open habitat settings with one as the other's predator.

It has been demonstrated for other groups that the elongation of the distal limb elements relative to proximal elements facilitates high-speed locomotion by increasing the relative proportion between the load and moment arms (Smith and Savage, '56). This relationship has also been shown to exist in bovids, with the most cursorial open country species having more elongated metapodials than species from forests or woodlands (Scott, '79, '85). This study of bovid hip and knee joint morphology complements the approach based on limb proportions. Together, these studies offer detailed information about bovid hindlimb biomechanics.

The studies presented and reviewed here provide a basis for understanding previously published correlations between different bovid taxa (ranging from species to tribe) and habitat. Analyses based on census data show that certain taxa are found in specific habitats (Estes, '74; Jarman, '74; Vrba, '80; Kingdon, '82; Greenacre and Vrba, '84). It seems that bovid locomotor adaptations are related to specific patterns of food search and predator avoidance strategies that are habitat specific.

Diet exerts fairly strong influences upon bovid behavior and morphology (Underwood, '83). The inverse correlation between food quality and body size is well known (Bell, '71; Jarman, '74) and provides a basis for understanding the dietary strategies of different bovid species. Bovids are herbivores—primarily grazers at the largest body sizes and folivores and frugivores at the smallest body sizes. Species at intermediate body sizes are mixed feeders. Although plant foods vary in seasonal abundance and local supply, grass, browse, new shoots, and fruit do not require active pursuit. The seasonally unpredictable nature of some plant foods may demand long-distance migrations for the largest

grazers or an intimate knowledge of the surrounding forest and fruit trees for the smallest folivores and frugivores (Jarman and Sinclair, '79; Maddock, '79).

There is then a general relationship between habitat and diet, with most grazers living in open habitats or savannas and most folivores and frugivores living in closed habitats or forests. Species occurring at the extremes of the diet and habitat spectrum are predicted to have locomotor adaptations that facilitate their food search in their specific habitats. A high degree of cursoriality will aid open country bovids in their pursuit of food over great distances, while greater maneuverability will facilitate food search in more closed habitat settings.

The problem of predator avoidance may exert greater constraints on bovid behavior and locomotion. Bovids demonstrate varied responses to predators. The largest bovids have the advantage of being larger than the majority of their predators and actively defend themselves in open habitats (Scott, '85). Other predator avoidance strategies are linked clearly to habitat structure and related to the amount of vegetation cover. Bovids moving through a dense understory encounter a structurally diverse substrate and generally follow a series of well-known paths. The strategy of predator avoidance followed by forest bovids relies upon crypsis and stealth as a way to blend into the available vegetation cover (Estes, '74; Jarman, '74).

Bovids that live in broken cover environments encounter a wide variety of vegetation that can range from dense bush or wooded savanna to tall grass and display equally diverse predator avoidance behaviors. These behaviors range from a "short run to cover" (Scott, '79) to crypsis (Estes, '74; Jarman, '74).

Bovids living in open country environments are subject to intense predatory pressures (Pienaar, '69; Kruuk, '72) but the open nature of the habitat precludes the effectiveness of crypsis and stealth. Instead, bovids living in open country utilize vigilance and try to outdistance their predators. There appears then to be strong selection pressure for highly cursorial locomotion in open habitats.

Social organization clearly plays an important role here also. Open country species that rely on vigilance are more social and form larger social units; species that rely on crypsis are usually solitary (Estes, '74; Jarman, '74). Consequently, much of bovid social organization in open country settings seems to

be related to identifying predators before they can approach close enough to pose a serious threat (Estes, '74).

The work presented here provides a methodology for studying the evolution of bovid locomotion. The dramatic radiation of bovids through the Neogene has been viewed as a progressive expansion of species from closed forest into increasingly open country environments (Thomas, '84a,b; Solounias, '82). The femoral character complexes found in bovids from closed habitats probably represent the plesiomorphic state (e.g., tribes Boselaphini, Cephalophini, Tragelaphini), while those from open habitats are apomorphic (e.g., tribes Hippotragini, Alcelaphini, Antilopini). This division of the femoral character complexes into polarity states is in general agreement with bovid phylogeny (Gentry, '70, '78; Solounias, '82; Vrba, '80).

A study of the fossil record of bovid evolution that addresses the characters investigated here should then provide morphological evidence for the predicted movement into intermediate and open habitats. This approach also offers a focus for studies of bovid social and dietary evolution. When combined with a parallel study of bovid predators, these data together will bear on questions regarding the degree and timing of coevolution (if any) between predators and prey. Future work will serve to document habitat evolution through the Neogene and, in turn, provide a much-needed indicator of terrestrial habitat change that is essential for reconstructing the environments of the past.

ACKNOWLEDGMENTS

I thank David Pilbeam, Nikos Solounias, John Barry, Steven Ward, Carl Gans, John Noss, Joyce Pohlman, Mahmood Raza, Katherine Scott, and three reviewers for their comments and discussion. The staff of Harvard University's Museum of Comparative Zoology (MCZ), Cambridge, and Dr. Guy Musser and his staff of the American Museum of Natural History, New York, kindly permitted me to measure bovid specimens in their care. L. Laszlo Meszoly of Harvard's MCZ drafted Figure 6. This work is drawn from my Ph.D. thesis submitted to the Departments of Anthropology and Earth and Planetary Sciences, Harvard University. The research was supported by a National Science Foundation graduate fellowship, grants in aid from the D. Dee Foundation, Harvard University, the Center for Advanced Study,

University of Nevada Reno, a Fulbright grant, and Smithsonian Foreign Currency Grant 20203700 to David Pilbeam and John Barry. The support of these individuals, institutions, and agencies is deeply appreciated.

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