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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.

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; Sustaita, 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). Bovids 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). Bovids 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