



Ecomorphology and phylogenetic risk: Implications for habitat reconstruction using fossil bovids



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ABSTRACT

Reconstructions of paleohabitats are necessary aids in understanding hominin evolution. The morphology of species from relevant sites, understood in terms of functional relationships to habitat (termed ecomorphology), offers a direct link to habitat. Bovids are a speciose radiation that includes many habitat specialists and are abundant in the fossil record. Thus, bovids are extremely common in ecomorphological analyses. However, bovid phylogeny and habitat preference are related, which raises the possibility that analyses linking habitat with morphology are not 'taxon free' but 'taxon-dependent.' Here we analyze eight relative dimensions and one shape index of the metatarsal for a sample of 72 bovid species and one antilocaprid. The selected variables have been previously shown to have strong associations with habitat and to have functional explanations for these associations. Phylogenetic generalized least squares analyses of these variables, including habitat and size, resulted in estimates for the parameter lambda (used to model phylogenetic signal) varying from zero to one. Thus, while phylogeny, morphology, and habitat all march together among the bovids, the odds that phylogeny confounds ecomorphological analyses may vary depending on particular morphological characteristics. While large values of lambda do not necessarily indicate that habitat differences are unimportant drivers of morphology, we consider the low value of lambda for relative metatarsal width suggestive that conclusions about habitat built on observations of this particular morphology carry with them less 'phylogenetic risk.'

We suggest that the way forward for ecomorphology is grounded in functionally relevant observations and careful consideration of phylogeny designed to bracket probable habitat preferences appropriately. Separate consideration of different morphological variables may help to determine the level of 'phylogenetic risk' attached to conclusions linking habitat and morphology.

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Introduction

Paleoanthropology is, at its core, about contextualizing the fossil evidence for human evolution by reconstructing the selection pressures and lifeways of fossil hominins. This central focus demands reconstructions of ancient environments and paleoecology. Thus, understanding the habitats available at fossil sites is a central paleoanthropological preoccupation and is one that only becomes more important with the recovery of more hominin fossils (e.g., Berger et al., 2010).

The lines of evidence leading to paleoecological reconstructions range across disciplines and a robust paleoecology cannot simply

rely on one line of inquiry. The available lines of evidence include geological evidence about depositional settings and climate, evidence for diets of species at sites (and hence vegetation) from dental microwear, dental mesowear and stable isotopes, evidence concerning vegetation from phytoliths and pollen, and evidence concerning the ecomorphology of fauna found at relevant sites. Ultimately, a robust paleoecological interpretation must rely on these lines of evidence collectively. Here we explore the intersection of phylogeny and ecomorphology in the Bovidae (which have been used most commonly in habitat reconstructions of fossil hominin sites) using the method of phylogenetic generalized least squares (PGLS) (see Nunn, 2011).

The extant radiation of the Bovidae is diverse and includes taxa found in a broad range of habitats. These range from dense forest to wide-open secondary grasslands to steep mountainous terrain. Thus, the value of bovids as habitat indicators has long been

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well-recognized (Gentry, 1970; Scott, 1979; Greenacre and Vrba, 1984; Kappelman, 1984, 1986, 1988, 1991; Scott, 1985; Shipman and Harris, 1988; Solounias and Dawson-Saunders, 1988; Kappelman et al., 1997). As bovids are often common at fossil sites of relevance to hominin evolution, they are an important part of hominin paleohabitat reconstructions.

Early paleohabitat reconstructions relied on taxonomic identifications based on dental and cranial characters and taxonomy was used as a proxy for paleohabitat (Vrba, 1980; Kappelman, 1984; Shipman and Harris, 1988). Thus, the presence of taxonomic groups whose extant representatives tend to be associated with a particular habitat was viewed as evidence for that habitat's existence in the past. This approach is limited by the possibility that fossil representatives of extant taxa may well have used different habitats (see Solounias and Dawson-Saunders, 1988). More recently, habitat preferences have been reconstructed based on ecomorphology (e.g., Kappelman, 1988; Scott et al., 1999; Kovarovic et al., 2002; DeGusta and Vrba, 2003, 2005; Plummer et al., 2008; Bishop et al., 2011; Curran, 2012; Meloro et al., 2013). Ecomorphology depends on an understanding of relevant functional morphology and is explicitly about adaptation and the relationships between phenotypes and performance (see especially Plummer et al., 2008). This taxon-free approach infers paleohabitats based on morphological characters that impart performance advantages in a specific habitat. For fossil sites, habitat-specific adaptations can fill the role of indicator species in extant settings.

Bovoid metapodials have been a common focus of analysis (Köhler, 1993; Plummer and Bishop, 1994; Kappelman et al., 1997; Scott, 2004; Kovarovic and Andrews, 2007; Bishop et al., 2011). Discriminant function analysis (DFA) is generally used to build models to assign fossil specimens to habitat types. However, the functional link between morphology and habitat has not always been discussed. For example, Plummer and Bishop (1994:48) left the functional morphology for future study with the suggestion that “joint stabilization, shaft shape, and lever arm length” were related to degree of cursoriality and predator avoidance strategy. An alternative to discriminant analyses has been to use canonical variates analysis to functionally link morphological variation with habitat in the form of a ‘Habitat Score’ (Scott and Maga, 2005; Curran, 2012). Through such analyses Habitat Scores can be compared for specimens from different sites to understand potential habitat differences in space and time. This approach contrasts with DFA by not making habitat category assignments but instead by creating a continuous variable that may be a meaningful morphological proxy for habitat variation. Discriminant function analysis always offers a habitat category assignment but the validity of these assignments may vary. In contrast, Habitat Scores summarize morphological variation likely related to habitat. In the case of bovid metapodials, Habitat Scores emphasize the importance of relative metapodial length and relative metapodial mid-shaft width (Scott and Maga, 2005). Elongate metapodials might potentially result from open habitats and cursoriality while broad metapodials could be linked with wet or rocky substrates and less predictable load directions.

These taxon-free approaches provide a novel way of dealing with the observation that fossil species can diverge in their ecological niche and habitat preferences from those of their nearest extant relatives. This is part of why ecomorphology has been of particular importance within paleoanthropology. The classic paper introducing bovid ecomorphology as a tool in paleoanthropology (Kappelman, 1991) was directed at the habitat of Fort Ternan, Kenya, in the Miocene and explicitly argues for the importance of a taxon-free approach when reconstructing ancient habitats based on fauna. In older geological contexts such as the case of Fort

Ternan (Kappelman, 1991; Scott et al., 1999), the taxon-free approach becomes essentially the only option, because species have had extremely long periods of time in which to diverge ecologically. Alternatively, in the case of more recent faunas, taxon-free and taxon-dependent approaches should merge (Kappelman et al., 1997). Indeed, in more recent archaeological contexts, ecomorphological analysis is certainly less necessary. Thus, ecomorphology is a solution to a particular kind of phylogenetic risk: the chance that fossils are ecologically different compared with their extant relatives. Here we refer to this as within-lineage ecological divergence risk or type A phylogenetic risk.

Recently, Klein et al. (2010) raised an important issue and argued for what is essentially an alternate form of phylogenetic risk. Based on a principle components analysis (PCA), Klein et al. (2010) found that species with similar habitat preferences often differed from each other in size and morphology as much as they differed from species that preferred different habitats. Thus, they argued that discriminant models previously used in habitat reconstructions must depend greatly on the taxonomic composition of the extant comparative samples used to create the classification. In other words, if different extant comparative samples produce different classification schemes, then ecomorphology is largely ‘taxon-dependent.’ The principal components used to make this argument were an overall size component (PC1) and a metapodial length component (PC2). Thus, two factors are potentially responsible for Klein et al.’s (2010) observation that bovids from the same habitat often differ greatly along their PCA axes. These factors are: 1) bovids of different size occupying the same habitats, and 2) bovids having different metapodial lengths as a result of factors other than locomotor adaptation to habitat (e.g., phylogeny, allometry).

With respect to the issue of size, there are large bovids found in both open and closed habitats and the same applies to small bovids. Thus, the finding of Klein et al. (2010) should not be particularly surprising, because bovids of differing size occupying the same habitat will differ dramatically, especially along the PC1 axis (a size component). One possible strategy for dealing with this issue is to build habitat-morphology models (discriminant or otherwise) that: 1) seek to eliminate size as a consideration, and 2) focus on constructing shape variables with clear and apparent functional links to habitat (see Scott and Maga, 2005; Curran, 2012).

An additional factor that might confound the relationship between habitat and metapodial length and also size might be phylogeny. If similarities in metapodial length are explainable by simple phylogenetic relatedness, then phylogeny would confound interpretation of a metapodial length-to-habitat link. This is potentially an issue for any shape variable hypothesized to have possible ecomorphological value. Thus, we see Klein et al.’s (2010) critique as pointing to a second type of phylogenetic risk: the chance that morphological similarity is better explained by phylogenetic signal than habitat-specific adaptation. Here we refer to this as phylogenetic signal risk or type B phylogenetic risk.

From a paleoanthropological perspective, study of type B phylogenetic risk provides an opportunity for improved paleohabitat reconstructions. The contention of Klein et al. (2010) is pessimistic in suggesting that any ecomorphological analysis can be confounded by phylogeny. Alternatively, if the magnitude of the potential issue can be understood and the circumstances where it may be a problem described, then paleoanthropology is equipped with a better tool for making inferences about paleohabitats.

We expect that ecomorphological and paleoecological analyses might be subject to both the types of phylogenetic risk discussed here. Thus, closely related taxa may be similar along some morphological axes due to phylogenetic signal while at the same time occupying the same habitats. It should also be noted that in

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