



Habitat preference of extant African bovids based on astragalus morphology: operationalizing ecomorphology for palaeoenvironmental reconstruction

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ABSTRACT

The habitat preferences of fauna found at palaeontological and archaeological sites can be used to investigate ancient environments and hominin habitat preferences. Here we present a discriminant function model linking astragalus morphology to four broadly defined habitat categories (open, light cover, heavy cover, and closed) using modern bovids of known ecology. Twenty-four measurements were taken on a sample of 286 astragali from 36 extant African antelope species. These measurements were used to generate ratios reflecting shape. An 11 variable discriminant function model was developed that had high classification success rates for complete astragali. Resubstitution analysis, jackknife analysis, and the classification of several “test samples” of specimens suggest that the predictive accuracy of this model is around 87%. The total classification success rates of 87% (jackknifed) or 93% (resubstitution) are considerably higher than those derived in another study of bovid astragalus ecomorphology (67%; [DeGusta, D., Vrba, E.S., 2003. A method for inferring palaeohabitats from the functional morphology of bovid astragali. *J. Archaeol. Sci.* 30, 1009–1022]) that used a more limited measurement scheme and a smaller sample of bovids than the present study. Different approaches to operationalizing ecomorphic analyses are considered in order to best extract accurate palaeoenvironmental information from palaeontological and archaeological datasets.

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1. Introduction

Palaeoenvironmental analysis is an essential part of palaeoanthropology, as human evolution is a result of the interaction between hominins and their abiotic and biotic surroundings. Detailed reconstructions of palaeohabitats based on palaeontological and geological evidence are necessary in order to understand the interplay between environmental change and hominin biological and behavioral evolution (deMenocal, 1995; Kingston, 2007; Plummer, 2004). However, for any particular palaeoanthropological locality, it is difficult to resolve what habitats were present, their relative proportions in a given place and time, and how these proportions may have changed over time.

Antelope (Mammalia: Bovidae) remains are often the most common fossils at hominin palaeontological and archaeological sites in Africa. Bovids span a large range of body sizes, have varied habitat preferences, and individual taxa often exhibit a degree of habitat specificity (Kappelman et al., 1997). Antelope astragali are

dense bones that are frequently preserved and easily recognisable due to their double pulley structure. Here we use discriminant function analysis (DFA) to relate astragalus morphometrics to habitat preference in modern bovids (see also DeGusta and Vrba, 2003). Based on this relationship we develop a mathematical model for predicting the habitat preference of extinct antelopes using measurements from their astragali.

The ecomorphological approach used here relies on links between morphology and environment rather than relying on taxonomic uniformitarianism. Whereas this relationship is defined using modern animals and their known habitat preferences, it depends on functional morphology rather than taxonomic relationships for its success. This contrasts with a taxonomic uniformitarian approach, where extinct animals are assigned ecological preferences largely on the basis of what their modern relatives do for a living. In reconstructing past environments it is important not to assume that the behavior and ecology of extinct taxa will always correspond to the behavior and ecology of their closest living relative (Plummer and Bishop, 1994; Sponheimer et al., 1999). Taxonomic uniformitarianism limits our ability to discover and understand the ways in which the past differs from the present, an important goal of palaeoenvironmental research.

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Further, understanding the palaeobiology of extinct mammals provides a framework for reconstructing the behavior and ecology of the hominins with which they lived.

2. What is ecomorphology?

Ecomorphology has been oversimplified as “functional morphology” in the recent zooarchaeological literature (DeGusta and Vrba, 2003, 2005), and so a brief description of ecomorphological research is warranted. Ecological morphology or ecomorphology provides one method of investigating the relationship between the phenotype of an organism and its environment (Van der Klaauw, 1948). Ecomorphology is an important field of research among organismal biologists studying extant and extinct vertebrates and invertebrates as well as plants (e.g., Aguirre et al., 2002; Arnold, 1983; Bock and von Wahlert, 1965; Garland and Losos, 1994; Hertel, 1994; Hertel and Ballance, 1999; Jones, 2003; Ricklefs and Miles, 1994; Van Valkenburgh, 1987; Wainwright, 1994; Wainwright and Bellwood, 2001; Wainwright and Reilly, 1994). Ecomorphic studies are implicitly about fitness and adaptation, with a central tenet being that organismal design provides limits on what an animal can and cannot do successfully. Phenotypic variation in a particular morphological, biochemical, or physiological trait will relate to Darwinian fitness in a population, if the trait in question is heritable and affects performance. Performance is the ability of individuals to perform ecologically relevant behaviors (e.g., acquire food, escape predation) on a daily basis. Thus, variation in traits within a population may relate to fitness, and variation in traits among populations and higher taxa may indicate adaptation to different lifestyles.

The investigation of the relationship between a phenotypic trait or trait complex and organismal performance is an important component of ecomorphic research (Aguirre et al., 2002; Brewer and Hertel, 2007; Sustaíta, 2008; Toro et al., 2004; Van Valkenburgh and Ruff, 1987). This investigation involves functional analysis to predict the consequences of morphological variation on the performance of the behaviors of interest. When feasible, these predictions can be tested with performance experiments in the laboratory or field (Wainwright, 1994). The performance-related aspects of organismal design impact ecology by constraining the resources that individuals can exploit (impacting niche partitioning) and by influencing individual fitness. Body size and oral aperture size of a suction-feeding reef fish, for example, provide discrete boundaries around what it might or might not be able to eat, providing important determinants of its potential feeding niche (Wainwright and Bellwood, 2001). The interaction of an individual with other members of its group, of populations within a species, and of species within a community all potentially influence population dynamics as well as community structure.

Ecomorphological studies are also useful in characterising and comparing fossil and modern communities (Damuth, 1992; Hertel, 1995; Ricklefs and Miles, 1994; Van Valkenburgh, 1988; Wainwright and Reilly, 1994). One approach is to make ecological inferences about species from their phenotypes (often morphology) and use this in investigating guild structure (Lewis, 1997; Werdelin and Lewis, 2001; Van Valkenburgh, 1985, 1988). For example, Hertel (1992, 1994) found that three basic feeding types and body size classes have evolved independently in the New and Old World vulture guilds, suggesting that competition has favored similar pathways of ecological separation. Analysis of community structure can be carried out using ecological diversity methods, where each species is reduced to a set of ecologically relevant variables (ecovariables), including diet (e.g., browser, grazer, frugivore), locomotor adaptation (e.g., terrestrial, arboreal) and body size (Fleming, 1973; Andrews et al., 1979; Reed, 1997). The frequency of ecovariables in different communities can be compared

as spectra, such as the relative frequency of different dietary ecovariables across a series of modern and fossil communities (Andrews et al., 1979; Fernandez-Jalvo et al., 1998). Alternatively, individual ecovariables, such as percentage of arboreal locomotion, can be compared across communities (Reed, 1997, 1998). Another approach is to classify species into ecological groups defined by their combination of diet, body size, and locomotor behavior and to use the absolute frequencies of these different ecological groups in different communities to construct a multidimensional eco-space. Distance in this eco-space measures ecological similarity, with more distant communities being more dissimilar to each other (Hertel and Lehman, 1998; Rodriguez, 2004; Rodriguez et al., 2006). In addition to comparing the structure of different communities, these approaches are useful for inferring the types and relative abundance of different habitats in a palaeocommunity. For example, mammalian body size distribution varies with environmental conditions and community structure, so that African montane forest communities have a very different body size distribution than woodland or bushland dominated communities (Andrews et al., 1979; Damuth, 1992). Functional morphology, then, should be viewed as a tool providing baseline information for many ecomorphological analyses, which often are concerned with higher order issues of community structure and palaeoenvironmental reconstruction.

In palaeoanthropology, ecomorphological analyses have frequently related specific morphologies in modern taxa to ecological parameters and, where strong correlations are demonstrated, have used these linkages to elucidate the ecology of fossil taxa exhibiting the same morphologies (Bishop, 1994; Bishop et al., 1999; DeGusta and Vrba, 2003, 2005; Kappelman, 1988, 1991; Kappelman et al., 1997; Lewis, 1997; Werdelin and Lewis, 2001; Plummer and Bishop, 1994; Spencer, 1997; Sponheimer et al., 1999). These analyses have often focused on reconstructing diet or habitat preferences of herbivores, and habitat preferences, prey size, stalking, and killing techniques for carnivores. For the African Bovidae, postcranial analyses have focused on reconstructing the habitat preferences of extinct taxa through study of their locomotor anatomy. Locomotor adaptation is intimately associated with ecology, as it is likely to reflect habitat structure, and is an important component of foraging and predator avoidance strategies. Kappelman (1988) found differences in the morphology of the femur in bovids from different habitats that he argued reflect differences in locomotor speed and frequency of direction change while running. These locomotor differences in turn are believed to relate to habitat-specific predator avoidance strategies and do not simply reflect the “...mechanical interaction between an organism and the physical substrates it moves across” as stated by DeGusta and Vrba (2003, p. 1009). Bovid from more open habitats escape predators by outrunning them, and exhibit features such as a cylindrical femoral head that enhance cursoriality and restrict limb movement to the parasagittal plane (Kappelman et al., 1997). Forest bovids are frequently territorial and tend to rely on crypsis and stealth to avoid predation. When they do flee from a predator they must move through structurally complex settings. The femora of forest bovids require more mobile hip joints to allow greater maneuverability when running amidst many low and medium-height obstacles (Kappelman, 1988). Bovid preferring habitats intermediate in structural complexity between forest and open country exhibit intermediate femoral morphologies. Whereas the morphological, functional, and ecological correlates among predator avoidance strategy, preferred habitat vegetative complexity, and postcranial morphology have been demonstrated best with the femur, our results on bovid humeri, radioulnae, tibiae, metapodials, calcanei, astragali, and phalanges are consistent with this framework (this study; Bishop et al., 2003, 2006; Plummer and Bishop, 1994; Plummer et al., 1999). Other researchers (DeGusta and Vrba, 2003, 2005; Kovarovic and

Andrews, 2007) have also noted a relationship between morphology and habitat preference in a variety of antelope postcranial elements.

3. Materials and methods

Here we analyse astragali from bovids living in four broadly defined habitat categories: open (grassland, arid country, ecotones bordering open country), light cover (light bush, tall grass), heavy cover (bush, woodland, densely vegetated swamp), and forest. These characterisations are based on the frameworks of Scott (1985), Kappelman (1986, 1988, 1991), and Kappelman et al. (1997) and represent a partitioning of the continuum of African habitat structure from those generally lacking trees and bush to those with a continuous tree canopy. Extant African antelopes were assigned to one of these four habitat preference categories based on modern behavioral observation of these taxa in the wild (Kappelman et al., 1997). As the term “preference” implies, these are not exclusive assignments and antelopes may be found in more than one of these categories during their lifetime. Alcelaphines (wildebeest and allies), for example, are bulk grazers that frequent grass-dominated habitats. Their predator avoidance strategy of vigilance and flight upon detection of a carnivore reflects their preference for open habitats (Jarman, 1974; Brashares et al., 2000). They sometimes move over long distances to acquire adequate forage (Jarman and Sinclair, 1979). However, most populations do not obtain enough water from their food, and will walk through other habitat types (e.g., riparian woodland) to reach water (Blumenschine, 1986; Estes, 1991). As discussed in Kappelman et al. (1997) and DeGusta and Vrba (2003), this categorisation retains environmentally relevant data within a simplified framework allowing statistical analysis and, as such, is a compromise between descriptive reality and analytical utility.

One of us (LCB) measured a sample of 286 astragali from 36 extant African antelope species from the collections of the American Museum of Natural History (New York, NY), the National Museum of Natural History (Washington, DC), and the Natural History Museum (London, UK) (Table 1). Error testing revealed no significant differences in the measurement scheme over time. Bovids weighing more than 250 kg (*Taurotragus* and *Syncerus*) were excluded to minimise differences in shape and size scaling that occur at the largest body masses (Scott, 1985), and because these genera may rely more on active defense than cursoriality or crypsis to avoid predation (Estes, 1991; Kappelman, 1988).

The taxonomic composition and habitat attributions of the bovid sample used here generally follow Kappelman et al. (1997) except that we included impala (*Aepyceros melampus*) in the light cover rather than the open habitat category. Impala are an edge (“ecotone”) species and mixed browsers/grazers that prefer open woodland bordering short to medium grassland (Dorst and Dandelot, 1970; Kingdon, 1997). Our inclusion of this taxon in the light cover category reflects their predilection to be near or utilise open woodland. The number of individuals measured per species ranged from 4 to 17 (median of 7). Measurements were taken on adult animals of both sexes. Wild-shot animals were measured when available; less than 5% of the individuals were zoo specimens, many of which had been wild-caught. Twenty-four measurements were taken on each astragalus (Fig. 1) and these were used to generate ratios reflecting shape. The set of measurements and ratios used in generating our discriminant function model is presented in Table 2. Summary statistics for the measurements and indices, by habitat group, are provided in Table 3.

Discriminant function analysis was used to test whether astragalus morphology could distinguish among bovids from different habitats (DeGusta and Vrba, 2003; Kappelman, 1986, 1988, 1991; Kovarovic and Andrews, 2007; Soulonias and Dawson-Saunders, 1988). DFA is a classification algorithm that classifies cases into

Table 1

Taxon list, sample size, and habitat preference category for specimens used in this analysis.

Subfamily	Tribe	Species	Sample size	Habitat
Bovinae				
	Tragelaphini	<i>Tragelaphus euryceros</i>	6	Heavy cover
		<i>Tragelaphus imberbis</i>	4	Heavy cover
		<i>Tragelaphus scriptus</i>	17	Forest
		<i>Tragelaphus spekei</i>	11	Heavy cover
		<i>Tragelaphus strepsiceros</i>	7	Heavy cover
	Cephalophini	<i>Cephalophus dorsalis</i>	5	Forest
		<i>Cephalophus leucogaster</i>	4	Forest
		<i>Cephalophus monticola</i>	4	Forest
		<i>Cephalophus natalensis</i>	4	Forest
		<i>Cephalophus nigrifrons</i>	4	Forest
		<i>Cephalophus silvicultor</i>	7	Forest
		<i>Cephalophus weynsi</i>	5	Forest
		<i>Sylvicapra grimmia</i>	17	Light Cover
Antilopinae				
	Neotragini	<i>Madoqua kirkii</i>	11	Heavy Cover
		<i>Neotragus moschatus</i>	4	Forest
		<i>Ourebia ourebia</i>	7	Light Cover
		<i>Raphicerus campestris</i>	5	Light Cover
	Antilopini	<i>Antidorcas marsupialis</i>	8	Open
		<i>Gazella granti</i>	10	Open
		<i>Gazella thomsoni</i>	8	Open
Hippotraginae				
	Reduncini	<i>Kobus ellipsiprymnus</i>	10	Heavy Cover
		<i>Kobus kob</i>	10	Light Cover
		<i>Kobus megaceros</i>	7	Heavy Cover
		<i>Redunca redunca</i>	10	Light Cover
		<i>Redunca arundinum</i>	7	Light Cover
		<i>Redunca fulvorufula</i>	8	Light Cover
	Hippotragini	<i>Addax nasomaculatus</i>	4	Open
		<i>Hippotragus equines</i>	4	Open
		<i>Hippotragus niger</i>	9	Open
		<i>Oryx gazella</i>	13	Open
Alcelaphinae				
	Aepycerotini	<i>Aepyceros melampus</i>	13	Light Cover
	Alcelaphini	<i>Alcelaphus buselaphus</i>	14	Open
		<i>Connochaetes gnou</i>	5	Open
		<i>Connochaetes taurinus</i>	6	Open
		<i>Damaliscus dorcas</i>	8	Open
		<i>Damaliscus lunatus</i>	10	Open

previously determined, naturally occurring groups (James, 1985). In this procedure, an equation (or function) is derived using the metrics and indices from the astragalus that best discriminate among habitat preference groups (hence the name discriminant function). Given the large number of measurements and ratios in this study, careful attention was paid to variable selection so that the most statistically robust model could be formulated. For the DFA, we used a stepwise procedure in SYSTAT v. 9.01 to assess the discriminatory power of different variable combinations. In addition to this procedure, we carried out extensive personal experimentation in both this study and a previous one (Plummer and Bishop, 1994). The variable list used here resulted from this experimentation. Significant differences were found among the within-group covariance matrices, so they were not pooled to calculate a linear discriminant function. Rather, a quadratic discriminant function was computed using the within-group covariance matrices (James, 1985; Reyment, 1991). Canonical

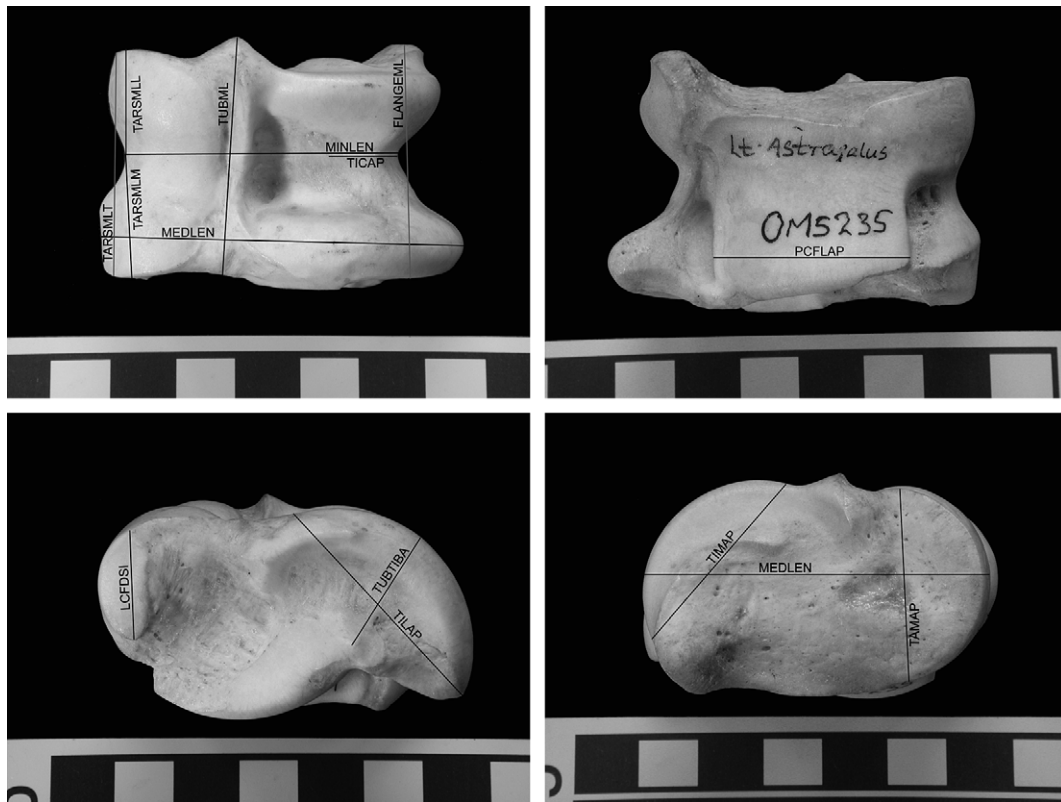


Fig. 1. Caliper measurements used in this study illustrated on bovid left astragalus. Clockwise, from upper left, anterior, posterior, lateral, and medial views. For description of measurements, see the text.

coefficients generated for each analysis indicated the relative contributions of different variables to the separation of the four habitat groups. Each observation was placed in the habitat category from which it had the smallest generalised squared (Mahalanobis) distance. The success of the generated model was indicated by multivariate statistics testing the significance of differences among group means, as well as by how well the discriminant function classified specimens of known habitat. Model accuracy was tested further using jackknife analysis. As a final test of predictive accuracy, we created two “test samples” of 36 specimens each that were withheld from analysis and treated as unknowns for classification by a function generated with the remaining specimens.

Table 2
Variables used in the analyses, illustrated in Fig. 1

Caliper measurements	Description
TARSMLT	Tarsal articulation M-L
TAMAP	Depth of medial portion of tarsal articulation
MINLEN	Minimum astragalus length
TUBTIBA	Tibial articulation to fibular tuberosity
Ratios	
LENRAT11	$FLANGEML/MEDLEN \times 100 =$ ML across flange of medial trochlea/medial length
LENRAT21	$TIMAP/MEDLEN \times 100 =$ length of tibial articulation, medial side/medial length
PCFRAT24	$PCFLAP/TUBML \times 100 =$ posterior calcaneal facet, lateral length/medio-lateral width at tuberosity
TICRAT2	$TICAP/TILAP \times 100 =$ tibial articulation, minimum length/tibial articulation, lateral length
SIRAT3	$LCFDSI/TUBTIBA \times 100 =$ distal lateral calcaneal facet, depth/tibial articulation to fibular tuberosity
TARAT5	$TARSMLM/TARSMLT \times 100 =$ tarsal articulation ML, medial side/tarsal articulation ML
TARAT9	$TARSMLM/TAMAP \times 100 =$ tarsal articulation ML, medial side/depth of medial portion of tarsal articulation

4. Results

4.1. DFA of modern astragali

The results of the complete astragalus discriminant function model are presented in Table 4. The classification algorithms for this model are available from the authors upon request. Three discriminant functions were calculated, accounting for 73.4%, 16.7% and 9.9% of the variance, respectively. The resubstitution classification success matrix (Table 4B) demonstrates that the function was effective at predicting habitat membership, with 265 of the 286 specimens being classified correctly (92.7%). Multivariate means of the different groups were significantly different ($p < 0.0001$) (Table 4C) demonstrating that the measurements and ratios used here can readily distinguish astragali from antelopes with different habitat preferences. Classification success was good across all four habitat groups, and for most species. *Kobus megaceros* had an anomalously high misclassification rate (42.9%) (Table 5). This species lives in floodplains, freshwater marshes, and swamps, which were classified here as “heavy cover” habitats. *Kobus megaceros* was also frequently misclassified into the light cover category by femoral discriminant function models, suggesting that this habitat category may be more appropriate for it (Kappelman et al., 1997). When specimens are analysed by a DFA model, they are assigned probabilities of their membership in one of the predetermined categories in question. These probabilities describe the likelihood that a particular specimen was drawn from a species preferring one of our four habitat classes. Of major importance is that almost all specimens were assigned to their preferred habitat with very high probabilities (mean probability for open = 97.6%, light cover = 92.5%, heavy cover = 94.5%, forest = 94.4%), lending further support to the model.

Table 3
Summary statistics of variables used in discriminant function model

	<i>n</i>	Mean	S.D.	Min	Max
TARSMILT					
Open	99	28.38	6.85	14.20	43.49
Light cover	77	19.12	4.17	12.53	27.45
Heavy cover	56	27.23	10.32	8.07	41.05
Forest	54	17.51	5.21	8.40	26.82
MINLEN					
Open	99	35.57	8.27	19.33	52.89
Light cover	77	26.47	5.62	17.34	37.37
Heavy cover	56	36.79	13.17	12.54	57.78
Forest	54	23.97	6.73	11.40	34.73
TUBTIBA					
Open	99	17.10	4.25	8.87	26.99
Light cover	77	11.52	2.50	6.93	16.96
Heavy cover	56	16.93	6.71	4.58	27.26
Forest	54	10.79	3.36	4.80	16.61
TAMAP					
Open	99	22.88	5.13	11.73	34.56
Light cover	77	15.30	3.64	9.66	22.56
Heavy cover	56	20.38	7.39	6.27	31.25
Forest	54	12.74	3.49	6.68	19.37
TARAT5 = (TARSMML/TARSMILT) × 100					
Open	99	46.24	2.27	40.09	50.78
Light cover	77	45.15	3.29	37.05	53.20
Heavy cover	56	45.69	3.08	37.96	52.74
Forest	54	44.70	3.18	37.85	51.37
TARAT9 = (TARSMML/TAMAP) × 100					
Open	99	57.14	3.68	48.40	66.59
Light cover	77	56.69	3.93	47.80	64.53
Heavy cover	56	60.31	6.34	46.62	72.65
Forest	54	61.00	4.65	50.30	76.12
TICRAT2 = (TICAP/TILAP) × 100					
Open	99	50.66	4.50	41.55	64.37
Light cover	77	53.61	4.55	41.30	61.39
Heavy cover	56	55.57	5.41	42.24	70.00
Forest	54	56.12	5.27	42.83	65.64
PCFRAT24 = (PCFLAP/TUBML) × 100					
Open	99	99.48	5.79	86.06	115.27
Light cover	77	100.28	5.22	88.59	109.64
Heavy cover	56	101.60	8.74	84.64	127.10
Forest	54	103.80	6.07	92.70	117.17
SIRAT3 = (LCFDSI/TUBTIBA) × 100					
Open	99	82.50	10.71	55.71	123.04
Light cover	77	92.39	13.51	70.62	134.92
Heavy cover	56	93.11	11.98	70.69	126.24
Forest	54	95.83	13.14	72.62	128.73
LENRAT11 = (FLANGML/MEDLEN) × 100					
Open	99	68.38	4.13	58.86	80.17
Light cover	77	64.00	2.98	56.62	71.37
Heavy cover	56	63.22	3.71	55.31	71.76
Forest	54	62.98	4.77	51.97	75.52
LENRAT21 = (TIMAP/MEDLEN) × 100					
Open	99	63.74	2.40	58.36	69.16
Light cover	77	59.96	2.41	52.34	64.87
Heavy cover	56	60.11	3.40	52.47	69.50
Forest	54	60.57	3.20	49.88	66.61

Kappelman et al. (1997) and DeGusta and Vrba (2003) noted that body mass was correlated somewhat with habitat structure, but was not driving the results of their respective discriminant function models. We found similar results in our model. Mean body masses for the taxa (sexes combined) in our four habitat categories are 133 kg for open, 39 kg for light cover, 136 kg for heavy cover, and 23 kg for forest. The fact that the classification success rates of the heavy cover taxa were similar to those of the light cover and forest taxa in both the resubstitution and jackknife analyses suggests that body mass is not the primary factor determining habitat assignment by the DFA. The relationship between mass and habitat assignment can be assessed

Table 4
Results of the astragalus discriminant function analysis

(A) Pooled within-class standardized canonical coefficients			
Canonical discriminant functions – standardized by within variances			
	1	2	3
TARSMILT	1.369	9.428*	1.073
MINLEN	−4.319*	0.037	3.591*
TUBTIBA	−0.741	0.824	−1.378
TAMAP	3.951*	−8.830*	−3.389*
LENRAT11	0.121	−0.158	0.107
LENRAT21	0.302	−0.183	−0.152
TARAT5	−0.030	2.049	1.305
TARAT9	−0.034	−2.435	−1.722
PCFRAT24	0.271	0.180	−0.660
TICRAT2	−0.114	0.125	−0.172
SIRAT3	−0.142	0.154	−0.210
% Variance	73.4	16.7	9.9

(B) Resubstitution classification results from quadratic discriminant function analysis (total correct = 92.7%)						
Classification matrix (cases in row categories classified into columns)						
Actual group	Number	Predicted group membership				Correct (%)
		Open	Light cover	Heavy cover	Forest	
Open	99	93	5	0	1	94
Light cover	77	1	70	3	3	91
Heavy cover	56	0	3	52	1	93
Forest	54	0	3	1	50	93

(C) Multivariate statistics testing hypothesis that class means are equal					
Statistic	Value	Approx. <i>F</i>	Num DF	Den DF	<i>Pr</i> > <i>F</i>
Wilks' lambda	0.124	25.009	33	802	<0.0001
Pillai's trace	1.371	20.975	33	822	<0.0001
Lawley–Hotelling trace	3.642	29.869	33	812	<0.0001

(D) Jackknifed classification results from quadratic discriminant function analysis (total correct = 87.1%)						
Actual group	Number	Predicted group membership				Correct (%)
		Open	Light cover	Heavy cover	Forest	
Open	99	91	5	2	1	92
Light cover	77	2	66	4	5	86
Heavy cover	56	3	4	47	2	84
Forest	54	0	5	4	45	83

Asterisks denote the highest values for each variable.

better using the data presented in Tables 3–6. We investigated the relationship between our variables and body size using femoral length as a proxy for body mass. Femoral length is strongly correlated with body mass for antelope of the size range investigated here (Scott, 1985). The log₁₀ transformed femoral length of bovids from our study sample was regressed on the log₁₀ transformed astragalus variables to test the degree of size dependence. The correlation coefficient and coefficient of determination between each variable and femoral length were calculated using SYSTAT v. 9.01 (Table 6). The four linear measurements used in the DFA model were strongly correlated with femoral length, whereas the ratios were not. The mean values of the linear measurements showed that the open and heavy cover samples, and light cover and forest samples, respectively, are similarly sized (Table 3). Yet as noted above, open country bovids are classified more accurately than heavy cover bovids, which have success rates similar to the light cover and forest samples. If body mass was driving habitat assignment, there should be a substantial amount of misclassification among categories with similarly sized animals, which is not the case (Table 4B).

4.2. Evaluating model success

The determination of model accuracy is a major concern in the use of DFA to study the palaeobiology of extinct species. If the

Table 5
Classification errors of discriminant function model

Taxon	Body mass	Habitat category	Number misclassified	Total sample	Percent misclassified (%)	Most likely reclassification
<i>Alcelaphus buselaphus</i>	155	Open	0	14	0.0	
<i>Damaliscus dorcas</i>	68	Open	0	8	0.0	
<i>Damaliscus lunatus</i>	136	Open	0	10	0.0	
<i>Connochaetes taurinus</i>	214	Open	0	6	0.0	
<i>Connochaetes gnou</i>	148	Open	0	5	0.0	
<i>Hippotragus niger</i>	228	Open	0	9	0.0	
<i>Addax nasomaculatus</i>	96	Open	1	4	25.0	Light cover
<i>Oryx gazella</i>	169	Open	0	13	0.0	
<i>Hippotragus equinus</i>	270	Open	0	4	0.0	
<i>Antidorcas marsupialis</i>	38	Open	1	8	12.5	Light cover
<i>Gazella thomsoni</i>	21	Open	2	8	25.0	Light cover, forest
<i>Gazella granti</i>	55	Open	2	10	20.0	Light cover
<i>Sylvicapra grimmia</i>	20	Light cover	3	17	17.6	Forest
<i>Aepyceros melampus</i>	53	Light cover	1	13	7.7	Open
<i>Ourebia ourebia</i>	17	Light cover	0	7	0.0	
<i>Raphicerus campestris</i>	11	Light cover	0	5	0.0	
<i>Kobus kob</i>	79	Light cover	2	10	20.0	Heavy cover
<i>Redunca redunca</i>	45	Light cover	1	10	10.0	Heavy cover
<i>Redunca arundinum</i>	58	Light cover	0	7	0.0	
<i>Redunca fulvorufula</i>	30	Light cover	0	8	0.0	
<i>Tragelaphus spekei</i>	78	Heavy cover	1	11	9.1	Forest
<i>Tragelaphus euryceros</i>	270	Heavy cover	0	6	0.0	
<i>Tragelaphus strepsiceros</i>	214	Heavy cover	0	7	0.0	
<i>Tragelaphus imberbis</i>	82	Heavy cover	0	4	0.0	
<i>Madoqua kirkii</i>	5	Heavy cover	0	11	0.0	
<i>Kobus ellipsiprymnus</i>	210	Heavy cover	0	10	0.0	
<i>Kobus megaceros</i>	90	Heavy cover	3	7	42.9	Light cover
<i>Tragelaphus scriptus</i>	43	Forest	1	17	5.9	Heavy cover
<i>Cephalophus natalensis</i>	13	Forest	0	4	0.0	
<i>Cephalophus leucogaster</i>	18	Forest	1	4	25.0	Light cover
<i>Cephalophus silvicultor</i>	63	Forest	0	7	0.0	
<i>Cephalophus monticola</i>	6	Forest	1	4	25.0	Light cover
<i>Cephalophus nigrifrons</i>	16	Forest	0	4	0.0	
<i>Cephalophus weynsi</i>	20	Forest	0	5	0.0	
<i>Cephalophus dorsalis</i>	22	Forest	0	5	0.0	
<i>Neotragus moschatus</i>	5	Forest	1	4	25.0	Light cover
Total misclassified			21	286	7.3	

Mixed sex body mass data from Kappelman et al. (1997) and Kingdon (1997).

explanatory power of a model developed with modern specimens is not high, its usefulness for assessing aspects of the ecology of extinct taxa will be limited. As noted by DeGusta and Vrba (2003), many studies using DFA to test the ability of skeletal metrics to predict bovid habitat preference or diet present a resubstitution analysis to assess model accuracy (e.g., Kappelman, 1991; Kappelman et al., 1997; Plummer and Bishop, 1994; Scott et al., 1999; Sponheimer et al., 1999). Resubstitution analysis tests the predictive accuracy of the function with the same data used to create it. In other words, the entire bovid sample was used to generate the discriminant function, and then the accuracy of this function was tested by using it to classify each specimen in the same dataset. Our

Table 6
The correlation coefficient (R) and the adjusted coefficient of determination (R^2) between the log of femoral length and the log of variables used in this study

Caliper measurements	R	Adjusted R^2	p
TARSM1T	0.980	0.961	9.9E-16
TAMAP	0.965	0.932	9.9E-16
MINLEN	0.987	0.974	9.9E-16
TUBTIBA	0.970	0.940	9.9E-16
Ratios			
LENRAT11	0.410	0.163	1.3E-08
LENRAT21	0.319	0.097	1.3E-05
PCFRAT24	0.446	0.194	4.5E-10
TICRAT2	0.294	0.082	6.6E-05
SIRAT3	0.374	0.135	2.7E-07
TARAT5	0.135	0.013	0.073
TARAT9	0.176	0.026	0.019

results for the resubstitution classification success matrix are summarised in Table 4B. More conservative measures of predictive accuracy test the discriminant function using specimens that were not used to generate it.

Here we provide two additional methods of testing the predictive accuracy of our model. The first is the classification success matrix generated using jackknife analysis (Table 4D). This matrix summarises the results of DFA in which each specimen in the sample was withheld from generating the discriminant function, and the resultant function was then used to predict the habitat preference of the “left out” specimen. The procedure was carried out 286 times (one for each specimen in the sample), and the summary of the function's predictive success is given in Table 4D. The overall accuracy of the model dropped from 92.7% to 87.1%, with the largest reductions being in the heavy cover and forest habitats. The model was still very accurate, with all classification success rates being 83% or higher. The open habitat category had the highest classification success rate in both models and only dropped 2% in accuracy from the resubstitution analysis to the jackknife analysis. This finding is theoretically consistent with the adaptive argument discussed above, in that the most marked morphological changes would be expected in the forms most reliant on cursoriality as a predator avoidance mechanism.

We also created “test samples” by removing one specimen per species ($n = 36$) to treat as unknowns to be classified with DFA using a function generated with the remaining 250 specimens (Table 7). This procedure was carried out twice (Test Sets 1 and 2) with different specimens being held out as unknowns. In each case

Table 7

Classification success rates and accuracy of predictions of held out specimens in Test Sets 1 and 2

Test Set 1: 250 specimens used to generate DFA model, 36 specimens (one per taxon) held out as unknowns				
Overall model success rate: 93.6% classified correctly in the resubstitution model, 86.0% classified correctly in the jackknifed model				
Held out specimens: 33 out of 36 classified correctly = 91.7%				
Species that missed	Actual habitat			Predicted habitat
<i>Tragelaphus imberbis</i>	Heavy cover			Open
<i>Antidorcas marsupialis</i>	Open			Light cover
<i>Gazella granti</i>	Open			Light cover
Actual and predicted habitat distributions of 36 unknown specimens				
	Open	Light cover	Heavy cover	Forest
Actual habitat representation	12 (33.3%)	8 (22.2%)	7 (19.4%)	9 (25.0%)
DFA habitat predictions	11 (30.6%)	10 (27.8%)	6 (16.7%)	9 (25.0%)
Difference	2.7%	5.6%	2.7%	0%
Test Set 2: 250 specimens used to generate DFA model, 36 specimens (one per taxon) held out as unknowns				
Overall model success rate: 93.2% classified correctly in the resubstitution model, 84.4% classified correctly in the jackknifed model				
Held out specimens: 34 out of 36 classified correctly = 94.4%				
Species that missed	Actual habitat			Predicted habitat
<i>Aepyceros melampus</i>	Light cover			Open
<i>Cephalophus natalensis</i>	Forest			Light cover
Actual and predicted habitat distributions of 36 unknown specimens				
	Open	Light cover	Heavy cover	Forest
Actual habitat representation	12 (33.3%)	8 (22.2%)	7 (19.4%)	9 (25.0%)
DFA habitat predictions	13 (36.1%)	8 (22.2%)	7 (19.4%)	8 (22.2%)
Difference	2.8%	0%	0%	2.8%

Thirty-six different specimens were used as unknowns in the two test sets.

a high frequency of the test specimens was classified correctly to habitat preference group (91.7% for Test Set 1 and 94.4% for Test Set 2). The species that were misclassified differed in each trial, suggesting that there is not a flaw in the classification of any particular taxon. For the overall sample, the resubstitution analysis, jackknife analysis, and use of test samples suggest that the predictive accuracy of this model is around 87% or perhaps a bit higher. The total classification success rates of 87.1% (jackknifed) or 92.7% (resubstitution) are considerably higher than that derived in another study of astragalus ecomorphology (67%; DeGusta and Vrba, 2003) using a more limited measurement scheme (nine measurements) and a smaller sample of bovids ($n=218$) than utilised here ($n=286$).

There are several different approaches to interpreting DFA output for ecomorphic analyses. The most common approach has been to derive a model with good predictive power and accept the DFA's habitat assignments for fossil specimens (Kappelman et al., 1997; complete metapodial models in Plummer and Bishop, 1994; Sponheimer et al., 1999). Effort is directed towards deriving models with high overall success rates (e.g., greater than 80%), so that there is a strong likelihood that fossil "unknowns" will be assigned

correctly to a habitat preference category. Concomitant with this approach is considering the probability with which each taxon is assigned to its preferred category. Probabilities of group assignment ranging around 50% or lower do not inspire much confidence even though it was classified correctly. As noted above, our model generated high correct classification (87%) with high probabilities of group assignment (>92%), providing an overall strong predictive model.

An alternative approach has recently been suggested, which uses the associated percentage probability (confidence value) of the habitat prediction of both the modern specimens used to create the DFA model as well as the fossil specimens under analysis (Table 8; DeGusta and Vrba, 2003, 2005). These probabilities represent the likelihood that a particular specimen belongs to each of the four habitat categories, and the habitat category with the highest probability is the predicted one. Their "confidence threshold" approach argues that all habitat predictions are not equal; specimens having high probability habitat predictions should be given the most weight in an analysis (DeGusta and Vrba, 2003). It was argued that this approach can yield a subset of fossil samples with a high chance (approximately 95%) of having a correct habitat preference

Table 8

Partial output from the resubstitution analysis of bovid astragali using our equivalents of DeGusta and Vrba's (2003) variables

Species	Known habitat	Predicted habitat	Probability (open)	Probability (light cover)	Probability (heavy cover)	Probability (forest)
<i>Alcelaphus buselaphus</i>	Open	Open	0.9640	0.0189	0.0120	0.0051
<i>Alcelaphus buselaphus</i>	Open	Open	0.9963	0.0010	0.0024	0.0003
<i>Gazella thomsoni</i>	Open	Light cover	0.2535	0.5953	0.0135	0.1377
<i>Gazella granti</i>	Open	Open	0.4059	0.2165	0.2252	0.1524
<i>Sylvicapra grimmia</i>	Light cover	Light cover	0.0212	0.5076	0.0343	0.4369
<i>Sylvicapra grimmia</i>	Light cover	Forest	0.0029	0.1842	0.0731	0.7399
<i>Tragelaphus strepsiceros</i>	Heavy cover	Heavy cover	0.0437	0.0609	0.8464	0.0491
<i>Tragelaphus imberbis</i>	Heavy cover	Heavy cover	0.0126	0.3116	0.5001	0.1756
<i>Cephalophus sylvicultor</i>	Forest	Forest	0.0037	0.0847	0.3760	0.5356
<i>Cephalophus sylvicultor</i>	Forest	Light cover	0.1842	0.4079	0.0973	0.3106

The known habitat is the preferred habitat of the species, whereas the predicted habitat is the habitat assigned by the DFA to each specimen. Three specimens have their erroneous habitat predictions in italics. The probabilities associating each specimen with each habitat category by the DFA are also provided. Only three specimens would pass a confidence threshold "filter" of 80% (probabilities in bold).

assignment, even from models that have relatively low (e.g., 65–70%) overall classification success rates. It is clear from their limited description of the approach that it leads to a winnowing of the data, particularly if specimens falling below the confidence threshold are considered “indeterminate to habitat.” The real question is whether the confidence obtained in the habitat predictions of a limited number of specimens offsets the data lost by disregarding or placing less weight on specimens falling below a particular confidence threshold. Moreover, can this approach obviate the need for developing DFA models with high overall success rates? If an analysis of habitat assignment probabilities yields equally useful results from models requiring few measurements and with modest overall success rates, it would greatly streamline data collection procedures. As these and other questions were not answered in the initial description of the methodology, we investigate the use of confidence thresholds further here.

4.3. The test model

DeGusta and Vrba (2003) generated a DFA for the bovid astragalus using eight linear measurements and a ratio. Our measurement scheme includes variables that are similar or identical to the variables used by them; therefore we used only our proxies of their variables with all our specimens to generate a DFA model for comparison. Interestingly, our overall success rate was similar to theirs, roughly 67% (Table 9). This allowed us to compare the results of simulated analyses of fossil samples using the confidence threshold method, coupled with a model with a modest overall success rate, to simply accepting at face value all habitat assignments produced by a model with a much higher overall success rate (our model described above). The first step in the confidence threshold method is to determine the probability value to be used

Table 9
DFA model using our dataset as proxies for DeGusta and Vrba's (2003) variables

(A) Our proxies for the variables used in DeGusta and Vrba (2003)						
Our caliper measurements	Description	Similar measure in DeGusta and Vrba (2003)				
MEDLEN	Medial length	LM				
LATLEN	Lateral length	LL				
TALAP	Tarsal articulation, depth of lateral portion	TD				
MAXSI	Maximum thickness	TI (approx.)				
TUBTIBA	Tibial articulation to fibular tuberosity	TP				
TARSMLT	Tarsal articulation, ML	WD				
MINLEN	Minimum astragalus length	LI				
TUBML	ML across tuberosity on dorsal surface, medial side	WI				
Ratios						
DVRAT	MINLEN/TUBML	LI/WI				
(B) Classification success matrices						
Classification success matrix from the resubstitution analysis (total correct = 68.5%)						
Actual group	Number	Predicted group membership				
		Open	Light cover	Heavy cover	Forest	Correct (%)
Open	99	76	12	10	1	77
Light cover	77	6	45	4	22	58
Heavy cover	56	5	4	35	12	63
Forest	54	2	7	5	40	74
Classification success matrix from the jackknife analysis (total correct = 64.7%)						
Actual group	Number	Predicted group membership				
		Open	Light cover	Heavy cover	Forest	Correct (%)
Open	99	75	13	10	1	76
Light cover	77	10	40	5	22	52
Heavy cover	56	7	5	31	13	55
Forest	54	2	8	5	39	72

Table 10
Specimens considered “indeterminate” using the confidence threshold approach

(A)					
Habitat	Number of specimens in analysis	Number of specimens considered indeterminate using 0.80 filter	Specimens considered indeterminate, by habitat (%)		
Open	99	48	48.5		
Light cover	77	73	94.8		
Heavy cover	56	42	75.0		
Forest	54	54	100.0		
(B)					
Habitat	Open	Light cover	Heavy cover	Forest	Total
Through filter (#)	53	2	12	2	69
Through filter (%)	76.8	2.9	17.4	2.9	100.0

(A) Number and percent of specimens in the confidence threshold test model considered indeterminate to habitat, using 80% as the probability threshold. Note that nearly all of the light cover and forest specimens are considered indeterminate. (B) Habitat distribution of the 69 specimens passing through the 80% probability filter. Note that most specimens are in the open habitat category, followed by heavy cover. These are the habitat categories that had the highest percentage of specimens passing through the 80% filter. The two individuals shown in the forest category are misclassified, light cover specimens.

as a cutoff point to minimise the misclassification rate to about 5% (Table 8). A probability threshold of 80% yields a misclassification rate of approximately 5.8%. In other words, all specimens with assigned habitat probabilities of less than 0.80 were considered to be “indeterminate to habitat” (Tables 8 and 10). According to DeGusta and Vrba (2003), these indeterminate specimens were included in the total number of specimens used to calculate the error rate rather than only those passing through the filter. We think this is somewhat misleading because including the indeterminate specimens inappropriately lowers the error rate. For example, if there were 100 specimens and only 30 passed through the filter, and six were classified incorrectly, then the error rate should be 6/30 or 17% rather than 6/100 or 6%. In reality the error rate is almost three times higher than suggested by their method.

Only 69 out of the 286 specimens used in this DFA had confidence values equal to or higher than 0.80. Sixty-five of these (94.2%) were classified correctly. Seventy-six percent (217 out of 286 individuals) had habitat probabilities less than 80%, and so were considered indeterminate. One hundred and thirty-one of these “indeterminate” specimens (60.4%) were actually correctly classified by the model, even though their probabilities fell below the threshold. So it is clear that a great deal of data is lost when using the confidence threshold-based method. Table 10 provides a breakdown of the number of specimens considered “indeterminate” by habitat, as well as the habitat distribution of the 69 specimens that passed through the 0.80 filter. What is notable here is that nearly all of the specimens in the light cover category and all of the forest specimens were considered indeterminate, and consequently very few of the specimens passing through the 0.80 filter were from these categories.

The ability of the confidence threshold approach to classify specimens of unknown habitat preference can be evaluated using our test samples. As described above, the test samples were constructed by drawing one specimen at random from each of the 36 species in our model. The procedure was carried out twice, forming two DFA models each with their associated test set of 36 individuals. Different individuals were held out for each test set, so they differed in composition. The test samples thus can be treated as unknowns, equivalent to 36 bones with unknown habitat affiliation recovered from a palaeontological or archaeological site. As shown in Table 11, the only specimens that passed through the confidence interval filter in the Test Set 1 sample were those preferring open habitats, even though specimens with the full range of habitat preferences were analysed. The Test Set 2 model correctly

Table 11

Results of the application of a confidence threshold of 80% to two test samples of 36 specimens each

Test Set 1: 250 specimens used to generate a DFA model with our proxies for the variables used by DeGusta and Vrba (2003). Thirty-six specimens were used as unknowns				
<i>Model success rate:</i> 66.4% classified correctly in the resubstitution model, 61% classified correctly in the jackknife model				
<i>Held out specimens:</i> 29 of 36 classified correctly = 80.6%				
Six specimens passed through 0.80 threshold. All were classified correctly, but were from only one habitat category (open)				
Actual habitat proportion representation of unknowns	Open 12 (33.3%)	Light cover 8 (22.2%)	Heavy cover 7 (19.4%)	Forest 9 (25.0%)
Habitat predictions using 80% threshold	6 (100%)	0	0	0
Difference (%)	66.6	22.2	19.4	25.0
Test Set 2: 250 specimens used to generate a DFA model with our proxies for the variables used by DeGusta and Vrba (2003). Thirty-six specimens were used as unknowns				
<i>Model success rate:</i> 68% classified correctly in the resubstitution model, 63% classified correctly in the jackknife model				
<i>Held out specimens:</i> 27 of 36 classified correctly = 75.0%				
Seven specimens passed through 0.80 threshold. All were classified correctly, but were from only two habitat categories (open, heavy cover)				
Actual habitat proportion representation of unknowns	Open 12 (33.3%)	Light cover 8 (22.2%)	Heavy cover 7 (19.4%)	Forest 9 (25.0%)
Habitat predictions using 80% threshold	4 (57.1%)	0	3 (42.9%)	0
Difference (%)	23.8	22.2	23.5	25.0

Note that only specimens from the open and, to a lesser degree, heavy cover categories passed through the confidence threshold filter.

classified specimens to both open and heavy cover, but none of the specimens from the light cover or forest habitat groups passed through the filter. In both test samples, the proportion representation of the predicted habitat preferences passing through the 0.80 filter deviated considerably from the actual habitat preferences of the test samples in question. So although the confidence threshold method can provide a subsample of specimens with a high probability of being classified correctly to habitat, bovids with different habitat preferences may not be equally likely to pass through the “filter.” This approach, when applied strictly, may distort the proportion representation of ecomorphs in an assemblage under analysis (Table 11).

This suggests that the consequences of confidence thresholds must be investigated fully before using them in the analysis of palaeontological or archaeological assemblages. Our simulated analysis of unknowns produced results that were biased against the light cover and forest habitat categories, even though the forest category had the second highest classification success rate (74%) in the resubstitution model (Table 9). Eliminating specimens with lower confidence of attribution may create more, rather than less, bias in the overall frequency of habitats represented. This has implications for using this method to reconstruct palaeohabitats, because some habitat categories (light cover and forest in this example) did not pass through the filter and so were not documented as being present.

In contrast to the confidence threshold method, the number of held out specimens classified correctly to habitat using our DFA model without a confidence threshold filter was much higher (Table 7). Moreover, comparison of the actual habitat preferences of the Test Sample 1 and 2 “unknowns” with those predicted by their respective DFA models shows that the proportion representation of the different ecomorphs in the held out samples was largely

retained. This suggests that when the goal of an ecomorphic analysis is both to have high confidence in habitat preference assignments as well as obtain information about the relative frequencies of different ecomorphs in a fossil or palaeontological assemblage, it is more prudent to use a model with a high success rate without a confidence threshold than a model with a modest overall success rate and a confidence threshold.

5. Functional interpretation

In their discussion of the morphological differences among astragali from different habitat groups, DeGusta and Vrba (2003, p. 1018) state that “It is tempting to assert specific functional correlates of these differences, but rigorous analysis of the biomechanics involved is preferable to such speculation.” Here we attempt to interpret our findings in the hope they will encourage future lines of inquiry. Fig. 2 presents notched box plots summarising the range of canonical scores for each habitat group. The first discriminant function accounts for 73.4% of sample dispersion (Table 4). As can be seen in Fig. 2, the open habitat morphotypes tend to have statistically significantly higher scores on function 1 than the samples from the other habitat groups. Two variables load heavily on function 1 (Table 4). MINLEN has a strongly negative loading whereas TAMAP has a strong positive loading. TAMAP indicates a wider distal condyle of the astragalus in the antero-posterior direction (Fig. 1). A wider arc gives a greater range of motion between two joints. The total velocity of a limb is the sum of the velocities at each movable joint, therefore increasing mobility at any given joint contributes to the overall speed of movement of the limb (Hildebrand and Goslow, 2001). This would be advantageous for animals living in more open habitats that rely on speed to outrun their predators.

Open habitat forms also have a shorter MINLEN. This variable suggests a more deeply notched astragalus in the proximo-distal direction, most notably in the proximal articulation with the tibia. A shorter MINLEN contributes to a deeper groove along the middle axis, which would form a more tightly interlocking joint and more restricted movement. Restricted lateral movements are found in more cursorial animals (Kappelman, 1988; Hildebrand and Goslow, 2001), which would be adaptive for open habitat dwellers.

The second discriminant function accounts for 16.7% of sample variance (Table 4). The heavy cover sample has statistically significantly higher scores on function 2 than the other three samples (Fig. 2). TARSMILT is loaded heavily on this axis. A greater TARSMILT suggests a wider base and more medio-lateral support for that articulation (Fig. 2). This would be advantageous in a more closed habitat that would select for greater emphasis on side to side movements (Kappelman, 1988; Hildebrand and Goslow, 2001). TAMAP is also loaded heavily on the axis but with a negative value (Table 4). In this case a narrower distal condyle was typical of heavy cover habitats, supporting the aforementioned interpretation. However, if this were true the same discrimination would be expected in the forest forms, which do not appear to differ from the more open habitat forms on this function. It may be that body size is important in this case, as the heavy cover forms are generally larger than the forest forms. Selection on greater support (a wider base) may be stronger for a larger body size and thus the smaller forest forms may tend to be more similar to less closed habitats.

The third discriminant function accounts for 9.9% of the sample variance. MINLEN has a strong positive loading on this function, whereas TAMAP has a strong negative loading. These were the same variables that loaded highly on the first discriminant function. Light cover bovids have statistically significantly higher scores than forest bovids with the open and heavy cover in between. This was supported by the first discriminant function except that in this case, the open habitat forms were more similar to the heavy cover

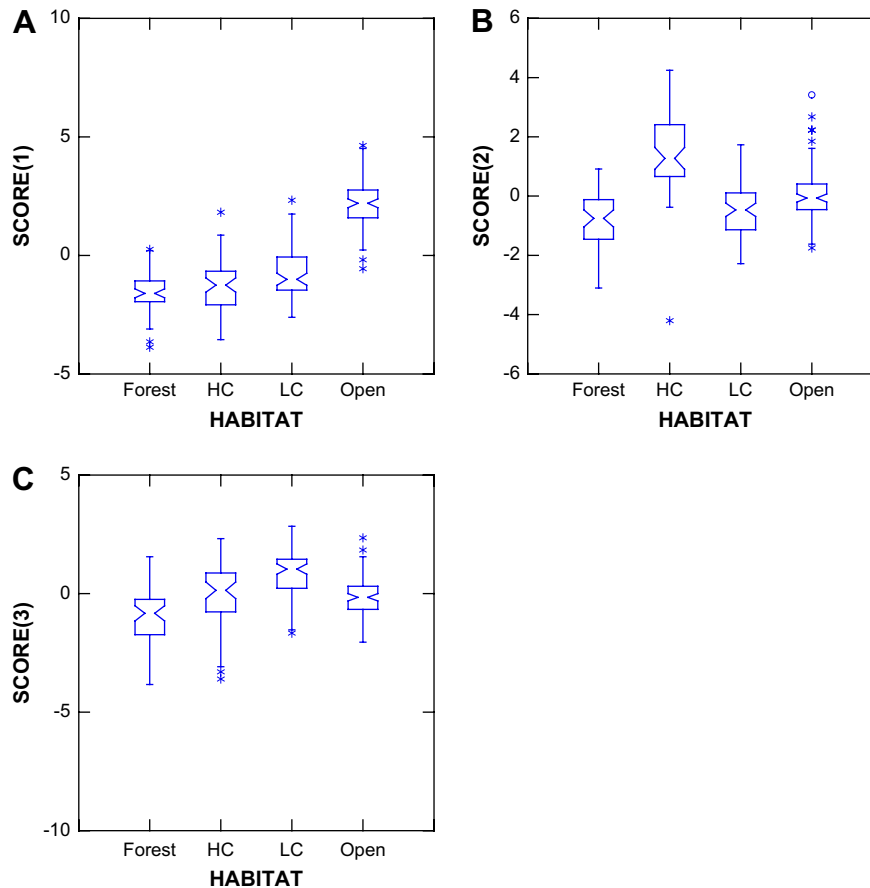


Fig. 2. Notched box plots summarising the range of canonical scores for each habitat group. The horizontal line at the point of constriction of each box represents the sample median. The upper and lower margins of the boxed areas are termed hinges. The median divides the sample distribution in halves, whereas the hinges split the halves into quarters. The outer confidence limits are encompassed by each box. If the boxed areas of two samples do not overlap, there is a high probability (95% or higher) that the samples in question were drawn from different populations.

(Fig. 2). Given this function only accounts for 9.9% of the variation, minor deviations from a “perfect” pattern are not surprising but the overall interpretations are consistent between the open/light cover groups and the heavy cover/forest groups.

6. Discussion

The use of cranial and postcranial ecomorphology to generate palaeoenvironmental information is becoming more common in palaeoanthropology (DeGusta and Vrba, 2003, 2005; Kovarovic and Andrews, 2007; Plummer and Bishop, 1994; Scott et al., 1999; Spencer, 1997).

Ecomorphological studies impart a greater value to fossils often not collected (e.g., limb fragments), which usually only need to be identified to taxonomic family. These underused specimens can be invaluable for palaeoecological analysis and can play a role in conceptualising past ecosystems. We have produced DFA models using the four habitat scheme provided here for complete and partial bovid humeri, radii, ulnae, tibiae, calcanei, astragali, and phalanges (Bishop et al., 2006; Plummer et al., 1999), as well as updated (with improved accuracy and using the four habitat scheme) metapodial models first described in Plummer and Bishop (1994). In combination with bovid femoral DFA models devised by Kappelman (e.g., Kappelman, 1988; Kappelman et al., 1997), suid postcranial DFA models developed by Bishop (Bishop, 1994; Bishop et al., 1999), bovid cranial and mandibular models for reconstructing dietary preferences (Spencer, 1997; Sponheimer et al., 1999), DFA models for bovid astragali and phalanges generated by DeGusta and Vrba (2003, 2005), and DFA models for a large number

of postcranial elements by Kovarovic and Andrews (2007), information on habitat structure as well as diet can likely be drawn from any reasonably large and well preserved fossil assemblage in the future. The development of DFA models using a broad array of bovid and suid skeletal elements will ultimately help mitigate the data lost by the differential destruction of particular elements or element portions by density-mediated processes, such as carnivore consumption (Faith and Behrensmeyer, 2006). As noted by Kovarovic and Andrews (2007), when analysing fossil assemblages, DFA models for different elements that differ significantly in accuracy should be assessed separately, to lessen the chance that specimens misclassified by the less accurate models drive palaeoenvironmental interpretation. Larger samples of fossils amenable to analysis will also allow more robust comparisons among different types of ecomorphic analysis, such as postcranial ecomorphology and ecomorphic assessments of community structure. It will allow more detailed comparisons among the gamut of ecomorphic approaches and other methods of palaeoenvironmental assessment, such as pollen analysis and stable isotopic analyses of pedogenic carbonates and enamel (Fernandez-Jalvo et al., 1998; Plummer and Bishop, 1994; Reed, 1997; Sponheimer et al., 1999).

As with any palaeoecological analysis, an assessment of the taphonomic history of a particular assemblage must be carried out in order to determine the biases that may have occurred in its formation (Andrews, 2006; Soligo and Andrews, 2005). Any systematic bias in an assemblage may alter the palaeoenvironmental signal. For example, in attritional assemblages formed in past and present African ecosystems there is frequently a strong bias against small (<15 kg) mammal taxa, such that their frequency in death

assemblages is often far lower than their frequency in living communities (Behrensmeier and Dechant Boaz, 1980; Behrensmeier and Chapman, 1993; Potts, 1988). Documenting bias and understanding its nature are critical for refining palaeoenvironmental interpretation (Soligo and Andrews, 2005).

The proportion representation of different ecomorphs in a fossil assemblage should be examined by size class, to determine whether the environmental signal given from small taxa is comparable to or significantly different from the signal derived from the skeletal elements of larger taxa. If there is little difference, then it may be justifiable to lump the data from the different-sized taxa together. However, if there is a taphonomic bias against a particular size class, and the ecomorphic signal is not uniform across size categories (e.g., if small taxa on average provided a more wooded signal than larger taxa and were less likely to be preserved), these discrepancies would need to be considered in palaeoenvironmental reconstruction. In assemblages accumulated by hominins or other animals, collection bias also needs to be assessed, as selection for animals of a particular size class and/or habitat preference might shift the environmental signal of the death assemblage away from that of the living community it was drawn from.

The degree of time averaging can influence the resultant environmental signal from a fossil assemblage, particularly if habitat margins shifted across the site locus during the depositional time frame (Cutler et al., 1999). Such habitat shifts could create a fossil assemblage containing cosmopolitan taxa as well as taxa with more restricted habitat preferences that typically would not have been found together at the same place and time. However, as long as habitat shifts were slow relative to sedimentation and time averaging, distinct habitat signals can be preserved in a fossil assemblage (Cutler et al., 1999). Because the habitat preferences of fossil forms should relate to the presence of those habitats in the region during the formation of the assemblage, ecomorphic analysis minimally documents the presence of habitats with a particular structure. If the sample of postcranial elements appropriate for ecomorphic analysis is large, more nuanced analyses can be conducted across space and through time. For example, frequency shifts in ecomorphs across a palaeolandscape might reflect differences in habitat structure across that landscape in the past. If there is a stratigraphically stacked set of isotaphonomic assemblages, shifts in the proportion representation of different ecomorphs could be related to the expansion or contraction of different habitat types over time (Fernandez-Jalvo et al., 1998; Plummer and Bishop, 1994). Regional indicators of habitat availability, such as the presence and proportion representation of different ecomorphs, can be compared with more local indicators, such as stable isotopic composition of pedogenic carbonates, to determine the extent to which regional and local environmental signals differ, and in the case of archaeological assemblages to potentially provide information on hominin foraging ecology.

7. Conclusion

We outline a method for reconstructing bovid habitat preference based on astragalus morphology. The accuracy of this model is high as assessed by resubstitution analysis, jackknife analysis, and through the use of several test samples. A test of the usefulness of applying confidence thresholds to DFA output as a means of improving accuracy suggests that this can have unintended consequences, particularly in biasing the results against certain habitat preference groups. We conclude that where accurate reconstruction of regional habitat structure and/or information on hominin foraging ecology is the goal, the best approach is still to develop DFA models with high overall success rates.

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