

Methods for inferring paleohabitats from the functional morphology of bovid phalanges

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Abstract

The functional morphology of postcranial remains can be used to infer habitat preference. This approach is typically considered an “ecomorphological” method, and has frequently been applied to bovid postcranial remains. Methods for predicting habitat preference from bovid postcrania currently exist for femora, metapodials, and astragali. Here we describe three methods for predicting paleohabitats using measurements of African bovid phalanges (proximal, intermediate, and distal). The proximal phalanx method correctly predicted the habitat preference for 130 of 183 modern bovid specimens (71.0%, 2.8 times better than chance, $p < 0.0001$). The intermediate phalanx method correctly predicted the habitat preference for 115 of 163 modern bovid specimens (70.6%, 2.8 times better than chance, $p < 0.0001$). The distal phalanx method correctly predicted the habitat preference for 87 of 122 modern bovid specimens (71.3%, 2.8 times better than chance, $p < 0.0001$). These accuracies compare well with those of existing such methods (1.8–3.4 times better than chance). Analysis of the probabilities associated with the habitat predictions allows confidence thresholds to be established that identify specific predictions which have <5% chance of being in error. This raises the effective accuracy of the methods to 95%. Extensive exploration and manipulation of the underlying data demonstrate that the habitat predictions are generally robust, and are relatively independent of body weight, taxonomy, and sample composition. These methods are broadly applicable, relatively accurate, and can be used to generate independent predictions of habitat from different elements, and thus constitute a useful approach to inferring past environments.

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1. Introduction

Accurate and precise reconstructions of past environments are required in order to test hypotheses about hominid biological and technological evolution [15,22,23]. One approach to reconstructing paleoenvironments is to use the functional morphology of mammalian postcranial fossils to infer their locomotor adaptations and, by association, their habitat prefer-

ences [1,2,4,5,8–11,13,14,19]. This approach is commonly termed an “ecological morphology” or “ecomorphology” method, though the use of these labels is generally avoided here since the approach is really that of functional morphology.

In theory, an organism’s locomotor anatomy should evince adaptations to the substrate(s) and environment(s) it locomotes across [7,17,18]. The habitat preference of an organism should thus be predictable, to varying degrees, from the functional morphology of its postcranial skeleton. Once the habitat preference(s) have been inferred from the functional morphology, they can be used to reconstruct aspects of the

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paleoenvironment. Of course, the morphology of an organism is constrained by its evolutionary history, and is not necessarily engineered for its current habitat. Phylogeny is thus a potentially confounding variable in attempting to infer habitat preference from functional morphology. In practice, though, the effect of phylogenetic constraint can be identified and excluded from the analysis by identifying anatomical features that co-vary with locomotion and habitat, rather than phylogeny, as described below.

In practice, paleohabitat reconstruction via functional morphology uses morphological characters—usually metric in nature (i.e. measurements) but sometimes non-metric (i.e. shape defined according to descriptive criteria)—that are potentially related to locomotion. The objective is to locate characters that co-vary with habitat preference, but do not co-vary with phylogeny. Such characters permit the accurate prediction of habitat preference independent of phylogeny/taxonomy. Characters thought to be potentially informative regarding locomotor mode (and thus habitat preference) are tested using samples of extant taxa whose habitat preferences are known. Their variation in extant taxa reveals whether they are, in fact, correlated with habitat preference. This empirically tests the link between the anatomical feature and habitat preference, and identifies characters which are primarily linked to habitat rather than phylogeny.

A variety of methods have been developed to use bovid postcranial elements in the functional morphology approach to paleohabitat prediction [1,2,4,8–11,13,14,19]. Gentry [5] rather informally described approximately 40 non-metric characters covering a range of bovid postcranial elements, and Köhler [13] described a similar number of non-metric characters of the metapodials and phalanges, though neither systematically tested their characters (see Ref. [3], for such a test). Kappelman [8–10] identified and tested nine metric characters of the femur, which allow habitat prediction with an accuracy of 81–85% using a four-category habitat scheme (Plains, Light Cover, Heavy Cover, and Forest; [11]). Plummer and Bishop [14] described and tested 19 metric characters of the metapodials, which allow habitat prediction with an accuracy of 62–89% using a three-category habitat grouping scheme (Open, Intermediate, and Closed). Elsewhere, we described eight metric characters of the bovid astragalus which predict habitat with 67% accuracy using four habitat categories [2].

Here we describe methods for predicting habitat preference from metric characters of bovid proximal, intermediate, and distal phalanges. Each of the three methods is entirely independent, and so any isolated bovid phalanx can be analyzed. Since bovid phalanges are frequently preserved (at least based on our examination of Ethiopian open-air Mio–Plio–Pleistocene sites),

this should increase the sample size available for bovid “ecomorphology” habitat reconstructions. In addition, the use of multiple elements can increase the confidence in such reconstructions if the results for different elements are congruent.

2. Materials

The methods described here were developed and tested using a sample of modern African bovids from the American Museum of Natural History. The taxonomic composition of the sample is given in Table 1. Only adult individuals (as determined by complete fusion of postcranial epiphyses) that were documented as wild-caught (non-captive) were included in the sample. Specimens with postcranial pathological processes were excluded. The specimens were sampled without regard to sex, since this parameter cannot currently be determined for isolated postcranial fossils. Phalanges were also sampled randomly with respect to forelimb and hindlimb, as there is currently no method for determining the placement of isolated phalanges. Measurements of a few articulated modern museum specimens suggest that, while forelimb and hindlimb phalanges can differ in absolute size within an individual, their proportions are relatively constant.

3. Methods

3.1. Measurements

Seven measurements (Fig. 1) developed for this study were taken on each proximal phalanx as follows:

Midline Length (LM)

The minimum proximal–distal dimension along the dorsal midline.

Proximal Width (WP)

The maximum medial–lateral dimension of the proximal end taken perpendicular to its major proximal–distal axis.

Intermediate Width (WI)

The medial–lateral dimension of the shaft at midshaft.

Distal Width (WD)

The maximum medial–lateral dimension of the distal articular end, taken perpendicular to its major proximal–distal axis.

Proximal Height (HP)

The midline dorsal–ventral dimension of the proximal articular end, taken perpendicular to its major proximal–distal axis.

Table 1
Taxonomic composition [6] and habitat assignments of the modern African bovid sample

Subfamily	Tribe	Species	Habitat group	# Prox Phx	# Int Phx	# Dist Phx		
Alcelaphinae	Aepycerotini	<i>Aepyceros melampus</i>	Light Cover	10	9	7		
		Alcelaphini						
		<i>Alcelaphus buselaphus</i>	Open	10	7	7		
		<i>Connochaetes gnou</i>	Open	1	1	1		
		<i>Connochaetes taurinus</i>	Open	7	6	5		
		<i>Damaliscus dorcas</i>	Open	6	6	3		
		<i>Damaliscus hunteri</i>	Open	2	1	0		
	<i>Damaliscus lunatus</i>	Open	4	4	3			
Antilopinae	Antilopini	<i>Antidorcas marsupialis</i>	Open	7	7	6		
		<i>Gazella granti</i>	Open	7	7	5		
		<i>Gazella thomsoni</i>	Open	4	3	2		
		<i>Litocranius walleri</i>	Open	4	3	1		
	Neotragini	<i>Madoqua kirki</i>	Forest	1	1	0		
		<i>Neotragus batesi</i>	Forest	2	2	2		
		<i>Ourebia ourebia</i>	Light Cover	8	8	0		
<i>Raphicerus campestris</i>		Light Cover	2	1	1			
Bovinae	Cephalophini	<i>Cephalophus niger</i>	Forest	1	1	1		
		<i>Cephalophus nigrifrons</i>	Forest	2	3	3		
		<i>Cephalophus sylvicultor</i>	Forest	5	5	4		
	Tragelaphini	<i>Taurotragus oryx</i>	Open	11	11	10		
		<i>Tragelaphus angasi</i>	Forest	3	1	0		
		<i>Tragelaphus buxtoni</i>	Heavy Cover	4	3	1		
		<i>Tragelaphus euryceros</i>	Heavy Cover	8	8	6		
		<i>Tragelaphus imberbis</i>	Heavy Cover	4	4	4		
		<i>Tragelaphus scriptus</i>	Forest	10	7	3		
		<i>Tragelaphus spekei</i>	Heavy Cover	6	6	6		
		<i>Tragelaphus strepiceros</i>	Heavy Cover	9	8	8		
		Hippotraginae	Hippotragini	<i>Addax nasamaculatus</i>	Open	4	4	4
				<i>Hippotragus niger</i>	Open	5	4	3
				<i>Oryx dammah</i>	Open	3	3	3
<i>Oryx gazella</i>	Open			4	4	3		
Reduncini	<i>Kobus ellipsiprymnus</i>		Heavy Cover	5	4	4		
	<i>Kobus kob</i>		Light Cover	4	3	3		
	<i>Kobus megaceros</i>		Heavy Cover	5	4	4		
	<i>Kobus vardoni</i>		Light Cover	2	1	1		
	<i>Redunca arundinum</i>		Light Cover	4	4	2		
	<i>Redunca fulvorufula</i>		Light Cover	7	7	4		
	<i>Redunca redunca</i>		Light Cover	2	2	2		
Total				183	163	122		

Intermediate Height (HI)

The midline dorsal–ventral dimension of the shaft at midshaft.

Distal Height (HD)

The midline dorsal–ventral dimension just proximal to the distal articular surface. One tip of the caliper should be placed on the dorsal surface just proximal to the distal articular surface, the other tip just proximal to the distal articular surface on the ventral surface. This results in a “diagonal” height (in lateral or medial view).

Seven measurements (Fig. 2) developed for this study were taken on each intermediate phalanx as follows:

Superior Length (LS)

The proximal–distal dimension of the dorsal surface, measured from the most proximal midline point of the dorsal surface of the proximal end to the most distal midline point on the distal articular surface.

Inferior Length (LI)

The proximal–distal dimension of the ventral surface, measured from the most proximal midline point of the ventral surface of the proximal end to the most distal midline point on the distal articular surface. The distal point for this measurement is the same as the distal point of the Superior Length (LS) metric.

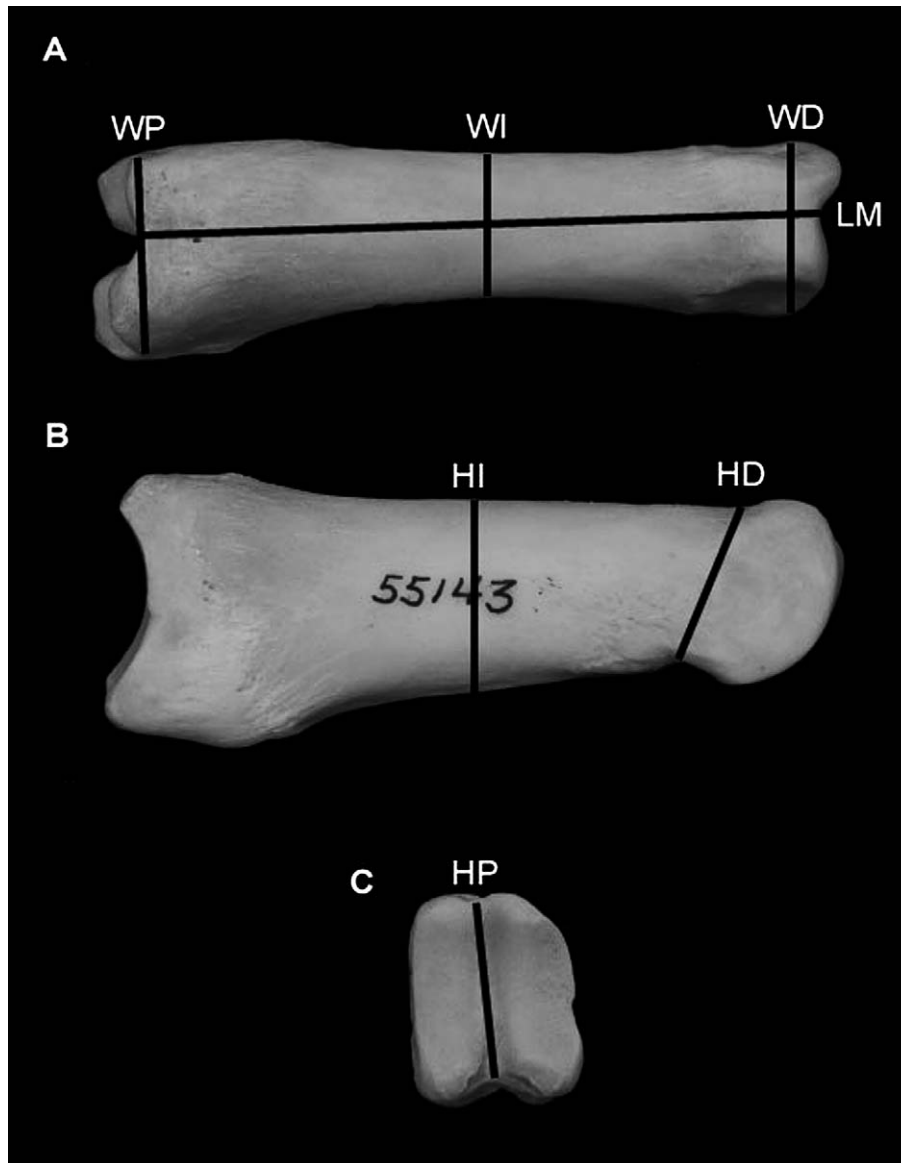


Fig. 1. (A) Dorsal view of proximal phalanx with midline length (LM), proximal width (WP), intermediate width (WI), and distal width (WD) measurements marked. (B) Side view of proximal phalanx with intermediate height (HI) and distal height (HD) measurements marked. (C) Proximal view of proximal phalanx with proximal height (HP) measurement marked.

Proximal Width (WP)

The maximum medial–lateral width of the proximal end, measured perpendicular to its major proximal–distal axis.

Distal Width (WD)

The maximum medial–lateral width of the distal end, measured perpendicular to its major proximal–distal axis.

Proximal–Medial Height (HM)

The dorsal–ventral dimension of the medial portion of the proximal articular facet, measured from the most ventral point to the most dorsal point. The most dorsal point for this metric is the same as the most dorsal point of the Proximal–Lateral Height metric.

The Proximal–Medial Height is almost always greater than the Proximal–Lateral Height.

Proximal–Lateral Height (HL)

The dorsal–ventral dimension of the lateral portion of the proximal articular facet, measured from the most ventral point to the most dorsal point. The most dorsal point for this metric is the same as the most dorsal point of the Proximal–Medial Height metric. The Proximal–Lateral Height is almost always less than the Proximal–Medial Height.

Distal Height (HD)

The dorsal–ventral dimension of the distal end, measured just proximal to the distal articular surface.

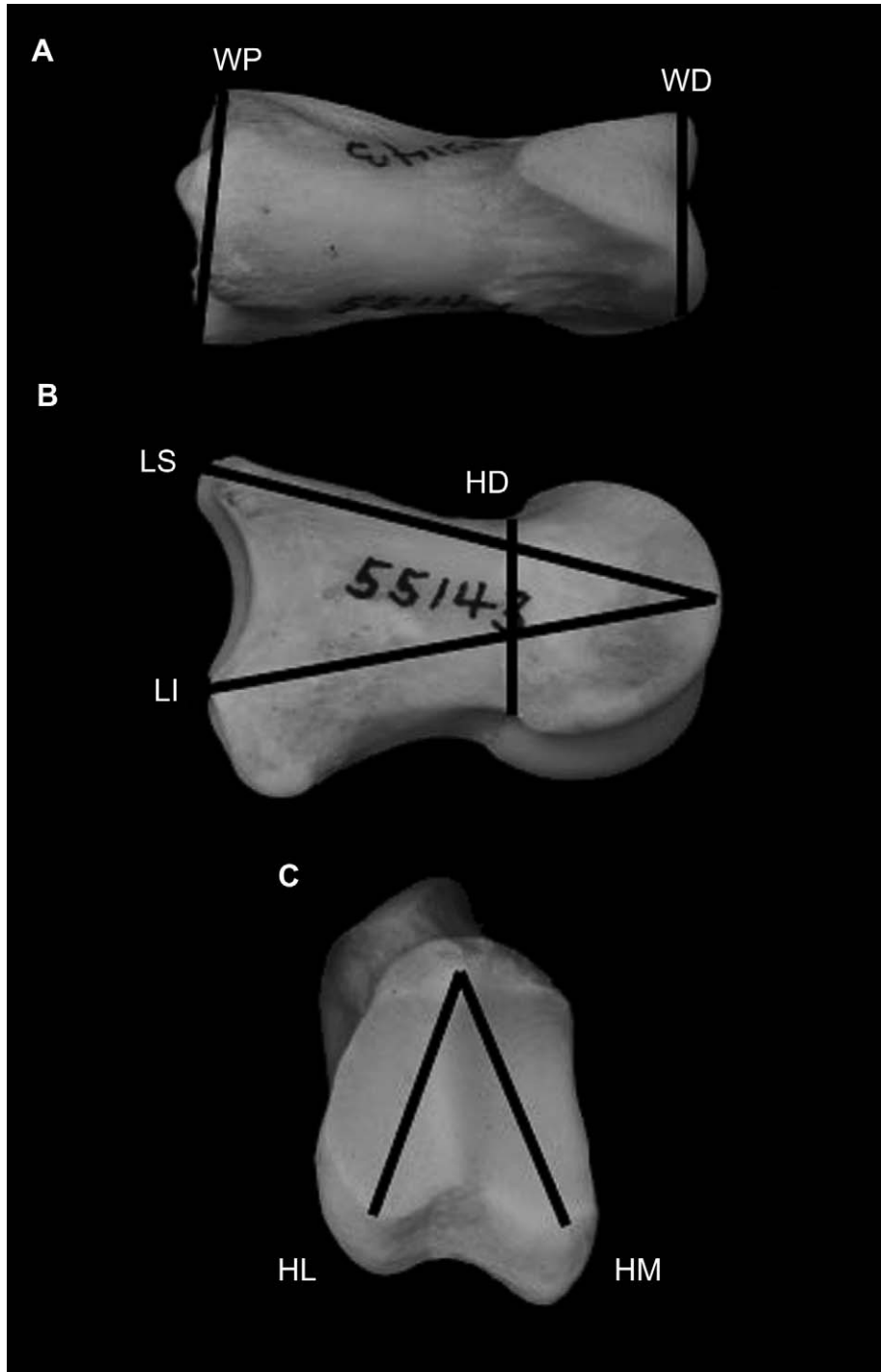


Fig. 2. (A) Dorsal view of intermediate phalanx with proximal width (WP) and distal width (WD) measurements marked. (B) Side view of intermediate phalanx with superior length (LS), inferior length (LI) and distal height (HD) measurements marked. (C) Proximal view of intermediate phalanx with proximal–lateral height (HL) and proximal–medial height (HM) measurements marked.

Five measurements (Fig. 3) developed for this study were taken on each distal phalanx as follows:

Superior Length (LS)

The proximal–distal dimension along the dorsal surface, from the dorsal-most point on the midline

of the proximal articular surface (non-articular projections extending dorsally from this are not included) to the distal-most point. In measuring this distance, care must be taken to avoid chipping or breaking the typically thin and fragile distal tips of distal phalanges.

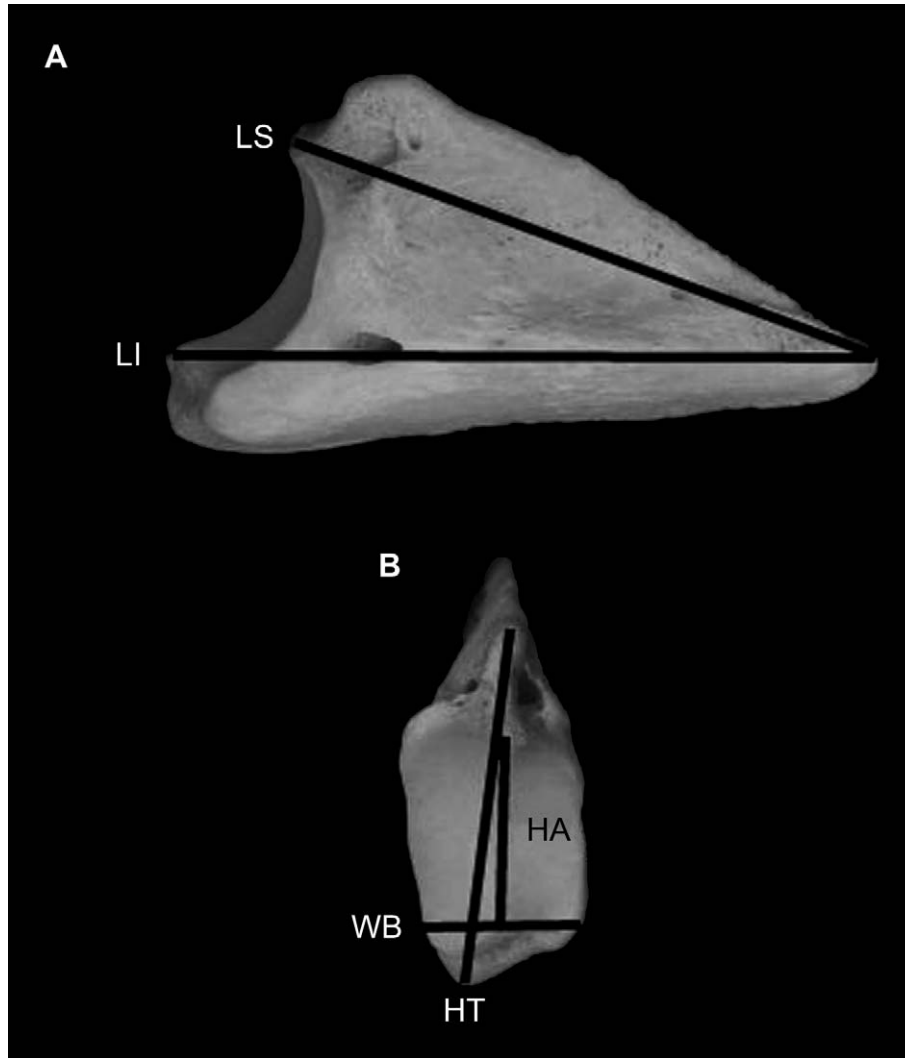


Fig. 3. (A) Side view of distal phalanx with superior length (LS) and inferior length (LI) measurements marked. (B) Proximal view of distal phalanx with basal width (WB), total height (HT), and articular facet height (HA) measurements marked.

Inferior Length (LI)

The proximal–distal dimension along the ventral surface, from the ventral-most point on the midline of the proximal articular surface (non-articular projections extending ventrally from this are not included) to the distal-most point. The distal-most point used is the same as for the Superior Length (LS) metric. In measuring this distance, care must be taken to avoid chipping or breaking the typically thin and fragile distal tips of distal phalanges.

Basal Width (WB)

The maximum medial–lateral dimension taken at the ventral base of the proximal articular facet.

Articular Facet Height (HA)

The ventral–dorsal dimension of the proximal articular facet, taken along the ridge separating the proximal facet into medial and lateral components

(one tip of the caliper is placed at the ventral terminus of the ridge and the other tip at the dorsal terminus).

Total Height (HT)

The maximum ventral–dorsal dimension of the proximal end, including non-articular projections.

The measurements were taken with digital calipers and recorded to the tenth of a millimeter. All measurements were taken by one individual (DD), eliminating concerns of interobserver error. The intraobserver error for each measurement was determined by measuring six specimens twice, with a separation of at least four days between measurements, and the results are given in Table 2. The measurements with relatively larger measurement error do not contribute significantly to the discriminant function results (as judged by their coefficients in the functions).

Table 2
Intraobserver measurement error

Metric	Mean % error	Range (%)
PP-LM	0.4	0.2–0.4
PP-WP	1.0	0.4–1.5
PP-WI	1.8	0.0–7.3
PP-WD	1.6	0.0–4.2
PP-HP	0.4	0.0–0.9
PP-HI	3.3	1.0–6.2
PP-HD	0.7	0.0–1.1
IP-LS	0.5	0.0–1.2
IP-LI	0.3	0.0–1.0
IP-WP	0.8	0.0–2.8
IP-WD	1.4	0.8–2.2
IP-HL	2.2	0.5–4.7
IP-HM	6.3	2.3–15.5
IP-HD	2.3	0.7–4.6
DP-LS	0.9	0.2–1.7
DP-LI	0.7	0.0–1.7
DP-HA	3.3	0.9–7.0
DP-HT	1.6	0.4–2.7
DP-WB	1.7	0.0–3.9

3.2. Habitat groups

All “ecomorphological” methods must use a habitat grouping scheme, in which the continuous range of possible habitats is partitioned into an arbitrary set of finite categories. We used the four-category scheme of Kappelman et al. [11], but performed our own assignment of bovid taxa to habitat categories [2]. Our assignments are given in Table 1. The “Forest” taxa are, naturally, forest-dwelling taxa. “Heavy Cover” taxa are those which frequent bush, woodland, swamp, and near-water habitats [11]. “Light Cover” taxa are those which frequent light bush, tall grass, and hilly areas [11]. “Open” taxa (the “plains” category in [11]) are those which frequent edge or ecotone, open country, and arid country [11]. This habitat grouping scheme is an arbitrary division of a continuous range, as any such scheme must be [11]. Furthermore, many bovid taxa range over several habitat types, and so the assignment of a taxon to a particular category is a “best fit” designation rather than an exclusive one.

3.3. Statistical analysis

We used the phalanx measurements and habitat preference information for a large sample of modern bovids to determine the degree to which habitat could be predicted from the measurements. Using the statistics program JMP (version 5.0 for the Macintosh, SAS Institute, Cary, NC) three discriminant functions were constructed to predict habitat preference from measurements of proximal, intermediate, and distal phalanges. Note that three separate discriminant functions are involved, derived from three separate data sets (proximal phalanx, intermediate phalanx, distal phalanx), so that

no associations between phalanges are needed to use these methods.

With those discriminant functions as a starting point, we carried out a variety of analyses to evaluate their accuracy and sensitivity to various factors. Each of the following analyses was done in turn for the proximal, intermediate, and distal phalanx data sets.

We examined the pattern of misclassifications from the original discriminant functions to establish the types of errors made. The original discriminant functions were generated from the raw measurements, so we examined the effect of using log-transformed data as the “inputs” for the discriminant functions. To investigate the distribution of the data, we examined plots of the various principal components, as well as the canonical variates. In order to further evaluate the morphometric differences between the habitat groups, we examined univariate and bivariate plots. We also derived regression equations to predict body weight from each element and developed discriminant functions to predict subsfamily and tribal membership.

We carried out a variety of analyses to evaluate the influence of body weight on the discriminant functions. In doing so, we used mixed-sex body weight means calculated from the ranges given in Kingdon [12]. We realize that the cautions of Smith and Jungers [20] regarding the source of body weight data apply here, and that substantial sexual dimorphism in some taxa makes mixed-sex means broad approximations, but only a general indication of body weight is necessary for our purposes. First, we compared the predicted body weights (from the regression equation) with the predicted habitat categories to assess the degree of co-variation between those predictions. Second, we constructed discriminant functions to predict habitat category from the principal components and compared those results to similar functions lacking the first principal component (demonstrably reflective of size and size-related shape). Finally, we examined the coefficients of the variables in the original discriminant function to evaluate their relative influence on the results.

The discriminant functions depend on the underlying data, rendering them potentially sensitive to characteristics of the sample used. We evaluated the sensitivity of the functions to sample composition in a variety of ways. First, we artificially equalized the number of specimens per species used in the sample and compared the results with the original discriminant functions. Second, we removed one species at a time from the analysis to evaluate the effects of taxon inclusion/exclusion. Finally, we withheld one specimen per species, as well as random sets of multiple specimens, to estimate the accuracy of the functions when applied to specimens not used in their generation. Discriminant functions are designed to emphasize the differences

Table 3
Summary statistics for the phalanx measurements by habitat group

Metric	Habitat group	Mean (mm)	Standard deviation	Range (mm)
PP-LM	Forest	36.6	11.4	14.4–55.9
	Heavy Cover	56.3	7.5	41.2–74.0
	Light Cover	43.3	8.6	24.0–56.7
	Open	55.0	10.5	31.2–74.0
PP-WP	Forest	10.8	3.2	4.0–14.7
	Heavy Cover	18.4	3.2	12.5–24.0
	Light Cover	11.7	2.5	7.1–16.0
	Open	18.5	5.8	8.9–31.4
PP-WI	Forest	9.5	2.7	3.6–12.9
	Heavy Cover	16.9	3.5	10.4–23.5
	Light Cover	9.4	2.1	5.5–13.4
	Open	15.2	5.6	6.4–29.0
PP-WD	Forest	10.0	2.9	3.8–13.8
	Heavy Cover	17.9	3.6	10.7–23.5
	Light Cover	10.9	2.5	6.4–15.2
	Open	17.2	5.9	7.5–30.9
PP-HP	Forest	15.7	4.6	6.0–22.4
	Heavy Cover	25.2	4.4	16.9–33.5
	Light Cover	16.2	3.7	8.8–22.0
	Open	23.0	6.5	11.9–37.6
PP-HI	Forest	11.7	3.5	4.1–17.2
	Heavy Cover	19.8	3.4	12.8–25.3
	Light Cover	11.7	2.3	6.8–16.5
	Open	17.7	5.6	8.8–31.2
PP-HD	Forest	9.0	2.7	3.3–13.0
	Heavy Cover	14.7	2.6	10.5–19.5
	Light Cover	9.7	1.7	6.0–11.7
	Open	14.0	3.7	7.2–23.1
IP-LS	Forest	23.9	6.6	11.5–32.6
	Heavy Cover	36.8	4.8	25.2–46.4
	Light Cover	26.4	5.1	17.4–34.8
	Open	33.7	7.6	19.7–48.2
IP-LI	Forest	22.8	6.2	11.5–31.4
	Heavy Cover	35.1	4.5	24.3–43.7
	Light Cover	24.9	4.6	17.0–33.6
	Open	31.8	7.2	18.7–46.9
IP-WP	Forest	10.1	3.1	4.1–15.1
	Heavy Cover	18.3	3.4	12.3–23.7
	Light Cover	10.5	2.3	6.6–14.9
	Open	16.9	5.9	8.0–30.4
IP-WD	Forest	8.2	2.6	3.1–11.9
	Heavy Cover	14.9	2.9	10.1–20.8
	Light Cover	9.1	1.8	5.9–13.2
	Open	15.2	4.9	7.0–26.0
IP-HL	Forest	11.4	3.7	4.0–16.4
	Heavy Cover	19.2	3.1	13.9–25.9
	Light Cover	12.4	2.6	8.3–16.2
	Open	17.6	5.6	9.4–29.9
IP-HM	Forest	9.7	3.2	3.6–15.6
	Heavy Cover	16.0	2.9	11.0–21.6
	Light Cover	10.3	2.3	6.6–14.3
	Open	14.6	4.4	6.6–25.3
IP-HD	Forest	9.4	3.1	3.4–14.7
	Heavy Cover	17.2	3.0	12.1–23.4
	Light Cover	9.9	2.2	6.3–13.5
	Open	15.5	6.0	7.3–31.3

Table 3 (continued)

Metric	Habitat group	Mean (mm)	Standard deviation	Range (mm)
DP-LS	Forest	23.0	6.0	10.8–28.8
	Heavy Cover	46.4	8.2	29.4–63.6
	Light Cover	29.2	5.9	18.1–40.2
	Open	41.4	11.6	18.7–65.5
DP-LI	Forest	25.7	7.0	11.6–32.6
	Heavy Cover	52.3	8.6	34.8–69.4
	Light Cover	33.0	6.6	19.8–45.5
	Open	46.3	12.8	21.2–72.3
DP-HA	Forest	8.8	2.6	4.4–12.3
	Heavy Cover	17.1	3.0	12.8–22.9
	Light Cover	11.8	1.7	8.1–14.2
	Open	15.8	4.6	8.3–27.5
DP-HT	Forest	13.7	4.7	5.4–18.5
	Heavy Cover	30.2	5.4	21.3–40.2
	Light Cover	22.5	3.5	14.6–26.6
	Open	31.6	9.7	16.3–51.4
DP-WB	Forest	7.7	2.6	3.2–10.9
	Heavy Cover	13.8	2.9	8.9–19.1
	Light Cover	9.4	1.6	5.8–12.5
	Open	14.7	4.2	6.8–22.2

between pre-determined categories [21], and so may be able to classify specimens with some accuracy even if the categories have no biological reality. To establish an empirical baseline of accuracy, we used a variety of clearly incorrect habitat assignments for our sample, and assessed the accuracy of the resulting discriminant functions in predicting the “wrong” habitats.

The predictions from a given discriminant function have differing probabilities of being correct, depending (in part) on the probability associated with the specific prediction. For each discriminant function, we identified a “threshold” probability (confidence value) such that specific predictions with a confidence value above that threshold have less than 5% error rate (equivalent to $p < 0.05$). This allows statistically significant predictions to be distinguished from those of more questionable reliability.

The results of these analyses, taken as a whole, provide insight on the reliability and sensitivity of the discriminant functions. The rationale for these explorations of the data is discussed further in DeGusta and Vrba [2]. We strongly urge others utilizing discriminant functions for habitat prediction (or related purposes) to carry out similar analyses.

4. Results

Three separate discriminant functions were generated which predict habitat preference group from measurements of, respectively, the proximal, intermediate, and distal phalanx of bovids. The functions themselves are

given in Appendix A. The JMP files with the discriminant functions, along with instructions on their use and all raw data (measurements), are available for download at <http://www.stanford.edu/~degusta>. Summary statistics for the measurements used are given in Table 3. The specific mistakes made by each discriminant function are detailed by taxon in Table 4 and by habitat group in Table 5.

The data set of modern bovid phalanx measurements can also be used to predict taxonomic affiliations, though that is not the focus of the current study. Using the taxonomy of Gentry [6] and the same set of phalanx measurements as described above, we were able to predict subfamily at 60–73% accuracy and tribe at 73–76% accuracy from measurements of each of the phalanges.

These “taxonomic” discriminant functions (available at <http://www.stanford.edu/~degusta>) may provide some additional insight into the nature of a fossil bovid assemblage, particularly if combined with predictions of body weight and habitat preference. The ability to predict taxonomic affiliation does not contradict the use of these measurements to predict function/habitat, since different discriminant functions are used to disentangle the co-existing influences of phylogeny and function.

4.1. Accuracy

The proximal phalanx discriminant function correctly predicted habitat group for 130 out of 183 bovids, for an overall accuracy of 71.0%. The intermediate phalanx

Table 4
Discriminant function habitat classifications by taxa

Species	Habitat group	Proximal phalanx		Intermediate phalanx		Distal phalanx	
		# Correctly classified	Misclassifications ^a	# Correctly classified	Misclassifications ^a	# Correctly classified	Misclassifications ^a
<i>Addax nasamaculatus</i>	Open	4		4		4	
<i>Aepyceros melampus</i>	Light Cover	10		7	2F	7	
<i>Alcelaphus buselaphus</i>	Open	8	2H	7		6	1H
<i>Antidorcas marsupialis</i>	Open	0	7L	3	4L	0	6L
<i>Cephalophus niger</i>	Forest	1		1		1	
<i>Cephalophus nigrifrons</i>	Forest	2		3		3	
<i>Cephalophus sylvicultor</i>	Forest	5		0	4L, 1H	4	
<i>Connochaetes gnou</i>	Open	1		1		1	
<i>Connochaetes taurinus</i>	Open	7		6		4	1H
<i>Damaliscus dorcas</i>	Open	6		5	1L	1	2L
<i>Damaliscus hunteri</i>	Open	2		1		—	
<i>Damaliscus lunatus</i>	Open	4		4		2	1H
<i>Gazella granti</i>	Open	4	3L	5	2L	0	5L
<i>Gazella thomsoni</i>	Open	0	3F, 1L	1	1F, 1L	0	2L
<i>Hippotragus niger</i>	Open	5		4		3	
<i>Kobus ellipsiprymnus</i>	Heavy Cover	1	3O, 1L	2	2O	0	4O
<i>Kobus kob</i>	Light Cover	2	1F, 1H	2	1O	0	3O
<i>Kobus megaceros</i>	Heavy Cover	0	3O, 2L	1	3L	3	1L
<i>Kobus vardonii</i>	Light Cover	1	1F	0	1H	1	
<i>Litocranius walleri</i>	Open	0	3L, 1F	0	3L	0	1L
<i>Madoqua kirki</i>	Forest	1		0	1L	—	
<i>Neotragus batesi</i>	Forest	2		2		2	
<i>Oryx dammah</i>	Open	2	1H	3		2	1H
<i>Oryx gazella</i>	Open	2	2H	4		3	
<i>Ourebia ourebia</i>	Light Cover	5	3F	4	3F, 1O	—	
<i>Raphicerus campestris</i>	Light Cover	0	2F	0	1F	0	1F
<i>Redunca arundinum</i>	Light Cover	4		4		1	1H
<i>Redunca fulvorufula</i>	Light Cover	6	1F	3	3F, 1O	4	
<i>Redunca redunca</i>	Light Cover	2		2		2	
<i>Taurotragus oryx</i>	Open	7	4H	7	4H	9	1H
<i>Tragelaphus angasi</i>	Forest	0	2H, 1L	1		—	
<i>Tragelaphus buxtoni</i>	Heavy Cover	3	1O	3		0	1O
<i>Tragelaphus euryceros</i>	Heavy Cover	7	1O	5	3O	6	
<i>Tragelaphus imberbis</i>	Heavy Cover	4		0	3F, 1L	1	3L
<i>Tragelaphus scriptus</i>	Forest	8	2L	6	1L	3	
<i>Tragelaphus spekei</i>	Heavy Cover	5	1O	6		6	
<i>Tragelaphus strepiceros</i>	Heavy Cover	9		8		8	

^a This column lists the specimens of those taxon that were misclassified, broken down by the habitat group (abbreviated using the initial letter of the group) that they were mistakenly assigned to by the discriminant function.

Table 5
Discriminant function habitat classifications by actual habitat type

Actual habitat	Classified as				Accuracy (actual) (%) ^b
	Forest	Heavy Cover	Light Cover	Open	
Proximal phalanx					
Forest	19	2	3	0	76.0
Heavy Cover	0	29	3	9	70.7
Light Cover	8	1	30	0	76.9
Open	4	9	14	52	65.8
Accuracy (pred) (%) ^a	61.3	73.2	60.0	85.3	71.0
Intermediate phalanx					
Forest	13	1	6	0	65.0
Heavy Cover	3	25	4	5	67.6
Light Cover	9	1	22	3	62.9
Open	1	4	11	55	77.5
Accuracy (pred) (%) ^a	50.0	80.6	51.2	87.3	70.6
Distal phalanx					
Forest	13	0	0	0	100
Heavy Cover	0	24	4	5	72.7
Light Cover	1	1	15	3	75.0
Open	0	5	16	35	62.5
Accuracy (pred) (%) ^a	92.9	80.0	42.9	81.4	71.3

^a “Accuracy (pred)” reports the accuracy of the classification by the predicted habitat groups. In other words, of those specimens predicted to belong to a particular habitat group, what percentages actually do.

^b “Accuracy (actual)” reports the accuracy of the classification by the actual habitat groups. In other words, of those specimens actually belonging to a particular habitat group, what percentages were properly classified.

discriminant function correctly predicted habitat group for 115 out of 163 bovids, for an overall accuracy of 70.6%. The distal phalanx discriminant function correctly predicted habitat group for 87 out of 122 bovids, for an overall accuracy of 71.3%. All three functions have an accuracy 2.8 times greater than chance alone ($p < 0.0001$ using Fisher’s exact test).

These “resubstitution” accuracies are only estimates of the likely ability of the functions to classify specimens not included in the sample used to generate the functions [2]. We therefore estimated the accuracy of the functions in a variety of other ways, as detailed in Section 3, and these estimates are reported in Table 6. In general, they confirm that the accuracy of the functions is in the vicinity of 70%, whereas the theoretical accuracy of a random function is 25% (with four habitat groups), and actual “random” functions (using intentionally incorrect habitat groupings) have accuracies in the range of 40–50%. The threshold confidence values which yield a misclassification rate of <5% are reported in Table 7. Specific predictions with higher confidence values than the reported thresholds can be thought of as statistically significant, assuming an α of 0.05. We do not suggest that specific predictions which fall short of statistical significance be ignored, just that they should be accorded less weight.

Table 6
Estimates of the accuracy of habitat classification

Element	Test	Accuracy
Proximal phalanx	Resubstitution	71% (130/183)
	Taxon balancing ^a	73% (270/370)
	Specimen jackknife ^b	73% (27/37)
	Species jackknife ^c	57% (102/181)
	Random jackknife ^d	64% (29/45)
	PCA ^e	71% (130/183)
Intermediate phalanx	PCA less PC1 ^f	63% (115/183)
	Resubstitution	71% (115/163)
	Taxon balancing ^a	73% (270/370)
	Specimen jackknife ^b	70% (26/37)
	Species jackknife ^c	52% (84/163)
	Random jackknife ^d	68% (28/41)
Distal phalanx	PCA ^e	71% (115/163)
	PCA less PC1 ^f	62% (101/163)
	Resubstitution	71% (87/122)
	Taxon balancing ^a	70% (231/330)
	Specimen jackknife ^b	64% (21/33)
	Species jackknife ^c	59% (72/122)
	Random jackknife ^d	74% (23/31)
	PCA ^e	71% (87/122)
	PCA less PC1 ^f	65% (79/122)

^a Equal numbers of specimens per species.

^b One specimen held out per species, in turn.

^c Each species held out in turn.

^d Random 25% of specimens held out.

^e Using principal components as source rather than individual metrics.

^f Using the principal components except the first component.

4.2. Morphotypes

While the discriminant functions assign phalanges to habitat groups in a statistical manner, it is also desirable to have a sense of the morphological differences that permit this sorting. The morphological differences between the phalanges of different habitat groups are best illustrated by a comparison of phalanx length (anterior–posterior), width (medial–lateral), and thickness (dorsal–ventral), as shown in Fig. 4. The overall pattern is of similarity between Forest and Light Cover taxa, on one hand, and Open and Heavy Cover taxa, on the other. In addition, the graphs show that *Taurotragus oryx* is an outlier, almost certainly due to its massive body weight. Similarly, *Tragelaphus spekei* has much longer phalanges than expected based on their width (and longer than expected based on its body weight). This is likely an adaptation for locomotion across the swampy terrain favored by *T. spekei*.

Table 7
Confidence value thresholds for significance

Phalanx	Cutoff (%)	Errors
Proximal	80	10/183 (5%)
Intermediate	75	7/163 (4%)
Distal	80	5/122 (4%)

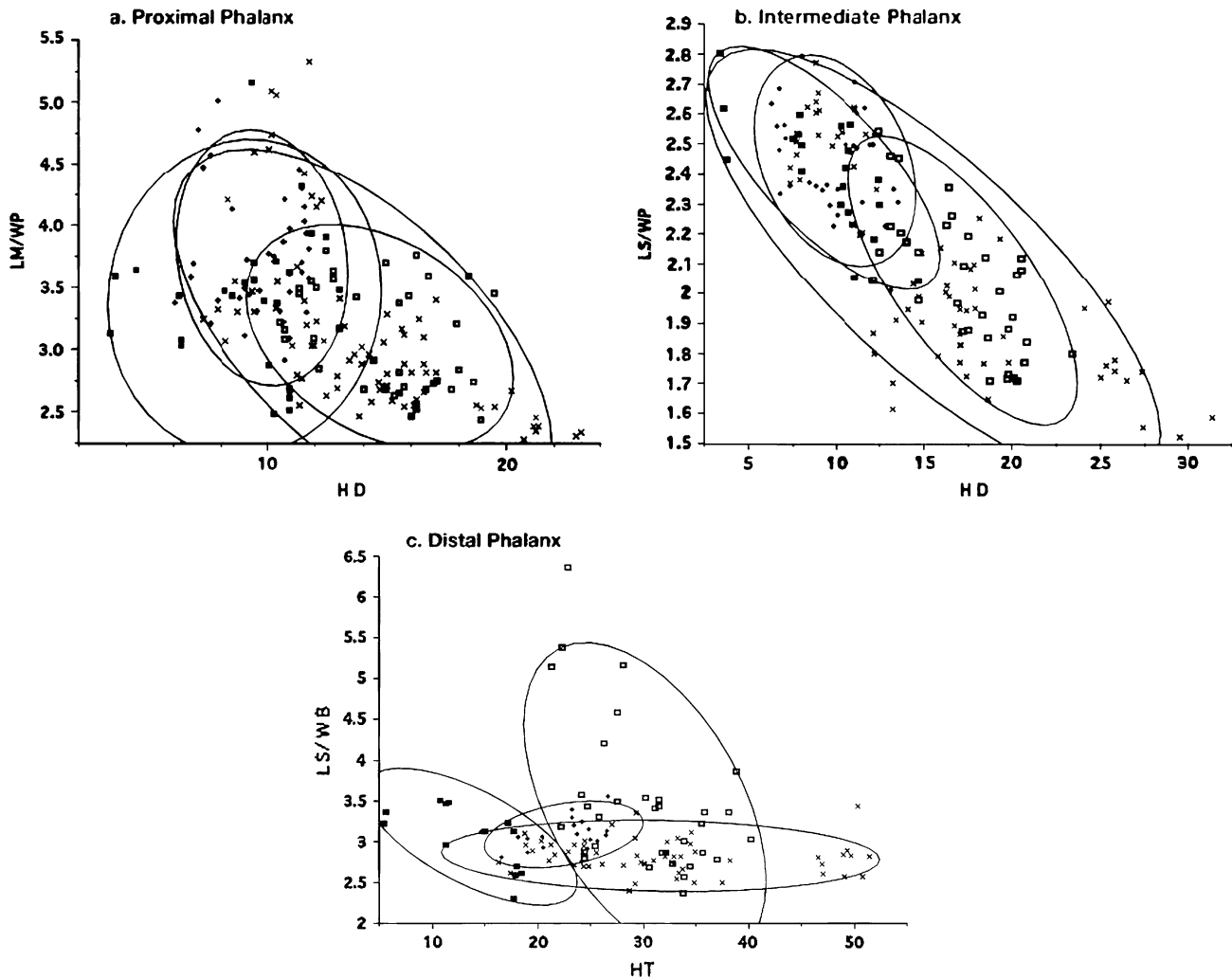


Fig. 4. Plots of phalangeal dimensions for the specimens in the modern African bovid sample. The actual habitat classifications for the specimens are denoted by symbols: closed boxes are Forest, open boxes are Heavy Cover, +s are Light Cover, and x's are Open. The ellipses represent 90% of each habitat group's distribution. (a) Proximal phalanx, LM/WP versus HD, in mm. (b) Intermediate phalanx, LS/WP versus HD, in mm. (c) Distal phalanx, LS/WB versus HT, in mm. See Section 3 for measurement abbreviations.

In general, Forest and Light Cover taxa have phalanges that are long relative to their width, whereas Open and Heavy Cover taxa have shorter phalanges relative to width. Open and Heavy Cover taxa, typically, have phalanges with greater dorsal–ventral height than those of Forest and Light Cover taxa. It is tempting to assert specific functional correlates of these differences, but rigorous analysis of the biomechanics involved is preferable to such speculation.

4.3. Body weight

Body weight is a potential complicating factor in analyses of this type. As described in Section 3, we carried out a variety of analyses to evaluate the influence of body weight on the results obtained.

Multiple regression (least squares) of the natural log of body weight against the three separate sets of phalanx

measurements demonstrates a strong correlation between these variables and body weight (adjusted R^2 of 0.89–0.91). The regression equations are provided in Appendix A since they can be used, with caution, to estimate the body weight of fossil bovids, which may be of interest [16–18].

A comparison of predicted body weights (from the regression equation) with the predicted habitat categories is given in Table 8, and shows that the two parameters vary independently [2]. A comparison of discriminant functions generated from the principal components with discriminant functions lacking the first principal component (demonstrably reflective of size and size-related shape) shows that approximately 6–9% of the discriminating power depends on size and size-related shape (Table 6). An examination of the coefficients of the variables in the original discriminant functions (see Appendix A) indicates that, for all three

Table 8
Predicted body weight ranges for predicted habitat groups

Predicted habitat group	Range of predicted body weights (kg)	Mean (kg)	SD
Proximal phalanx			
Forest	10–78	35	17
Heavy Cover	51–649	214	156
Light Cover	20–285	56	38
Open	47–979	211	199
Intermediate phalanx			
Forest	9–83	38	21
Heavy Cover	59–698	231	162
Light Cover	12–94	53	21
Open	23–795	193	168
Distal phalanx			
Forest	11–50	31	13
Heavy Cover	61–746	183	131
Light Cover	29–88	55	15
Open	67–826	261	212

functions, the most influential variable is a ratio, which is demonstrably independent of body size. These results provide clear evidence that size and body weight are not the primary determinants of the habitat predictions.

4.4. Sample issues

The predictions of the discriminant function are inevitably a result of the modern sample used to generate it. Several analyses, as described in Section 3, were carried out to investigate the sensitivity of the results to the taxonomic and specimen composition of our modern sample (Table 6). They indicate that the discriminant functions are, as expected, sensitive to the inclusion of a few particular species, but are otherwise robust. For example, artificially balancing the numbers of individuals in each species did not produce significant changes in the habitat predictions for any of the discriminant functions [2]. The specimens whose habitat predictions shifted were uniformly those with low confidence values, supporting the use of such values to assess the reliability of specific predictions.

5. Discussion

The accuracy of a discriminant function must be considered relative to the number of groups it is attempting to discriminate between—a random function will, on average, be 33% accurate for a three habitat category scheme (e.g., [14]), but only 25% accurate for a four-category habitat scheme (e.g., [11]). The standardized accuracies (resubstitution accuracy divided by number of habitat categories) of different discriminant functions for predicting habitat from bovid postcrania are given in Table 9.

Table 9
Accuracy of habitat predictions from bovid postcranial elements

Element	Portion	Accuracy ^a	Source
Femur	Complete	3.4×	[11]
Femur	Proximal	3.2×	[11]
Distal phalanx	Complete	2.8×	this study
Intermediate phalanx	Complete	2.8×	this study
Proximal phalanx	Complete	2.8×	this study
Astragalus	Complete	2.7×	[2]
Metatarsal	Complete	2.7×	[14]
Metacarpal	Complete	2.5×	[14]
Metatarsal	Distal	2.1×	[14]
Metacarpal	Distal	2.0×	[14]
Metatarsal	Proximal	1.9×	[14]
Metacarpal	Proximal	1.8×	[14]

^a Accuracy expressed relative to chance (times better than random function).

All three phalanx discriminant functions predict habitat category 2.8 times better than chance, which is superior to the accuracy of the various metapodial methods [14] and slightly better than the astragalus method [2]. The phalanx methods are not quite as accurate as Kappelman et al.'s [11] femur-based methods, but the frequent preservation of phalanges is a redeeming feature. In addition, the use of the confidence values to identify specific predictions which are statistically significant results in effective 95% accuracy for phalanx (and astragalus) predictions (Table 7), which is much greater than that currently obtainable for femora or metapodials. In addition, extensive manipulation and exploration of the data indicate that the phalanx and astragalus results are robust. Similar manipulations should be carried out on the raw data sets underlying the femoral [11] and, especially, metapodial [14] methods to evaluate their sensitivity to, for example, taxonomic composition and unequal sample sizes of included taxa.

The accuracy and broad applicability of habitat predictions based on measurements of bovid phalanges make these techniques a useful addition to similar methods which use other bovid elements. Even so, every method has its limitations, which include both the inherent limits of the approach and the limits of the particular implementation of that approach. Bovid “ecomorphology” is no exception in this regard. The inherent limitations include the difficulty of constructing a habitat grouping scheme that is both sufficiently precise and sufficiently accurate, especially since some bovid species use a range of habitat types. This approach also assumes that characters found to be indicative of habitat in modern bovids are similarly indicative of habitat in fossil bovids. This is likely to be a reasonable assumption, because modern bovids are taxonomically and geographically diverse, and because the mechanical principles which condition functional morphology do not change over time, but this is still an

assumption. As with any method, the less-than-100% accuracy is a limitation, though at least the accuracy of specific predictions is quantifiable in this approach. Finally, these methods represent only one approach to inferring paleohabitats. The most robust reconstructions of paleoenvironments are those which draw on multiple lines of evidence (geological, geochemical, paleobotanical, archaeological, “faunal list” approaches, etc.), so the results of “ecomorphological” studies should not be viewed in isolation.

In addition to these inherent limits, a more refined understanding of the functional anatomy of the bovid phalanges, as they relate to the biomechanics of locomotion, would likely provide deeper insight into the current results. Such biomechanical data would provide a direct test of the link between phalanx morphology and locomotion, strengthening the inferences made here. Unfortunately, such data are not currently available in the literature. In addition, while the statistical manipulation of taxa and specimens suggests that these results will be stable as the sample is expanded, the incorporation of additional specimens and species is needed in order to establish this conclusively. Furthermore, the overlap between Forest and Light Cover morphotypes, and between Open and Heavy Cover morphotypes, questions whether a simple “Closed” versus “Open” dichotomy is tenable. Finally, the applicability of these methods to non-African bovids is currently unknown.

6. Conclusion

The use of the functional morphology of bovid postcrania to infer paleohabitats has been shown to be a useful technique (e.g., [11]). The extension of this method to the phalanges should increase the value of this approach. With such methods now available for variety of elements (femora, metapodials, astragali, proximal phalanges, intermediate phalanges, and distal phalanges), habitat predictions can be based on larger sample sizes. Since predictions generated from different elements are independent, the analysis of different elements from a single fossil site should produce more reliable estimates of past environments. This in turn should improve our understanding of past environments, and the technological and biological evolution that occurred in them.

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Appendix A. Discriminant functions for habitat prediction

The following equations are the discriminant functions generated from the modern African bovid data using JMP (version 5.0 for the Macintosh, SAS Institute, Cary, NC). All calculations use the measurements reported in millimeters. For measurement abbreviations, see Section 3.

Proximal phalanx

$$\text{Probability of Forest Habitat} = \frac{e^{-0.5\text{DIST}[F]}}{\text{DIST}[Z]}$$

$$\text{Probability of Heavy Cover Habitat} = \frac{e^{-0.5\text{DIST}[H]}}{\text{DIST}[Z]}$$

$$\text{Probability of Light Cover Habitat} = \frac{e^{-0.5\text{DIST}[L]}}{\text{DIST}[Z]}$$

$$\text{Probability of Open Habitat} = \frac{e^{-0.5\text{DIST}[O]}}{\text{DIST}[Z]}$$

where

$$\begin{aligned} \text{DIST}[F] = & \text{DIST}[Z] + (13.0\text{LM}) + (-62.4\text{WP}) \\ & + (14.3\text{WI}) + (11.7\text{WD}) + (-7.2\text{HP}) \\ & + (-3.1\text{HI}) + (10.9\text{HD}) + \left[-210.7 \frac{\text{LM}}{\text{WP}} \right] + 358.3 \end{aligned}$$

$$\begin{aligned} \text{DIST}[H] = & \text{DIST}[Z] + (11.9\text{LM}) + (-59.6\text{WP}) \\ & + (13.6\text{WI}) + (11.1\text{WD}) + (-5.5\text{HP}) \\ & + (-4.3\text{HI}) + (9.9\text{HD}) + \left[-201.5 \frac{\text{LM}}{\text{WP}} \right] + 349.1 \end{aligned}$$

$$\begin{aligned} \text{DIST}[L] = & \text{DIST}[Z] + (12.9\text{LM}) + (-64.4\text{WP}) \\ & + (15.2\text{WI}) + (11.1\text{WD}) + (-6.4\text{HP}) \\ & + (-2.1\text{HI}) + (10.1\text{HD}) + \left[-215.7 \frac{\text{LM}}{\text{WP}} \right] + 382.8 \end{aligned}$$

$$\begin{aligned} \text{DIST}[O] = & \text{DIST}[Z] + (12.8\text{LM}) + (-67.1\text{WP}) \\ & + (15.6\text{WI}) + (12.6\text{WD}) + (-5.1\text{HP}) \\ & + (-2.6\text{HI}) + (9.3\text{HD}) + \left[-215.7 \frac{\text{LM}}{\text{WP}} \right] + 398.2 \end{aligned}$$

$$\begin{aligned} \text{DIST}[Z] = & e^{-0.5\text{DIST}[F]} + e^{-0.5\text{DIST}[H]} \\ & + e^{-0.5\text{DIST}[L]} + e^{-0.5\text{DIST}[O]} \end{aligned}$$

Intermediate phalanx

$$\text{Probability of Forest Habitat} = \frac{e^{-0.5\text{DIST}[F]}}{\text{DIST}[Z]}$$

$$\text{Probability of Heavy Cover Habitat} = \frac{e^{-0.5\text{DIST}[H]}}{\text{DIST}[Z]}$$

$$\text{Probability of Light Cover Habitat} = \frac{e^{-0.5\text{DIST}[L]}}{\text{DIST}[Z]}$$

$$\text{Probability of Open Habitat} = \frac{e^{-0.5\text{DIST}[O]}}{\text{DIST}[Z]}$$

where

$$\begin{aligned} \text{DIST}[F] = & \text{DIST}[Z] + (9.5\text{LS}) + (-16.4\text{LI}) + (36.4\text{WP}) \\ & + (128.3\text{WD}) + (-6.6\text{HL}) + (-0.2\text{HM}) \\ & + (-145.5\text{HD}) + \left[-2562.5 \frac{\text{WD}}{\text{HD}} \right] + 1223.8 \end{aligned}$$

$$\begin{aligned} \text{DIST}[H] = & \text{DIST}[Z] + (9.7\text{LS}) + (-17.4\text{LI}) + (36.3\text{WP}) \\ & + (130.8\text{WD}) + (-7.0\text{HL}) + (0.1\text{HM}) \\ & + (-147.6\text{HD}) + \left[-2607.0 \frac{\text{WD}}{\text{HD}} \right] + 1285.9 \end{aligned}$$

$$\begin{aligned} \text{DIST}[L] = & \text{DIST}[Z] + (8.3\text{LS}) + (-15.7\text{LI}) + (37.8\text{WP}) \\ & + (129.7\text{WD}) + (-6.9\text{HL}) + (-0.4\text{HM}) \\ & + (-147.9\text{HD}) + \left[-2606.3 \frac{\text{WD}}{\text{HD}} \right] + 1270.7 \end{aligned}$$

$$\begin{aligned} \text{DIST}[O] = & \text{DIST}[Z] + (9.2\text{LS}) + (-16.7\text{LI}) + (41.4\text{WP}) \\ & + (130.1\text{WD}) + (-6.9\text{HL}) + (0.5\text{HM}) \\ & + (-153.1\text{HD}) + \left[-2695.1 \frac{\text{WD}}{\text{HD}} \right] + 1366.1 \end{aligned}$$

$$\begin{aligned} \text{DIST}[Z] = & e^{-0.5\text{DIST}[F]} + e^{-0.5\text{DIST}[H]} \\ & + e^{-0.5\text{DIST}[L]} + e^{-0.5\text{DIST}[O]} \end{aligned}$$

Distal phalanx

$$\text{Probability of Forest Habitat} = \frac{e^{-0.5\text{DIST}[F]}}{\text{DIST}[Z]}$$

$$\text{Probability of Heavy Cover Habitat} = \frac{e^{-0.5\text{DIST}[H]}}{\text{DIST}[Z]}$$

$$\text{Probability of Light Cover Habitat} = \frac{e^{-0.5\text{DIST}[L]}}{\text{DIST}[Z]}$$

$$\text{Probability of Open Habitat} = \frac{e^{-0.5\text{DIST}[O]}}{\text{DIST}[Z]}$$

where

$$\begin{aligned} \text{DIST}[F] = & \text{DIST}[Z] + (34.7\text{LS}) + (-0.3\text{LI}) \\ & + (-6.0\text{HA}) + (0.4\text{HT}) \\ & + (-95.8\text{WB}) + \left[-401.9 \frac{\text{LS}}{\text{WB}} \right] + 614.7 \end{aligned}$$

$$\begin{aligned} \text{DIST}[H] = & \text{DIST}[Z] + (35.4\text{LS}) + (-2.1\text{LI}) \\ & + (-6.3\text{HA}) + (0.0\text{HT}) + (-92.4\text{WB}) \\ & + \left[-394.3 \frac{\text{LS}}{\text{WB}} \right] + 612.5 \end{aligned}$$

$$\begin{aligned} \text{DIST}[L] = & \text{DIST}[Z] + (35.0\text{LS}) + (-1.3\text{LI}) \\ & + (-4.4\text{HA}) + (-1.0\text{HT}) + (-92.4\text{WB}) \\ & + \left[-393.7 \frac{\text{LS}}{\text{WB}} \right] + 592.8 \end{aligned}$$

$$\begin{aligned} \text{DIST}[O] = & \text{DIST}[Z] + (34.7\text{LS}) + (-1.3\text{LI}) \\ & + (-3.5\text{HA}) + (-1.2\text{HT}) + (-93.6\text{WB}) \\ & + \left[-392.8 \frac{\text{LS}}{\text{WB}} \right] + 600.1 \end{aligned}$$

$$\begin{aligned} \text{DIST}[Z] = & e^{-0.5\text{DIST}[F]} + e^{-0.5\text{DIST}[H]} \\ & + e^{-0.5\text{DIST}[L]} + e^{-0.5\text{DIST}[O]} \end{aligned}$$

Regression equations for body weight prediction

All calculations use the measurements reported in millimeters. For measurement abbreviations, see Section 3.

Proximal phalanx

$$\begin{aligned} \ln \text{Body Weight (kg)} = & 1.450 + 0.012\text{LM} \\ & + 0.046\text{WP} - 0.004\text{WI} + 0.025\text{WD} \\ & + 0.067\text{HP} + 0.022\text{HI} - 0.032\text{HD} \end{aligned}$$

Intermediate phalanx

$$\begin{aligned} \ln \text{Body Weight (kg)} = & 1.224 + 0.102\text{LS} \\ & - 0.063\text{LI} + 0.012\text{WP} + 0.068\text{WD} \\ & + 0.038\text{HL} + 0.047\text{HM} - 0.028\text{HD} \end{aligned}$$

Distal phalanx

$$\begin{aligned} \ln \text{Body Weight (kg)} = & 1.790 - 0.031\text{LS} + 0.035\text{LI} \\ & + 0.022\text{HA} + 0.051\text{HT} + 0.059\text{WB} \end{aligned}$$

References

- [1] L.C. Bishop, Pigs and the Ancestors: Hominids, Suids, and Environments During the Plio–Pleistocene of East Africa, PhD dissertation, Yale University, 1994.
- [2] D. DeGusta, E.S. Vrba, A method for inferring paleohabitats from the functional morphology of bovid astragali, *Journal of Archaeological Science* 30 (2003) 1009–1022.
- [3] D. DeGusta, E.S. Vrba, Methods for inferring paleohabitats from discrete traits of the bovid postcranial skeleton, *Journal of Archaeological Science*, in press, doi:10.1016/j.jas.2005.02.011.
- [4] S. Elton, Locomotor and habitat classifications of cercopithecoid postcranial material from Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2, South Africa, *Palaeontologica Africana* 37 (2001) 115–126.
- [5] A.W. Gentry, The Bovidae (Mammalia) of the Fort Ternan fossil fauna, in: L.S.B. Leakey, R.J.G. Savage (Eds.), *Fossil Vertebrates of Africa*, vol. 2, Academic Press, London, 1970, pp. 243–323.
- [6] A.W. Gentry, The subfamilies and tribes of the family Bovidae, *Mammal Review* 22 (1992) 1–32.
- [7] H.A. Hespeneide, Ecological inferences from morphological data, *Annual Review of Ecology and Systematics* 4 (1973) 213–229.
- [8] J. Kappelman, The Paleocology and Chronology of the Middle Miocene Hominoids from the Chinji Formation of Pakistan, PhD dissertation, Harvard University, 1987.
- [9] J. Kappelman, Morphology and locomotor adaptations of the bovid femur in relation to habitat, *Journal of Morphology* 198 (1988) 119–130.
- [10] J. Kappelman, The paleoenvironment of *Kenyapithecus* at Fort Ternan, *Journal of Human Evolution* 20 (1991) 95–129.
- [11] J. Kappelman, T. Plummer, L. Bishop, A. Duncan, S. Appleton, Bovids as indicators of Plio–Pleistocene paleoenvironments in East Africa, *Journal of Human Evolution* 32 (1997) 229–256.
- [12] J. Kingdon, *East African Mammals*, Academic Press, London, 1982.
- [13] M. Köhler, Skeleton and habitat of recent and fossil Ruminants, *Münchner Geowissenschaftliche Abhandlungen* 25 (1993) 1–88.
- [14] T.W. Plummer, L.C. Bishop, Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains, *Journal of Human Evolution* 27 (1994) 147–175.
- [15] R. Potts, A.K. Behrensmeyer, P. Ditchfield, Paleolandscape variation and Early Pleistocene hominid activities: members 1 and 7, Olorgesailie Formation, Kenya, *Journal of Human Evolution* 37 (1999) 747–788.
- [16] K.M. Scott, Adaptation and Allometry in Bovid Postcranial Proportions, PhD dissertation, Yale University, 1979.
- [17] K.M. Scott, Allometric trends and locomotor adaptations in the Bovidae, *Bulletin of the American Museum of Natural History* 197 (1985) 197–288.
- [18] K.M. Scott, Postcranial dimensions of ungulates as predictors of body mass, in: J. Damuth, B.J. MacFadden (Eds.), *Body Size in Mammalian Paleobiology*, Cambridge University Press, Cambridge, 1990, pp. 301–335.
- [19] R.S. Scott, J. Kappelman, J. Kelley, The paleoenvironment of *Sivapithecus parvada*, *Journal of Human Evolution* 36 (1999) 245–274.
- [20] R.J. Smith, W.L. Jungers, Body mass in comparative primatology, *Journal of Human Evolution* 32 (1997) 523–559.
- [21] G.N. van Vaark, W. Schaafsma, Advances in the quantitative analysis of skeletal morphology, in: S.R. Saunders, M.A. Katzenberg (Eds.), *Skeletal Biology of Past Peoples: Research Methods*, Wiley Liss, New York, 1992, pp. 225–257.
- [22] E.S. Vrba, Ecological and adaptive changes associated with early hominid evolution, in: E. Delson (Ed.), *Ancestors: The Hard Evidence*, Alan R. Liss, New York, 1985, pp. 63–71.
- [23] E.S. Vrba, On the connections between paleoclimate and evolution, in: E.S. Vrba, G.H. Denton, T.C. Partridge, L.H. Buckle (Eds.), *Paleoclimate and Evolution with Emphasis on Human Origins*, Yale University Press, New Haven, 1995, pp. 24–48.