Cats in the forest: predicting habitat adaptations from humerus morphometry in extant and fossil Felidae (Carnivora)

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RRH: MORPHOMETRIC HABITAT-ADAPTATION

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Abstract.—Mammalian carnivores are rarely incorporated in paleoenvironmental reconstructions, largely due to their rarity within the fossil record. However, multivariate statistical modelling can be used successfully to quantify specific anatomical features as environmental predictors. Here we explore morphological variability of the humerus in a closely related group of predators (Felidae) to investigate the relationship between morphometric descriptors and habitat categories. Linear measurements of the humerus are analysed in three different morphometric combinations (log transformed, size free and ratio) and distinct ways of categorising habitat adaptations are explored. Open, Mixed and Closed categories are defined according to distinct criteria based on traditional descriptions of species, distributions and biome occupancy. Extensive exploratory work is presented using linear discriminant analyses and several fossils are included to provide paleoecological reconstructions. No significant differences are found in the predictive power of distinct morphometric descriptors or habitat criteria, although sample splitting into small and large cat guilds greatly improves the stability of LDA models. Significant insights emerge for three long-canine cats: *Smilodon populator*, *Paramachairodus orientalis* and *Dinofelis* sp. from Olduvai Gorge (East Africa). *S. populator* and *P. orientalis*are are both predicted to have been closed-habitat adapted taxa. The false “sabre tooth” *Dinofelis* sp. from Olduvai Gorge is predicted to be adapted to mixed habitat. The application of felid humerus ecomorphology to the carnivoran record of Olduvai Gorge shows that older stratigraphic levels (Bed I, 1.99-1.79 Ma) included a broader range of environments when compared to Bed II and Bed V, where there is an abundance of open adapted cats.

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Introduction

The functional morphological adaptations of the postcranial skeleton can be powerful indicators of locomotion and habitat exploitation. For fossil species whose behaviour cannot be observed directly, identifying such adaptations and linking them to habitat are important aspects of paleobiological reconstruction. This approach also informs paleoecological and paleoenvironmental reconstruction, with these ‘ecomorphological’ methods shedding light not only on the animals themselves but also on the environments they inhabited. A relatively large number of ecomorphic studies, focused mostly on bovids from Plio-Pleistocene African paleontological sites (Kappelman 1988; Plummer and Bishop 1994; Kappelman et al. 1997; DeGusta and Vrba 2003, 2005a, b; Kovarovic and Andrews 2007; Plummer et al. 2008), have informed paleohabitat reconstruction. Although other taxa, such as primates (Elton 2001, 2002, 2006), marsupials (Bassarova et al. 2009) and suids (Bishop 1999), have been subject to similar analyses, terrestrial carnivorans (fissiped Carnivora) are generally under-represented in these studies (Gonyea 1976; Lewis 1997). Conventionally, it is assumed that morphological diversity in the carnivorans reflects adaptations to specific functions (e.g., foraging and feeding, posture) more than the environment they occupy (Ewer 1973; Van Valkenburgh 1985, 1987, 1988, 1989, 1999, 2007; Bicknevicius and Van Valkenburgh 1996; Anyonge 1996; Janis and Wilhem 1993; Garland and Janis 1993; Carrano 1999; Farlow and Pianka 2002; Wroe et al. 2005; Meloro 2011a, b). Due to their large geographic ranges and high trophic levels, carnivorans tend to be more eurybiomic -able to exploit numerous habitats and biomes- than other mammalian clades (Hernández-Fernández and Vrba 2006). This reinforces the largely unexplored notion that carnivorans are ‘generalists’ in their skeletal adaptations to habitat and hence have limited value when included in studies that aim to reconstruct palaeohabitat.

Neglecting carnivoran fauna when undertaking ecomorphic-based paleoenvironmental reconstructions may exclude important information about local and regional habitats and how these are exploited by different members of mammalian communities. It is thus important to address whether the carnivoran skeleton can yield sufficiently detailed information about functional morphology related to habitat adaptations. There is definite potential for their use. Within the genus *Panthera*, there are obvious differences in habitat exploitation between the extant lion (*Panthera leo*), which tends to hunt in an open, savanna environment, and the tiger (*Panthera tigris*), which is more restricted to tropical and temperate forested areas. This indicates that even though carnivorans are eurytopic and eurybiomic, niche differentiation does occur. It can further be inferred that if this differentiation has reasonably deep evolutionary roots, there may be adaptations, even if subtle, to these different habitats. Indeed, distinct skeletal metrics that correlate with habitat exploitation in large carnivorous predators have already been identified and used to explore adaptation to habitat in both extant and extinct taxa (Lewis 1997; Meloro 2011b). Although few morphometric surveys have subsequently been performed that specifically examine the correlations between skeletal morphology and habitat adaptations in terrestrial carnivorans (but see Polly 2010), several studies have indicated the strong relationship between appendicular skeleton morphometry and locomotion or behaviour (Anyonge 1996; Andersson and Werdelin 2003; Andersson 2004; Schutz and Guralnick 2007; Polly 2008; Polly and MacLeod 2008; Meachen-Samuel and Van Valkenburgh 2009; Lewis and Lague 2010).

Here, we explore the relationships between the functional morphology of the carnivoran postcranial skeleton and habitat preferences, focusing on a single family of fissiped carnivorans, the Felidae. We develop models based on modern species and apply these to fossil felids. The felids, or cats, are a speciose and widespread family of ‘hypercarnivores’ (Ewer 1973; Gittleman 1985; Martin 1989; Kitchener 1991; Turner and

Antón 1997; Sunquist and Sunquist 2002). This results in relative dental homogeneity within the family (Holliday and Steppan 2004; Meloro and Raia 2010), but other skull features differ according to the prey they specialise on (Christiansen 2008; Slater and Van Valkenburgh 2008; Meachel-Samuel and Van Valkenburgh 2009b; Meloro 2011a). The most exceptional skull and postcranial morphologies are seen in the extinct sabre- and dirk- toothed cats (distinguished by extremely long canine teeth), as a possible result of extreme adaptations to a specialised hunting technique (Christiansen 2008; Slater and Van Valkenburgh 2008; Antón et al. 2004, 2005; Palmqvist et al. 2007; McHenry et al. 2007). Felids vary greatly in size, with the smallest members (such as the black-footed cat, *Felis nigripes*) having body masses under 2kg and the largest extant forms (such as the tiger, *Panthera tigris*) weighing as much as 300kg (Kitchner et al. 2010). Some extinct taxa, such as the dirk-toothed *Smilodon populator,* were likely to have been even larger than this, exceeding 400kg (Christiansen and Harris 2005). This body mass diversity is reflected in locomotion, with smaller taxa generally being much more arboreal than bigger forms (Gittleman 1985; Kitchener 1991; Turner and Antón 1997; Sunquist and Sunquist 2002; Kitchner et al. 2010). The felids also exploit an array of habitats, commensurate with their near-cosmopolitan distribution. Many species show distinct habitat preferences (e.g. the leopard *Panthera pardus* is a typical habitat generalist that can be found in woodlands as well as deserts), while others are restricted to specific environmental conditions (e.g. the Andean cat *Leopardus jacobita* occurs only in association with rocky outcrops in the arid zones of the high Andes, typically above 4200 m) (Macdonald et al. 2010). This broad range of adaptations at the interspecific level occurs also in the appendicular skeleton (Kitchener et al. 2010) suggesting that a degree of co-variation should occur between habitat adaptation and functional morphology.

We restrict our analyses to a single bone, the humerus. The humerus has been shown in primates to be highly informative about locomotor adaptations and habitat preferences

(Elton 2001, 2002, 2006), and forelimb bone proportion (radius/humerus length) have been used to distinguish adaptation to different habitats in previous studies of felids and carnivorans (Gonyea 1978; Lewis 1997; Meachen-Samuels and Van Valkenburgh 2009; Meloro 2011b). The humerus is one of the three long bones of the forelimb, and articulates proximally with the scapula, providing information about shoulder function including rotation, extension and flexion, and distally with the radius and ulna, reflecting elbow flexion and extension. Consequently, as well as reflecting foraging behaviour (Ruff 2002; Meachen-Samuels and Van Valkenburgh 2009, 2010; Lewis and Lague 2010), variation in humeral morphology can differentiate between cursorial and non-cursorial animals and thus reflects differences in habitats exploited (Andersson and Werdelin 2003).

Our focus on a single bone does not imply that only this bone may be informative, but rather aims to identify its potential for paleobiological and paleoenvironemental reconstruction. Associated skeletons and skeletal regions are rare in the fossil record, so any method that aims to reconstruct the paleobiology of fossil specimens must take this into account. Most ecomorphic studies focus on single bones (cf. Polly 2010), and some (e.g., Elton 2001, 2002, 2006) on epiphyses only, given that these are the long bone parts most likely to be preserved. We therefore present a broad range of statistical analyses designed to improve the resolution of existing methods.

We also aim to identify an objective habitat classification for use in ecomorphic analyses. It is usual for three or four habitat categories to be defined *a priori* (Kappelman et al. 1997; Bishop 1999; Elton 2001, 2002; DeGusta and Vrba 2003, 2005a, b; Plummer et al. 2008), although some have used as many as seven (Kovarovic and Andrews 2007). Notwithstanding the relatively large number of studies correlating habitat adaptations and long bone morphology, there is no consensus about how to categorise large mammals in discrete and distinct habitats objectively. Most studies rely on reviews of biology and ethology to categorise the most common environments exploited by different species. These are often defined as ‘open’ (for example, grassland), ‘mixed’ (mixture of grassland and tree-cover) and ‘closed’ (forest). In her study of the Plio-Pleistocene East African carnivore guild, Lewis (1997) assigned carnivoran species to these three habitat types, defining ‘mixed’ as having around 20% canopy cover, ‘open’ as having less than this, and ‘closed’ as having more than 20%. An alternative advocated by some authors (e.g., Hernández-Fernández 2001; Hernández-Fernández and Pelaéz-Campomanes 2003) is to categorise environmental preferences based on number of biomes occurring in their geographical range. However, few published studies have addressed the issue of habitat categorisation in detail. Here, we explore how to define habitat categories, quantifying presence/absence in particular environments and examining species’ preferences across biomes and habitats.

Early ecomorphic studies (e.g., Kappelman 1988) used ratios as a means of size-correcting morphometric data. This approach was later questioned (De Gusta and Vrba 2005a, b; Kovaric and Andrews 2007), with simple linear measurements argued to be equally informative as ratios in the discriminant analyses that form the basis of ecomorphic studies. Given that previous studies of carnivorans similar to ours used ratios only (Van Valkenburgh 1987; Lewis 1997), here we examine the utility of simple raw measurements versus ratios and residuals (another common way of generating ‘size free’ data) as predictors of habitat preference.

In short, we seek to assess whether the humeral morphometry of one family of carnivorans, the felids, allows the recovery of useful information about habitat exploitation. The methods surrounding ecomorphic reconstruction are assessed, in order to determine whether the way in which habitat is categorised for the taxa in the modern comparative sample influences analytic results, and to examine particular types of scaling methods and modern comparative ‘training’ sets. In addition, we investigate whether it is possible to recover accurate information from highly fragmentary material, using data from the epiphyses of modern specimens as a proxy for the data collected from incomplete fossils. Finally, we use the methods we develop to reconstruct the habitat preferences of three extinct felids, *Paramachairodus orientalis* and *Smilodon populator* and *Dinofelis* sp. as well as fragmentary fossil material from different stratigraphic intervals of the hominin East African fossil site Olduvai Gorge. This approach provides an example of how felid humerus ecomorphology can be used to inform paleoenvironmental reconstruction.

Materials and Methods

Sample Size

Complete and incomplete humeri belonging to both extant and extinct members of the Felidae, housed in the Natural History Museum London (B.M.N.H., London), Royal Museum for Central Africa (R.M.C.A., Tervuren), National Museum of Scotland (NMS, Edinburgh) and Kenya National Museum (KNM, Nairobi) (Electronic Supplementary Material), were included in the ecomorphological analyses. For each modern specimen, taxonomy was reassessed following species accounts in the IUCN red list (IUCN 2009). When accurate geographic information was available, modern specimens belonging to species with large geographic ranges (the wild cat, *Felis silvestris*), lion (*Panthera leo*), leopard (*Panthera pardus*) and tiger (*Panthera tigris*) were assigned to subspecies (Table 1). A total of 111 extant specimens across 11 genera were included in the analyses (Supplementary Table 1). Sample size was not equally distributed across taxa ($\chi^2 = 94.901$, df = 34, $p < 0.0001$). Inevitably, most of the extant sample was biased in favour of trophy hunted species (e.g., lions and leopards). To get maximum taxonomic and hence environmental coverage, non-pathological captive specimens were included (13% of the sample). Several of these specimens derive from captive breeding centres where general conditions for the animal approximate their natural environment (A. Kitchener personal communication 2009). For this study, it is assumed that captivity is a negligible source of morphometric variation (but see O’Regan and Kitchener 2005). Thirty-one percent of the specimens had either no locality recorded or were only located to a continent, with the rest of the sample being wild-caught with good locality data. Approximately half the extant sample could not be assigned to sex; within the rest of the sample, males and females were equally distributed. Sexual dimorphism is generally high in felids (Gittleman and Van Valkenburgh 1997), but as it is uncorrelated with habitat adaptation at interspecific level, here it is assumed to be a negligible source of morphometric variation. Both sexes were pooled in the analyses.

Two complete specimens (one fossil, one cast) of sabre toothed cats of the subfamily Machairodontinae plus five humeri from Olduvai Gorge were included in the fossil sample. Of the sabre toothed cats, *Paramachairodus orientalis* (BMNH M8960) is represented by a complete but slightly deformed humerus from Pikermi, Greece (a late Miocene fossil site) while *Smilodon populator* (the biggest Pleistocene dirk tooth cat from South America) specimen was a cast from a complete skeleton housed in the Natural History Museum, London. The material from Olduvai Gorge includes two complete humeri belonging to *Dinofelis* sp. indet D (OLD 74/54, OLD 74/348, Werdelin and Lewis 2001) from Bed I, and three distal fragments housed at the NHM of London: M20240 recorded from DKI 25 IV 35 and tentatively assigned to *Panthera* sp. from Bed I, M14676 belonging to *Panthera leo* from Bed II (cf. Leakey 1965) and M14677 classified as *Panthera leo* from Bed V (Upper Pleistocene). We excluded from the analyses only one incomplete humerus from Bed I (OLD 5067 FLK NI I 4, *Panthera pardus*) for which measurements were too few to be considered.

Linear Measurements and Error Estimation

Forty linear measurements of the humerus (Table 2) were taken to 0.5 mm by a single observer (CM) using an osteometric board (for greatest bone length), spreading callipers (for physiological length) or Sylvac digital callipers interfaced to a laptop computer. Most measurements were taken on the left humerus. If that was not available the right was substituted, assuming that as asymmetry was fluctuating and not directional no systematic bias would be introduced.

Measurement error was calculated measuring the same specimen of serval (*Leptailurus serval* BMNH 1981.988) three times on separate occasions (cf. DeGusta and Vrba 2003, 2005a. b). Overall, the mean error was less than 5%, consistent with that seen in other studies. The mean error estimate for each measurement is given in Table 2. A similar survey was also computed for other four species of Carnivora belonging to different size classes and yielding very similar errors (C. Meloro unpublished data).

Given that the sample represents a wide range of cats with attendant differences in body mass (1 kg – 200 kg), the measurements were log transformed for statistical analyses. This enables assumptions of normality to be met and scales the data (cf. Kovarovic and Andrews 2007). Initial examinations showed that the percentage of correctly classified cases in discriminant analyses when data are log transformed were always higher than when raw data were used.

Habitat categorisation

Four different ways of determining habitat categories were examined and compared (Table 1). These used (A) presence or absence in particular biomes (based on raw data from Ortolani and Caro 1996) to assign species to one of three categories (open, mixed, closed); (B) descriptions from the IUCN specialist group on cats that were then used to assign species to the above categories; (C) a GIS-based approach to assign each specimen to grassland or forest biome; (D) a similar GIS-based method assigning specimens to open/closed biome.

Presence or absence in particular biomes (A).—Data from Ortolani and Caro (1996), who recorded the presence or absence of each carnivoran species in a series of broad biomes, were used to assign each felid species to one of three categories (open/mixed/closed). The biomes used by Ortolani and Caro (1996) were temperate forest, tropical forest, grassland, arctic, riparian, and desert. Species were first given a habitat score, by recording presence in tropical or temperate forest as +1, presence in grassland, arctic or desert as -1; riparian was not considered because it is generally associated with semi-aquatic species like otters and no felids occurred exclusively in this category. Absence was recorded as 0. These scores were summed, with positive values used to indicate preference for closed environments (presence in forests), zero values preference to mixed environments (balanced between forest and open environments), while negative scores indicate preference for open environments. For example, the lion is recorded in grassland (-1) and desert (-1), which sum to -2 and is thus categorised as ’open‘. The European lynx (*Lynx lynx*) occurs in temperate forest (+1) and grassland (-1), summing to zero and thus is assigned to ’Mixed‘. For several taxa we did not possess the Ortolani and Caro (1996) categorisations, and consequently we recorded their presence into biomes according to the IUCN species description (see B).

Descriptions from the IUCN specialist group (B).—Data on habitat preferences from the IUCN cat specialist group (IUCN 2009) were used to subjectively assign each species to one of three categories (open/mixed/closed). For instance, the lion, described as preferring “open woodland-thick bush, scrub, grass complexes” was scored as ‘open’. The European lynx, described as preferring ‘forested areas’ as well as being present in ‘more open, thinly wooded, thick scrub woodland and barren, rocky areas above the treeline, alpine tundra’ is scored as mixed. In many cases, categorisation using this method correlates with results of method (A) but some differences exist; e.g., the Scottish wild cat (*Felis silvestris grampia*) is considered as 'mixed' (Coniferous forest + Mediterranean shrubland) using this method, rather than 'open'.

GIS-based approach – grassland vs forest (C).—The third method used a specimen-specific rather than a broad species-based approach. Each individual skeleton with accurate locality data (longitude and latitude) was plotted using DIVA-GIS software Version 5.2.0.2. Open-source shape files showing species-specific range maps for the Carnivora, taken from Greneyer et al. (2006), were used to check for potential outliers. These maps were also used to identify species centroid coordinates (where the geographic range was continuous and not fragmented), assumed to be a representative locality for captive specimens or those with no recorded locality. The WWF world ecoregion polygon (Olson et al. 2001), describing 14 ecoregions (plus two categories: rock and ice, and lake), was overlaid on the range maps allowing an ecoregion (biome) to be extracted for each specimen locality. The ecoregions extracted for the sampled localities were ascribed either to 'forest' (e.g., tropical and subtropical moist, dry broadleaf forest, temperate coniferous forest) or 'grassland/shrubland' (e.g., montane grassland and shrubland, tropical and subtropical grassland, savanna and shrublands, deserts and xeric shrublands). In this way each individual extant specimen could be confidently ascribed to 'forest' or 'grassland/shrubland'.

GIS-based approach – open vs closed (D).—The fourth method built on the principles of method (C), but instead of simply extracting a single habitat category for each specimen, the Xtools of ESRI ArcGIS 3.2 (ESRI 1992) was used to assess the interaction between the species geographic range and ecoregion polygons to quantify the relative proportion of each biome occupied by individual taxa. In order to assign species to either 'open', 'mixed' or 'closed', the 14 biomes were classified as either 'forest' or 'grassland/shrubland' as in method C. For each species, the relative percentages of occurrence in 'forest' or 'grassland/

biomes were summarised in a ratio that is equal to % occurrence grassland divided by % occurrence forest. Species with a ratio between 0 and 0.9 were classified as ‘Closed’, between 0.9 to 1.1 ‘mixed’, and those species above 1.1 ‘open’. Seventy two percent of geographic range of lion was found in ‘grassland/shrubland’ biomes with 25% in ‘forest’ biomes (3% is in the biome ‘lake’ or ‘rocks & ice’ that here are not considered), giving a ratio of 2.88. Consequently, all skeletal specimens of lion are classified as ‘open’. The Eurasian lynx (*Lynx lynx*), in contrast, has a ratio of 0.63 (38% in grassland and 61% in forest biomes) and is considered ’closed‘.

Scaling Measurements

Three separate datasets, derived from different measurement scaling/size correction methods, were analysed to examine their relative efficacy. Dataset (1) contained log transformed linear measurements. Dataset (2) was obtained by applying univariate regression models of log maximum length versus all the other logged variables, then using the unstandardised residuals as “size free” variables. Only one of these residuals, log Physiological Length (n = 112, r_s = 0.230, p = 0.012) was correlated with log Maximum Length. Dataset (3) used log transformed linear measurements combined in 27 functional ratios (Supplementary Table 2; after Bishop 1999; Elton 2001, 2002). Six ratios did not exhibit any correlation with Log Maximum length while the majority of them were negatively influenced by humerus length. All the ratios were retained for statistical analyses.

We used the software PASW Statistic 18 to perform Linear Discriminant Analysis (LDA) with a Forward Stepwise procedure (with an F entry probability of p = 0.05). This option allows for the selection of the most appropriate morphometric variables for discriminating pre-assigned categories (Hair et al. 1998). Although the more relaxed criterion of F = 0.15 used by several previous studies (Kappelman et al. 1997; Bishop 1999; Elton

2001, 2002; Plummer et al. 2008) generally leads to the inclusion of more variables in the models, the more stringent criterion used here should select a smaller number of the most powerful discriminatory variables, which could be an advantage when applying the methods to fragmentary fossils. The modern specimens of known habitat were used as a ‘training set’ to assign fossil specimens, with no *a priori* habitat classification to a category.

For the whole humerus dataset, twelve separate LDAs were undertaken, combining each scaled dataset and each habitat categorisation method. For all models, the validity of LDA was interpreted based on the Wilk’s lambda statistics and percentage of correctly classified specimens after cross-validation. In addition, LDA models were also performed on a subset of variables that could simulate bias introduced by the analyses of fossils. In this case, we selected a subsample of variables from the proximal or distal epiphyses of specific bones and re-ran the discriminant analyses on that subset (cf., Elton 2001, 2002).

Nested Ecological Analyses

Meloro (2011a) recently demonstrated that LDA model performance can be improved if dataset are split according to ecologically meaningful groups. Since the target of our study is to predict habitat adaptation of large fossil species, we performed a nested ecological analysis splitting our felid sample by a body mass threshold of 7 kg, based on the findings of studies by Van Valkenburgh (1985, 1988, 1996) and Meloro and O’Higgins (2011). The majority of small cats (< 7 kg) tend to hunt prey smaller than themselves and are capable of an arboreal lifestyle (Meachen-Samuels and Van Valkenburgh 2009, Table 1). Consequently, their humerus morphometry is expected to correlate differently to specific habitat adaptations when compared to larger species. Lewis and Lague (2010) have also demonstrated that long bone allometry of felids (including the humerus) is better described by a second polynomial regression suggesting allometric differences occur between small and larger taxa.

Since the number of 'small cat' (< 7 kg) specimens is relatively low (n = 29) we could not perform any meaningful LDA model because of the large number of variables compared to the actual sample. However, the dataset of large taxa (>7 kg, N = 82 specimens) was re-analysed separately to test if LDA models improved when compared to the overall dataset. Based on the results of the general analyses, we also restrict big cats LDA models to dataset 1 only (log transformed measurement).

Sensitivity analyses

In order to validate the efficacy of our LDA models to make predictions irrespective of unequal taxonomic sample size (Kovarovic et al. 2011), we performed two kinds of sensitivity analyses. First, we repeated the most accurate LDA after removing from the original sample all the specimens belonging to a particularly abundant taxon. We repeated the LDA by excluding first *Felis silvestris grampia* (N = 9, the most abundant small felid), then *Panthera pardus* (N = 12, representative mixed medium size felid) and finally *Panthera leo* (N = 17, the most abundant large felid).

A second sensitivity analysis was conducted to test for the effect of sample size (number of specimens) or body mass (in grams, log transformed) on percentage of correctly classified specimens for the 32 extant species sampled. Non-parametric Spearman correlation was applied to identify positive or negative significant correlations based on the results from all the LDA models.

Results

Whole Humerus

For the whole humerus dataset, all twelve data combinations yielded statistically significant ($p < 0.0001$) Wilk's lamba values in the linear discriminant analysis (LDA; Table

3). Only one function was extracted for the discriminant model based on habitat categorisation Method C, compared to two functions for the others (that explained 70 % and 30 % of variance in the mean respectively).

The stepwise procedure reduced the number of variables selected in the models. Between six and nine (a mean of eight) variables were selected for models using habitat categorisation Methods A, B and C (using ‘open’-‘mixed’-‘closed’ categories). For models using Method C (which uses only two habitat categories - ‘forest’ and ‘grassland’) the number of variables decreased to four, three or two depending on the measurement scaling dataset used. Some variables are selected reasonably consistently regardless of habitat categorisation or measurement scaling dataset (Fig. 1, section Logged data). Mediolateral head articular surface, bicipital groove depth, head surface height and mediolateral subspinosus scar are commonly selected for the proximal end, while distal epiphysis maximum mediolateral, olecranon fossa projection, trochlea superior-inferior medial border, and extensor carpi scar length are commonly selected measurements from the distal portion (Fig. 1). These variables also tend to be selected in the models of the “size free” data set (see Fig. 1, section Size-free). Data from the proximal humerus are generally selected more frequently than those from the distal humerus (Fig 1). In the analyses using ratios, anteroposterior maximum head diameter / mediolateral head articular surface width, bicipital groove ratio, trochlea ratio, the trochlea and the olecranon fossa ratios are all frequently selected (Fig. 2). Both proximal and distal data were equally selected in ratio-based models (Fig. 2).

Table 4 shows percentages of correctly classified specimens for each of the twelve models using ‘leave one out’ classification in the LDA. A combination of logged linear measurements with habitat categorisation Method A gives the most consistent and accurate classifications (see also Fig. 3). Residuals and ratios are less consistent and effective overall.

Analyses using habitat categorisation Methods C and D are less accurate than those using the other two methods.

Proximal and Distal epiphyses

The proximal and distal humeral models were derived from logged linear measurements and ratios; residuals were not used because corrections were based on whole humerus length, which would not be available for fragmented fossil specimens. Sixteen linear discriminant models (using each of the four habitat categorisation Methods, and two Datasets divided into proximal and distal elements) were therefore derived. All but one of the discriminant functions were significant ($p < 0.001$). The exception was the model using habitat categorisation Method B (IUCN categorisation) and ratios for the distal humerus, in which the second extracted function was non-significant ($p = 0.32$). Again, the stepwise procedure considerably reduced the number of variables selected (Figs. 1 and 2). For logged linear measurements a range of six to nine variables were selected for proximal models (with greater tubercle mediolateral length selected most often) and three to six for distal (with distal mediolateral width and trochlea superior-inferior medial border being frequently selected) (Fig. 1); for ratios it ranged from one – anteroposterior maximum head diameter/mediolateral head articular surface width – to six for proximal models, and to five for distal models (Fig. 2).

There was marked dissimilarity in the percentage of correctly classified specimens for the different models (Table 5). For the proximal humerus, the model with the best classification rate used habitat categorisation Method A (Ortolani and Caro habitat) and Dataset 1 (logged linear measurements). For the distal humerus, habitat categorisation Methods C (GIS sample based) and D (geographic range based) along with Dataset 3 (ratios) gave the best results (Table 5). In general, the proximal humerus models gave better classification results than those for the distal humerus.

Big Cats

Discriminant functions were significant at $p < 0.05$, except for the distal humerus model using logged linear measurements and habitat categorisation Method C. The stepwise procedure reduced the number of variables to as little as one (for proximal humerus only, logged greater tubercle mediolateral width for habitat categorisation Method D) to as many as 10 (logged humerus measurements on the whole humerus for habitat categorisation Method D). Proximal humerus measurements were selected more frequently than distal ones (Fig. 4), with bicipital groove descriptors being one of the most informative in the whole humerus and proximal humerus analyses (see Fig. 4). Mediolateral width at the distal end is the most frequently selected variable in the distal models. The highest percentage of correctly classified specimens is in models for the whole humerus using logged linear measurements, with habitat categorisation Methods A and D giving the best results (Table 6) and Method C markedly worse. Accuracy declines with the use of proximal and distal elements on their own, with distal models being on average the least good classifiers (Table 6).

Summary of Models

When percentage of correctly classified cases is compared across different dataset without taking different habitat methodologies into account there are no differences in predictive power for the categories Open (Kruskal-Wallis $\chi^2_{(9)} = 14.820$, $p = 0.096$) and Mixed (K-W $\chi^2_{(6)} = 16.075$, $p = 0.065$). The predictive power for the Closed category changes according to the Dataset used (K-W $\chi^2_{(9)} =22.393$, $p = 0.008$), with models based on Dataset 1 (logged linear measurements) having the highest percentage of correctly classified cases (Fig.

5A). To compare the predictive accuracy of distinct habitat categorisations, percentage of correctly classified cases from different datasets were pooled. There are no statistically significant differences between reclassification rates for the different habitat categorisation Methods (all K-W $p > 0.1$, Fig. 5B). In general, the Habitat criterion D models obtain the highest correct prediction rate for the category "Open" but not for "Closed" (Fig. 5B). When only big cats are considered, the category "Closed" using Habitat criterion A is predicted at a ca 90% accuracy; this result is never achieved in any other LDA models. Consequently, the Ortolani and Caro (1996) criterion is probably the best to fit data for ecomorphology data of big cats (Fig. 5B).

Figure 6 illustrates the major differences between the proximal and distal epiphyses of three taxa close to the centroids for the different habitat categories (open / mixed / closed). Open adapted specimens exhibit on average a larger subspinus scar, a higher head, a larger distal epiphysis and a higher trochlea when compared to the closed adapted taxa.

Sensitivity analyses.

The LDA models excluding specific taxa were applied to discriminate habitat categorisation Method A (Ortolani & Caro) for Dataset 1 (logged data). Excluding *Felis silvestris grampia*, the LDA yields two significant functions (at $p < 0.0001$) associated with ten measurements. The percentage of correctly classified cases is high for Closed (81.8), followed by Open (79.5) and Mixed (69.0). The exclusion of the leopard also shows little impact on the LDA model (significant after a selection of 8 variables) with percentage of correctly classified cases improving for Closed (92.7) and Mixed (70.6) but not for Open (66.7). On the other hand, the exclusion of all lion specimens rendered the LDA model non-significant (significant only after adding at least seven lion specimens).

Species show distinct percentages of correctly classified cases depending on the analyses (Table 7). A positive correlation is recorded between number of specimens and log body weight ($r_{spearman} = 0.547$, $p < 0.0001$). Number of specimens also correlates positively with percentage of correct cases when applying Habitat A (Ortolani & Caro) for dataset logged ($r_{spearman} = 0.362$, $p < 0.004$) and for dataset “size free” ($r_{spearman} = 0.522$, $p < 0.002$). For the latter dataset there is also a positive correlation between log BW and percentage correct cases ($r_{spearman} = 0.357$, $p < 0.044$). No other significant correlations emerged, suggesting no influence of sample size and body mass on the other LDA models.

Application to Fossil Specimens

Habitat prediction of fossil specimens varies according to the methodology and the dataset used (Fig. 7). The sabre-tooth/dirk-toothed cats *Paramachairodus orientalis* and *Smilodon populator* are generally predicted as adapted for Closed habitat, while *Dinofelis* sp. exhibits a broader range of adaptations, being classified in similar proportions into Open, Mixed or Closed habitat depending on the analyses.

As all fossil specimens are large felids, the models based on the big cats Dataset 1 (logged linear measurements) using Habitat Method A are the most accurate for complete specimens. With this classification scheme, both *Paramachairodus orientalis* and *Smilodon populator* are classified as Closed, while *Dinofelis* sp. (Old 74/01) is classified as Mixed. For the proximal humerus analyses we chose the Dataset 1 Method A for big cats, which yielded the best rate of cross-validation accuracy (average 72.6 %) when compared to the other methods. Again, *P. orientalis* and *S. populator* are classified as Closed, and both *Dinofelis* sp. from Olduvai Bed I as Mixed.. Dataset 1 Method B (IUCN classification scheme) had the better rate of classification for the distal humerus of big cats (average 69.03%) and it validates adaptation to Closed habitat in *P. orientalis* and *S. populator*; both *Dinofelis* specimens from Bed I are classified as Open. The distal fragment *Panthera* sp. (M 20240) from Bed I is predicted as Closed while the two distal fragments of lions from Bed II and Bed V are predicted as Open. The fossil humeri of cats from Olduvai Gorge show that a broad range of habitats was present at Bed I when compared to Bed II and Bed V (Upper Pleistocene).

Discussion

Our results clearly indicate that accurate information about habitat exploitation can be recovered from the felid humerus, notwithstanding the cosmopolitan and eurybiomic nature of the family (Kitchener 1991; Turner and Antón 1997; Sunquist and Sunquist 2002; Kitchener et al. 2010). Single bones, even if fragmentary, can be ecologically informative. Previous work (Gonyea 1976; Anyonge 1996; Lewis 1997; Meloro 2011b) has demonstrated that comparative long bone indices, such as intermembral index, can be used to reconstruct habitat preference and locomotor strategy in a broad range of large carnivores. However, the probability of fossilisation for mammalian carnivores is generally low (Damuth 1982) and even lower for particularly large felids (Gittleman and Harvey 1982; Gittleman 1985; Turner and Antón 1997), so few relatively complete and associated skeletons are recovered. Developing accurate models based on single bones and bone elements is thus important. The re-substitution rates for the felid humerus in this study are similar to those observed in discriminant analyses from other studies of large mammals, including bovids, suids and primates (Kappelman et al. 1997; Bishop 1999; Elton 2001, 2002; DeGusta and Vrba 2003, 2005a, b; Kovarovic and Andrews 2007; Plummer et al. 2008). This indicates that carnivorans, important components of past and present biotas, can be as paleoecologically informative as their prey (Hernández-Fernández 2001; Hernández-Fernández and Pelaéz-Campomanes 2003; Hernández Fernández et al. 2006; Hernández Fernández and Vrba 2006).

One promising avenue of future research will be to combine ecomorphic-based reconstructions of past habitats for different mammalian groups likely to be sympatric and contemporaneous to construct a more holistic picture of the environmental context of ecological communities. This approach has recently been used by Polly (2010), who examined calcaneum ecomorphology in different North American carnivoran communities. Taking this further, using multiple carnivorans and prey species from the same locality may provide a depth of information about biome and paleoenvironment that cannot be recovered by focusing on specimens from a single species, genus or even family.

The analyses we present here highlight several methodological issues. Attempts to correct the data using residuals or ratios to take size into account did not increase the accuracy of the statistical models, and indeed in many cases yielded resubstitution rates that were lower than the logged linear measurements. These results therefore lend support to the use of minimally-manipulated data in ecomorphic analysis of large mammals (*sensu* DeGusta and Vrba 2003). Investigations on the teeth of much smaller mammals, voles, suggested similar conclusions, indicating that residual or ratio-based scaling of morphometric data are not always justified, must be validated through experimentation and must be appropriate to the question being addressed (Navarro et al. 2004). Using logged linear measurements retains a significant size signal. For ecomorphic reconstruction using felids, it is likely that size, known to be hugely biologically and ecologically influential in carnivorans (Gittleman 1985; Carbone et al. 1996, 2007) as well as mammals as a whole (Damuth and McFadden 1990), is an important explanatory and discriminatory variable when considering habitat adaptation. This has also been noted for primates (Elton 2001, 2002) and bovids (Plummer et al. 2008).

One challenge when retaining a size signal by using logged linear measurements is accounting for allometric effects, especially if scaling factors differ between taxonomic groups or adaptive grades. In the discriminant analyses, resubstitution rates improved on the whole when the modern sample was divided according to size, with seven kilograms the threshold between ‘small’ and ‘big’ cats. This clearly points to scaling differences within the felids, also noted in other studies (Bertram and Biewener 1990; Christiansen 1999; Lewis and Lague 2010). There is no hard-and-fast rule about where the threshold should be drawn, however, with one study on interspecific scaling of the carnivoran postcranium pegging the size threshold at 100kg (Bertram and Biewener 1990) and another at 50kg (Christiansen 1999). Another potential threshold is at 25kg, based on metabolism and hunting behaviour, because carnivorans bigger than this tend to kill prey larger than themselves (Carbone et al. 1999, 2007). The choice of threshold should be appropriate to the question being addressed. In the case of the present study, seven kilograms is the most meaningful threshold, as shown in previous research on locomotor behaviour (Van Valkenburgh 1985, 1987). Specifically, arboreality is primarily dictated by body mass (Van Valkenburgh 1987); in Felidae, the majority of taxa with mean body masses less than seven kilograms tend to use arboreal substrates frequently while bigger forms such as caracal, serval, lynxes and most of the pantherine cats tend to be more terrestrial, albeit with many taxa being scansorial as well arboreal (Meachen-Samuels and Van Valkenburgh 2009). This does not preclude the exploitation of closed habitats in taxa larger than seven kilograms, as seen in Table 2, but does highlight a grade shift in the felids. Separation of these two grades results in more accurate discrimination for modern specimens, so a similar separation method (using estimates of mass based on the size of the bone) should be employed for fossil felid specimens, as supported by the more consistent allocation of fossils to habitat types in our study when using the big cat modern training set rather than the full modern sample.

There were no statistically significant differences in the discriminatory power of GIS-based habitat categories (Methods C and D) versus more traditional ways of assigning taxa to groups (Methods A and B) based on species’ biology (see Fig. 5B). However, in the discriminant analyses, some habitat categorisation methods worked better than others. For the whole humerus and proximal humerus, Method A gave the most accurate and consistent resubstitution results when using the whole modern training set. When using the big cats training set, Method A along with Method D, yielded the best results. The GIS-based Methods (C and D) developed here, which use specimen-specific information based on geographic location, may have a significant drawback in that their accuracy relies on the sample having a representative geographical distribution. This is often problematic with museum collections, as specimens tend to be drawn from a relatively small number of localities, often chosen for ease of access (Cardini et al. 2007). Smaller or forest specimens may thus be less well represented than the larger, charismatic open landscape animals, which certainly seems to be the case for our sample. The overall habitat classification may thus be skewed. On balance, therefore, Method A, based on data from Ortolani and Caro (1996), who recorded the presence or absence of carnivoran species rather than individual specimens in broad biomes, seems to provide the best habitat categorisation for extant species of big cats.

Unsurprisingly, the resubstitution rates were higher for models using the whole humerus compared to those employing either the proximal or distal epiphyses separately. The proximal humerus was the most functionally informative in our felid sample, demonstrated both by the dominance of proximal humerus measurements in the stepwise LDA and the better resubstitution results from the analyses using only the proximal region compared to distal. The proximal humerus is also highly informative in cercopithecid primates, although the distal humerus is also a good discriminator (Elton 2001). In felids, variables such as greater tubercle mediolateral width, bicipital groove depth and width, head articular surface height and width of *subspinosus* tuberosity (Fig. 6) are constantly selected in most models, and generally have a low degree of measurement error. Similar measurements, albeit contained in ratios, were selected in primate models (Elton 2001), suggesting that they may be functionally informative across a number of mammalian groups. The greater tubercle is the attachment site for the *supra* and *subspinosus* muscle complex, part of the rotator cuff of the shoulder. The bicipital groove (or sulcus intertubercularis) is the passage for the tendon and nerve of the *biceps* muscle (Reighard and Jennings 1901; Barone 1980). These muscles facilitate movement in the vertical and lateral planes, between the scapula and the humerus. They are implicated in both prey capture and climbing, activities that are linked to habitat adaptations in the Felidae (Ewer 1973; Kitchener et al. 2010).

In felids, models based on the distal humerus were less consistent and accurate, and relatively few measurements were selected in the stepwise procedure for the whole humerus. Measurements that most frequently emerged were maximum mediolateral width of the distal humerus and trochlea superior-inferior medial length (Fig. 6), as well as the size of the *extensor carpii* tuberosity to a lesser extent. The error is relatively low for these measurements. Both distal mediolateral width and trochlea superior-inferior provide information about elbow functional morphology. The trochlea has been identified as functionally informative in other studies of Carnivora as a whole (Andersson and Werdelin 2003; Andersson 2004) because of its role in supination as well as its high correlation with body mass. The *extensor carpii* muscle influences movements of the forepaw that are needed in prey grappling and climbing (Barone 1980).

One major purpose of ecomorphic discriminant analysis is to reconstruct the habitat preferences of extinct taxa. The results from our study give useful insights into the paleobiology and paleoecology of the sabre/dirk toothed cats *Smilodon populator* and *Paramachairodus orientalis* and the enigmatic false sabre *Dinofelis* sp.. The most robust combination of logged linear measurements, habitat categorisation Method A and the big cat modern training set, supported strongly the assignment of both sabre cats to the 'closed' category while *Dinofelis* sp. is predicted as 'mixed'. This is in line with previous research that suggested that the large, specialist stalker *S. populator* needed to exploit environments with extensive forest cover (Gonyea 1976; Kurtén and Werdelin 1990; Christian and Harris 2005). Paleoecological data on *P. orientalis* are generally scanty, although its European counterpart (*Pristinosmilus ogygia*) has been suggested to be a better climber than the leopard (Salesa et al. 2005, 2006, 2009). Polly and MacLeod (2008) also predicted semidigitigrade locomotor behaviour for this big cat, indicating climbing ability and possibly supporting an adaptation to mixed-closed environments. Lewis (1997) and Werdelin and Lewis (2001) reported adaptations in *Dinofelis* sp. to climb trees for carcass transport and possibly to 'mixed/closed' habitat exploitation. Our analyses suggest that this taxon was probably more eurybiomic and capable of adapting to a range environments including open grassland. These findings are supported by the allometric investigation of Lewis and League (2010) who recognised that the *Dinofelis* humerus had similarities with medium sized 'mixed' cats such as the leopard and the puma. Predictions for the fragmentary material of *Panthera* sp. of Olduvai Gorge Bed I are more enigmatic and possibly suggest that the specimen does not belong to *P. leo* but to a large cat with adaptations to 'closed' habitats. The fossil lions included in our analyses are consistently assigned to the 'Open' category, the same category as the modern lion. This suggests the habitat preferences of African Pleistocene lions were broadly similar to those of extant forms.

Overall, these results strongly encourage the inclusion of felids in paleoenvironmental reconstructions. It clearly emerges that a broad range of habitats existed at Olduvai Bed I, with possibly more forested conditions compared to later intervals of Bed II and Bed V (Upper Pleistocene). This conclusion is supported by other studies (Fernàndez-Jalvo et al. 1998, Plummer and Bishop 1994; Plummer et al. 2009), and more robust results might emerge by combining ecomorphology of a broader range of mammalian species. Louys et al. (2011) recently demonstrated that broad ecological categories within mammalian communities correlate with percentage of vegetation cover in extant tropical ecosystems, thus future ‘taxon free’ studies have the potential to predict multidimensional environmental variables.

Inevitably, a small number of incongruences emerged in the multiple models used to assign the fossil specimens to habitat category, with some resubstitutions into the ‘mixed’ category for both sabre toothed cats and lions. This may reflect measurement error or statistical inaccuracy. Alternatively, it may hint at adaptations in extinct animals to environments that are unknown in the modern world. Fossils may inhabit functional categories of their own (Albrecht 1992), which may lead to unexpected results in discriminant analysis. Similarly, habitats in the past may not resemble those seen today. This has been suggested based on faunal evidence for Olduvai Bed I, which had woodland that was much more species-rich than that seen today. It is therefore possible that significant differences exist between the function and structure of past and present ecosystems (Fernàndez-Jalvo et al. 1998).

Conclusion

The results presented in this paper show that the use of carnivorans has great promise in paleoecological reconstructions. For felids, the best linear discriminant function model, which predicted habitat categories at a very high rate of accuracy (over 90% for ‘mixed’ and ‘closed’ categories in jack-knifed classifications), used logged linear measurements in a training set comprising big (> 7 kg) species. This suggests that the use of logged linear measurements could be preferable to residual or ratio-based scaled data, although this should be verified on a study-by-study basis and with reference to the question being addressed. It also indicates that a narrower, grade-based modern comparative sample and training set might be more appropriate than one comprising a larger number of species. The choice of habitat categorisation method is less straightforward, but a broad, biome-based classification using as much robust and comparable data from the literature, objectively weighted, may be the preferable option. The proximal humerus appears to be highly functionally informative, in line with earlier ecomorphic research (Elton 2001). The high reclassification results for the proximal humerus on its own as well as the whole humerus indicates that even isolated, fragmentary bones can yield useful information about habitat preferences in fossils. The fossil sabre tooth *Smilodon populator* and *Paramachairodus orientalis* show adaptations to closed environments while *Dinofelis* sp. from Olduvai Bed I clearly belongs to the 'mixed' category. This interpretation, together with results emerging from other fragmentary fossil cats, validates previous paleoenvironmental reconstructions of Olduvai Gorge, with older stratigraphic intervals (Bed I) being characterised by higher abundance of forested taxa.

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Tables

Table 1. Habitat categories and basic ecological data for felid species analysed (body weight averaged between males and females from IUCN, 2009; locomotion as in Meachen-Samuels and Van Valkenburgh, 2009). Habitat C is summarised as percentage of specimens (= Spec.) recorded in Forest or Grassland.

Species	BW(kg)	Locomotion	Habitat A	Habitat B	% Spec. Forest	Spec. Grass	Habitat D
Acinonyx jubatus	40.917	Terrestrial	Open	Open	50	50	Open
Caracal aurata	6.200	Terrestrial	Closed	Closed	100	0	Closed
Caracal caracal	11.500	Scansorial	Open	Open	50	50	Mixed
Felis chaus	5.150	Terrestrial	Mixed	Mixed	100	0	Closed
Felis margarita	2.500	Terrestrial	Open	Open	0	100	Open
Felis nigripes	1.525	Terrestrial	Open	Open	0	100	Mixed
Felis silvestris grampia	4.167	Scansorial	Closed	Mixed	100	0	Closed
Felis silvestris lybica	4.833	Scansorial	Open	Open	33	67	Mixed
Leopardus geoffroy	4.350	Terrestrial	Mixed	Mixed	100	0	Open
Leopardus guigna	2.200	unknown	Closed	Closed	100	0	Closed
Leopardus pardalis	10.131	Scansorial	Closed	Closed	0	100	Closed
Leopardus wiedii	3.200	Arboreal	Closed	Closed	100	0	Closed
Leptailurus serval	12.250	Terrestrial	Open	Open	0	100	Mixed
Lynx canadensis	10.025	Terrestrial	Mixed	Closed	100	0	Mixed
Lynx lynx	20.100	Scansorial	Mixed	Mixed	67	33	Closed
Lynx pardinus	11.050	Terrestrial	Mixed	Mixed	100	0	Closed
Lynx rufus	9.300	Scansorial	Open	Mixed	0	100	Open
Neofelis nebulosa	15.500	Arboreal	Closed	Closed	100	0	Closed
Panthera leo	150.529	Terrestrial	Open	Open	20	80	Open
Panthera leo persica	147.500	Terrestrial	Open	Open	100	0	Open
Panthera onca	79.167	Scansorial	Closed	Closed	100	0	Closed
Panthera pardus	35.042	Scansorial	Mixed	Mixed	50	50	Mixed
Panthera pardus fusca	49.667	Scansorial	Mixed	Mixed	100	0	Mixed
Panthera tigris	169.375	Terrestrial	Closed	Closed	100	0	Closed
Panthera tigris altaica	243.000	Terrestrial	Closed	Closed	100	0	Closed
Panthera uncia	42.188	Scansorial	Closed	Open	0	100	Open
Pardofelis badia	1.950	unknown	Closed	Closed	100	0	Closed
Pardofelis marmorata	4.000	Arboreal	Closed	Closed	100	0	Closed
Pardofelis temminckii	11.750	Scansorial	Mixed	Mixed	100	0	Closed
Prionailurus bengalensis	5.050	Scansorial	Closed	Closed	100	0	Closed
Prionailurus planiceps	2.000	Terrestrial	Closed	Closed	100	0	Closed

Prionailurus rubiginosus	1.350	unknown	Mixed	Mixed	100	0	Closed
Prionailurus viverrinus	9.625	Terrestrial	Closed	Closed	100	0	Closed
Puma concolor	57.125	Scansorial	Mixed	Mixed	100	0	Closed
Puma jaguarundi	5.150	Scansorial	Closed	Mixed	100	0	Closed

TABLE 2. Measurement error and description for 40 humerus linear measurements. Only absolute values of differences in multiple measurement comparison are reported.

ID	**Description**	**Error**
L	Length (L)	0.12%
PhL	Physiological L-from central tip of epiphyses	0.62%
DtL	Deltopectoral crest Max L	1.32%
DtPhL	Deltopectoral crest Physiological L	2.57%
Mds_ML	Midshaft Mediolateral (ML)	0.10%
Mds_AP	Midshaft AnteriorPosterior (AP)	1.77%
APmH	AP max Head	0.14%
APartH	AP articular surface Head	5.07%
APsH	AP Head shaft	1.05%
ML_H	ML Head max	0.66%
ML_artH	ML Head articular surface	1.69%
H_H	Head surface Height	0.42%
BcG_W	Bicipital Groove Width	4.48%
BcG_D	Bicipital Groove Depth	1.45%
GT_AP	Greater Tubercle max AP	1.47%
GT_ML	Greater Tubercle max ML	0.00%
Sb_ML	Subspinosus scar ML	2.89%
Sb_AP	Subspinosus scar AP	3.32%
LT_AP	Lesser Tubercle max AP	0.16%
LT_ML	Lesser Tubercle max ML	0.00%
Dst_ML	Distal epiphysis maximum ML	0.14%
Dst_AP1	Distal epiphysis AP medial articular surface	5.15%
Dst_AP2	Dist epiphysis AP lateral articular surface	1.27%
TrL	Trochlea Max L	1.52%
CpL	Capitulum Max L	2.90%
TrAP	AP_Trochlea at the midpoint	0.11%
Cd_L1	Trochlea superior-inferior maximum L	1.15%
Cd_L2	Trochlea superior-inferior medium L	1.85%
Cd_L3	Trochlea superior-inferior minimum L	5.24%
Pj_Tr	Projection of Trochlea in vertical plane	2.13%
Dst_art_ML	ML distal Articular surface	2.38%
Of_ML	Olecranon fossa ML	0.72%
Of_H	Olecranon fossa Height	8.22%
Of_Pr	Olecranon fossa projection	0.64%
PrTb_L	Pronator tubercle L	3.16%
UmF_L	Ulnar medial fossa L	1.00%
UlF_ML	Ulnar lateral fossa ML	5.78%
UlF_AP	Ulnar lateral fossa AP	12.23%
UlF_pj	Ulnar lateral fossa depth	5.20%
ExC_L	Extensor carpii scar L	1.14%

TABLE 3. Wilk's lambda for 12 discriminant analyses based on overall measurements. All values are associated to a $p < 0.0001$.

	Habitat A	Habitat B	Habitat C	Habitat D
Logged (1)	0.241	0.299	0.794	0.271
Size free (2)	0.297	0.349	0.859	0.385
Ratios (3)	0.368	0.557	0.86	0.415

TABLE 4. Percentage of correctly classified cases after leave one out procedure for 12 discriminant models based on the overall dataset.

		Habitat A	Habitat B	Habitat C	Habitat D
Logged (1)	Open	74.4	71.4	70.6	69.7
	Mixed	75.9	69.4		69.0
	Closed	78.6	71.9	61.9	75.0
Size free (2)	Open	82.1	69.1	64.7	60.6
	Mixed	62.1	58.3		62.1
	Closed	66.7	75.0	40.5	70.8
Ratios (3)	Open	71.8	71.4	67.7	69.7
	Mixed	65.5	44.4		75.9
	Closed	64.3	59.4	64.3	60.4

TABLE 5. Percentage of correctly classified cases after leave one out procedure for 16 discriminant models using proximal or distal humerus region.

		Habitat A	Habitat B	Habitat C	Habitat D
Proximal log (1)	Open	66.7	64.3	73.8	81.8
	Mixed	65.5	63.9		44.8
	Closed	69	65.6	64.7	68.8
Proximal ratio (3)	Open	66.7	64.3	52.4	75.8
	Mixed	72.4	47.2		72.4
	Closed	57.1	59.4	66.2	43.8
Distal raw (1)	Open	66.7	71.4	57.1	66.7
	Mixed	41.4	44.4		62.1
	Closed	67.4	30.3	69.6	57.1
Distal ratio (3)	Open	69.2	78.6	76.2	81.8
	Mixed	58.6	19.4		34.5
	Closed	53.5	39.4	58	49

TABLE 6. Percentage of correctly classified cases after leave one out procedure for 11 discriminant models based on subsample of large felids.

		Habitat A	Habitat B	Habitat C	Habitat D
Log (1)	Open	81.2	85.7	67.6	85.7
	Mixed	91.7	90.5		97.5
	Closed	95.5	72.7	61.4	80.8
Proximal Log (1)	Open	75	71.4	73.5	78.6
	Mixed	79.2	61.9		41.7
	Closed	63.6	72.7	68.2	19.2
Distal Log (1)	Open	75	78.6	n.s	74.3
	Mixed	58.3	70.8		57.1
	Closed	54.5	57.7	n.s	54.5

TABLE 7. Percentage of correctly classified cases (numbers are in decimals, 1.00 = 100%) for each species based on a selection of LDA analyses performed on the whole humerus measurement dataset. Meth = Habitat categorisation. In bold all the 100% correct cases.

	Logged Data				Size free Data				Ratios			
Species	Meth A	Meth B	Meth C	Meth D	Meth A	Meth B	Meth C	Meth D	Meth A	Meth B	Meth C	Meth D
Acinonyx jubatus	**1.00**	**1.00**	0.67	**1.00**	**1.00**	**1.00**	0.67	**1.00**	**1.00**	**1.00**	0.33	0.83
Caracal aurata	0.50	0.50	0.50	**1.00**	0.00	0.50	**1.00**	**1.00**	0.00	0.00	0.50	0.00
Caracal caracal	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	0.00	0.50	0.50	**1.00**	0.50	**1.00**
Felis chaus	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.50	0.50	0.50	0.00
Felis margarita	0.00	0.00	0.50	0.50	**1.00**	**1.00**	0.50	**1.00**	0.00	0.00	0.50	0.00
Felis marmorata	**1.00**	0.00	**1.00**	**1.00**	0.00	0.00	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	0.00
Felis nigripes	0.50	0.50	0.00	0.00	**1.00**	**1.00**	**1.00**	0.00	0.00	0.50	0.00	0.00
Felis silvestris grampia	**1.00**	**1.00**	**1.00**	0.89	0.78	0.67	0.78	0.56	**1.00**	0.67	**1.00**	0.89
Felis silvestris lybica	0.00	0.33	0.33	0.33	**1.00**	**1.00**	0.67	0.00	0.67	0.33	0.33	0.67
Leopardus geoffroy	0.50	**1.00**	0.00	0.00	0.50	0.00	0.50	0.50	0.50	0.50	0.50	0.00
Leopardus guigna	0.00	**1.00**	**1.00**	**1.00**	0.00	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**
Leopardus pardalis	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**
Leopardus wiedii	0.00	0.00	**1.00**	**1.00**	0.00	0.00	**1.00**	0.00	0.00	0.00	0.00	0.00
Leptailurus serval	0.83	0.50	0.50	**1.00**	0.67	0.83	0.83	0.83	0.50	0.33	0.67	0.83
Lynx canadensis	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	0.75	0.25	**1.00**	**1.00**	0.75	**1.00**	0.75
Lynx lynx	**1.00**	0.67	0.67	0.67	**1.00**	**1.00**	0.67	0.33	**1.00**	**1.00**	0.33	0.00
Lynx pardinus	**1.00**	0.50	**1.00**	**1.00**	**1.00**	0.50	0.50	**1.00**	**1.00**	0.00	**1.00**	**1.00**
Lynx rufus	0.00	**1.00**	0.00	0.00	0.00	**1.00**	0.00	**1.00**	**1.00**	**1.00**	**1.00**	0.00
Neofelis nebulosa	**1.00**	0.67	0.00	0.33	0.67	0.67	0.33	0.67	0.67	0.33	0.67	0.67
Panthera leo	0.88	0.94	0.47	0.88	0.76	0.53	0.18	0.53	0.88	0.82	0.65	0.94
Panthera onca	**1.00**	0.67	0.67	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	0.00	0.67	**1.00**	0.33
Panthera pardus	0.92	0.67	0.67	0.58	0.50	0.75	0.75	0.67	0.50	0.17	0.42	0.83
Panthera tigris	0.00	0.25	**1.00**	0.25	0.75	0.50	**1.00**	0.75	0.00	0.25	0.75	0.25
Panthera uncia	0.75	0.25	**1.00**	0.25	0.50	0.00	**1.00**	0.25	0.75	**1.00**	**1.00**	0.50
Pardofelis badia	**1.00**	**1.00**	**1.00**	**1.00**	0.00	**1.00**	**1.00**	0.00	0.00	0.00	**1.00**	**1.00**
Pardofelis temmincki	0.00	0.00	0.00	**1.00**	**1.00**	0.00	0.00	**1.00**	**1.00**	0.00	0.00	**1.00**
Prionailurus bengalensis	**1.00**	0.67	**1.00**	0.33	**1.00**	0.67	0.67	0.33	**1.00**	0.67	0.67	**1.00**
Prionailurus planiceps	**1.00**	**1.00**	**1.00**	**1.00**	0.00	**1.00**	0.00	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**
Prionailurus rubiginosus	0.00	**1.00**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**1.00**	**1.00**	**1.00**

Prionailurus viverrinus	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	0.75	0.75	0.75	0.75
Puma concolor	0.50	0.00	**1.00**	0.50	0.50	0.50	**1.00**	**1.00**	0.50	0.50	0.50	0.00
Puma jaguarundi	0.00	**1.00**	**1.00**	0.00	0.00	0.00	**1.00**	**1.00**	0.00	0.00	**1.00**	0.00

Figure captions

FIGURE 1. Variable selection by each categorisation scheme (= Meth) is indicated in grey. Results from different dataset are reported including the whole bone LDA models (=Log data), the “size-free” LDA model after regressing out bone length, and the epiphyses log data (proximal and distal separated by line). Meth A = Presence or absence in particular biomes; Meth B = Descriptions from IUCN specialist group; Meth C = GIS-based approach, grassland vs forest; Meth D = GIS-based approach – open vs closed

FIGURE 2. Variable selection by each categorisation scheme (= Meth) is indicated in grey. Results from the ratio datasets (whole bone or epiphyses only) are reported. Meth A = Presence or absence in particular biomes; Meth B = Descriptions from IUCN specialist group; Meth C = GIS-based approach, grassland vs forest; Meth D = GIS-based approach – open vs closed

FIGURE 3. Plot of the discriminant functions extracted for habitat A (Ortolani and Caro, 1996) when using logged linear measurements (number of variables selected = 8).

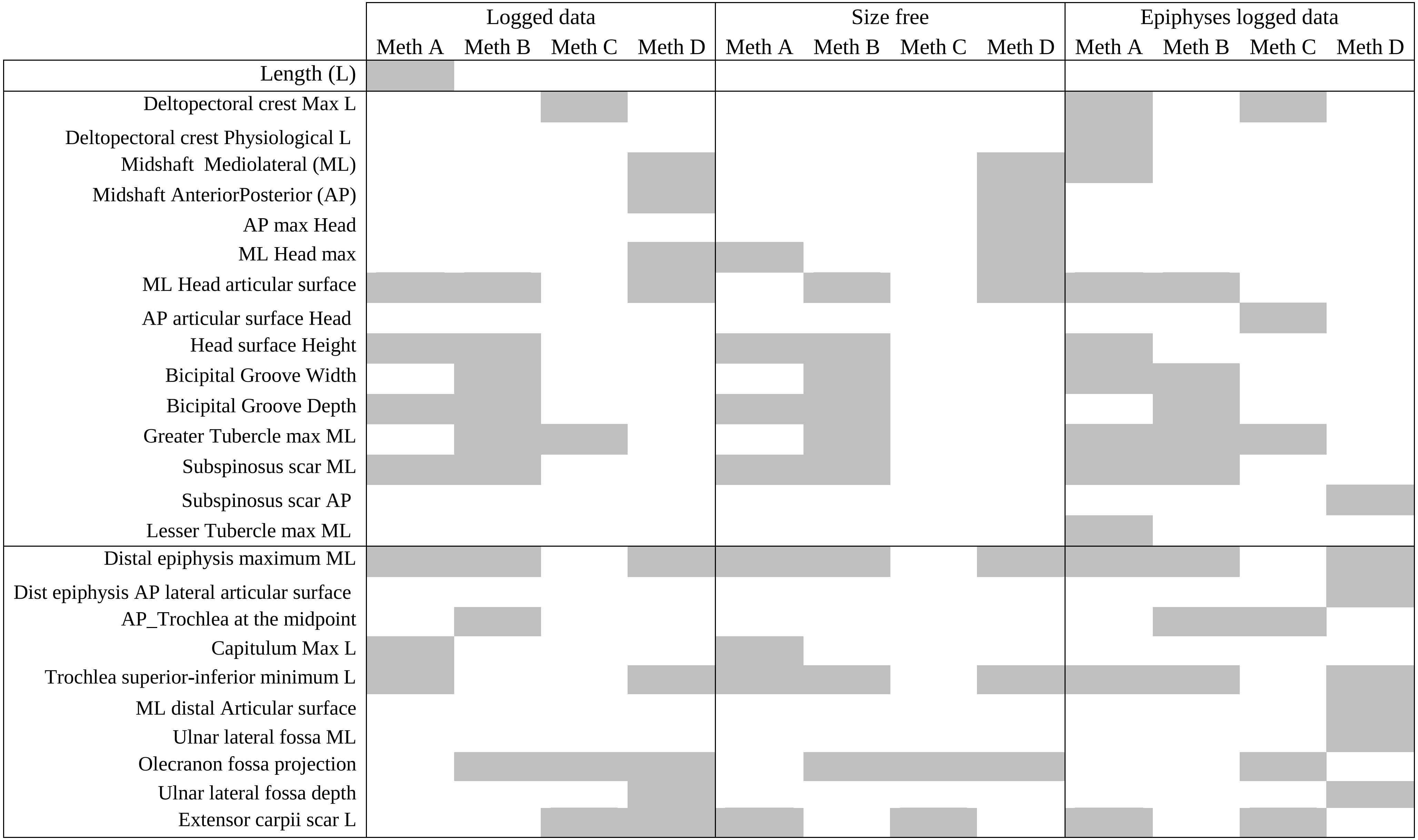
FIGURE 4. Variable selection by each categorisation scheme (= Meth) is indicated in grey. Results from the whole log dataset and epiphyses log dataset of a subsample of large cats are reported. Meth A = Presence or absence in particular biomes; Meth B = Descriptions from IUCN specialist group; Meth C = GIS-based approach, grassland vs forest; Meth D = GIS-based approach – open vs closed

FIGURE 5. Box and whisker plot of percentage of correctly classified cases summarised in 40 LDA models. Central bar indicates the mean value, top and bottom of box indicate the 25% and 75% quartiles, whiskers indicate maximum and minimum values. Abbreviations are: DistalBig= dataset of distal logged data for only big cats; DistalRatio = dataset of distal ratios; DistalRaw= dataset of distal logged data; ProximalBig= dataset of proximal logged data for only big cats; ProxRatio = dataset of proximal ratios; ProxRaw= dataset of proximal logged data; Ratio = dataset of ratios; Raw = dataset of logged data; RawBig = dataset of logged data for big cats only; Residual=dataset “size free”. Habitat A = Presence or absence in particular biomes; Habitat B = Descriptions from IUCN specialist group; Habitat C = GIS-based approach, grassland vs forest; Habitat D = GIS-based approach – open vs closed

FIGURE 6. Schematic representation of proximal and distal humerus epiphyses for three taxa that closely resemble in the DF scores the centroid of each habitat categorisation. Sb_ML = Subspinosus scar ML; H_H = Head surface Height; Dst_ML = Distal epiphysis maximum ML; Cd_L3 = Trochlea superior-inferior minimum L

FIGURE 7. Percentage of predicted cases for fossil specimens. Stratigraphy of specimens from Olduvai is also indicated.

FIGURE 1



	Logged data				Size free				Epiphyses logged data			
	Meth A	Meth B	Meth C	Meth D	Meth A	Meth B	Meth C	Meth D	Meth A	Meth B	Meth C	Meth D
Length (L)	■											
Deltopectoral crest Max L			■						■		■	
Deltopectoral crest Physiological L									■			
Midshaft Mediolateral (ML)				■				■	■			
Midshaft AnteriorPosterior (AP)				■				■				
AP max Head								■				
ML Head max				■	■			■				
ML Head articular surface	■	■		■		■		■	■	■		
AP articular surface Head											■	
Head surface Height	■	■			■	■			■			
Bicipital Groove Width		■				■			■	■		
Bicipital Groove Depth	■	■			■	■				■		
Greater Tubercle max ML		■	■			■			■	■	■	
Subspinosus scar ML	■	■			■	■			■	■		
Subspinosus scar AP												■
Lesser Tubercle max ML									■			
Distal epiphysis maximum ML	■	■		■	■	■		■	■	■		■
Dist epiphysis AP lateral articular surface												■
AP_Trochlea at the midpoint		■								■	■	
Capitulum Max L	■				■							
Trochlea superior-inferior minimum L	■			■	■	■		■	■	■		■
ML distal Articular surface												■
Ulnar lateral fossa ML												■
Olecranon fossa projection		■	■	■		■	■	■			■	
Ulnar lateral fossa depth				■								■
Extensor carpii scar L			■	■	■		■		■		■	

TWO COLUMNS (148 mm)

FIGURE 2

	Ratios whole bone				Ratios Epiphyses			
	Meth A	Meth B	Meth C	Meth D	Meth A	Meth B	Meth C	Meth D
Deltopectoral crest Max L / Deltopectoral crest Physiological length	▨			▨	▨	▨		▨
Midshaft ML / AP				▨				▨
AP max Head / ML Head max				▨				▨
AP max Head / ML Head articular surface	▨		▨	▨		▨	▨	▨
AP max Head / Head surface Height	▨							
AP articular surface Head / Head surface Height					▨			
Bicipital Groove Width / Groove Depth	▨	▨				▨		▨
Greater Tubercle max AP / Greater Tubercle max ML		▨				▨		
Subspinosus scar ML / Subspinosus scar AP		▨			▨			▨
Lesser Tubercle max AP / Lesser Tubercle max ML	▨							
Distal epiphysis maximum ML / Capitulum L	▨				▨			
Trochlea Max L / AP Trochlea at the midpoint		▨		▨		▨		
Trochlea Max L / Capitulum L	▨							
Trochlea Max L / Trochlea superior-inferior maximum L	▨				▨			
Trochlea superior-inferior maximum L / AP_Trochlea at the midpoint				▨				▨
Trochlea superior-inferior max. L / Trochlea superior-inferior min. L	▨			▨	▨			
Olecranon fossa Height / Olecranon fossa projection		▨	▨					
Ulnar lateral fossa ML / Ulnar lateral fossa AP		▨				▨		▨
Pronator tubercle L / Ulnar medial fossa L					▨			
Pronator tubercle L / Extensor carpii scar L			▨				▨	

TWO COLUMNS (148 mm)

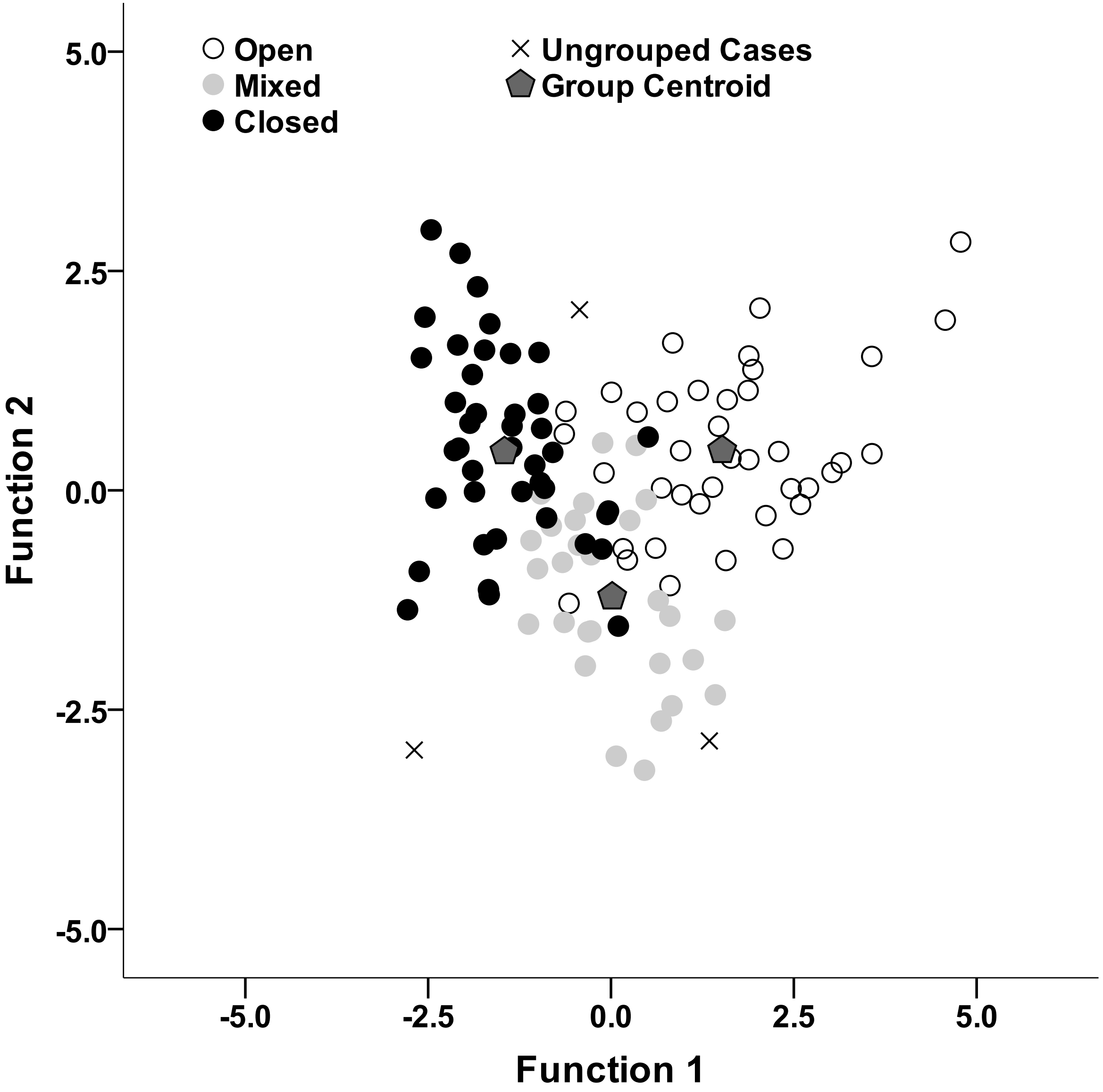


FIGURE 3

ONE COLUMN (72 mm)

FIGURE 4

	Logged data				Epiphyses logged only			
	Meth A	Meth B	Meth C	Meth D	Meth A	Meth B	Meth C	Meth D
Length (L)	■			■				
Deltopectoral crest Max L							■	
Midshaft Mediolateral (ML)				■	■			
AP max Head				■				
AP articular surface Head							■	
AP Head shaft						■		
ML Head max	■	■		■				
ML Head articular surface					■	■		
Head surface Height	■	■			■			
Bicipital Groove Width	■		■	■				
Bicipital Groove Depth	■	■		■	■	■		
Greater Tubercle max ML	■		■		■		■	■
Subspinosus scar ML	■	■			■	■		
Distal epiphysis maximum ML	■	■			■	■		■
Dist epiphysis AP lateral articular surface					■			
Trochlea Max L				■				
AP_Trochlea at the midpoint				■		■		■
Trochlea superior-inferior maximum L				■				
Trochlea superior-inferior minimum L					■			
ML distal Articular surface				■				
Olecranon fossa ML	■	■						
Olecranon fossa projection						■		■
Pronator tubercle L						■		
Ulnar lateral fossa ML				■				■
Ulnar lateral fossa depth								■

TWO COLUMNS (148 mm)

FIGURE 5

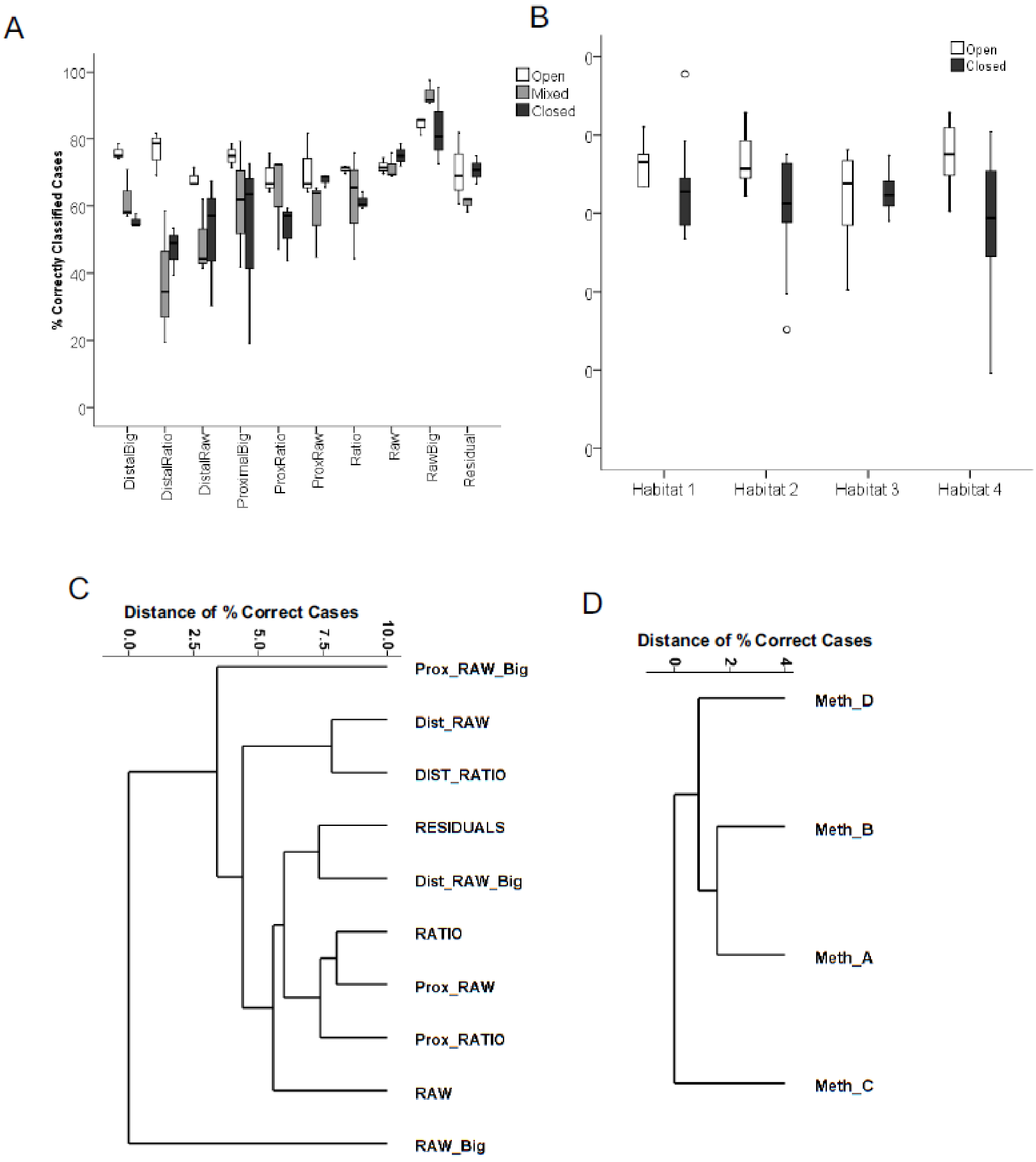
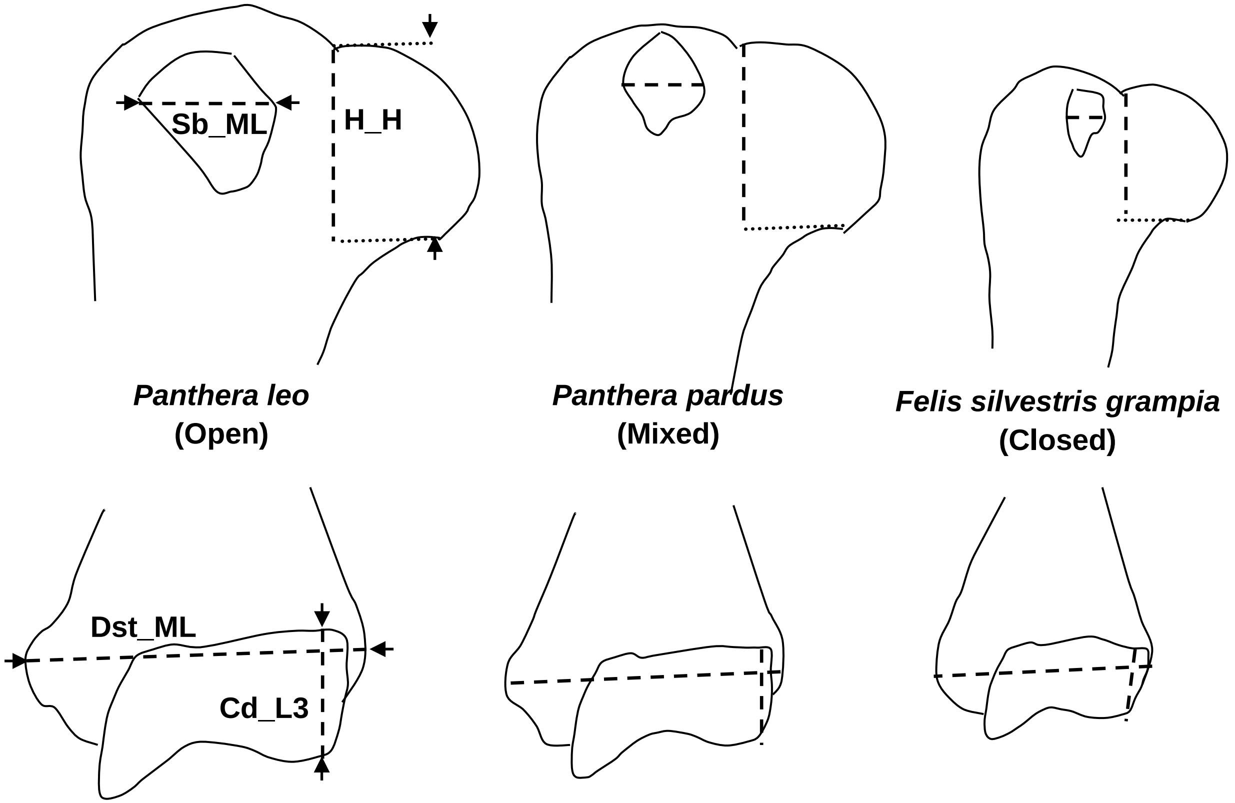
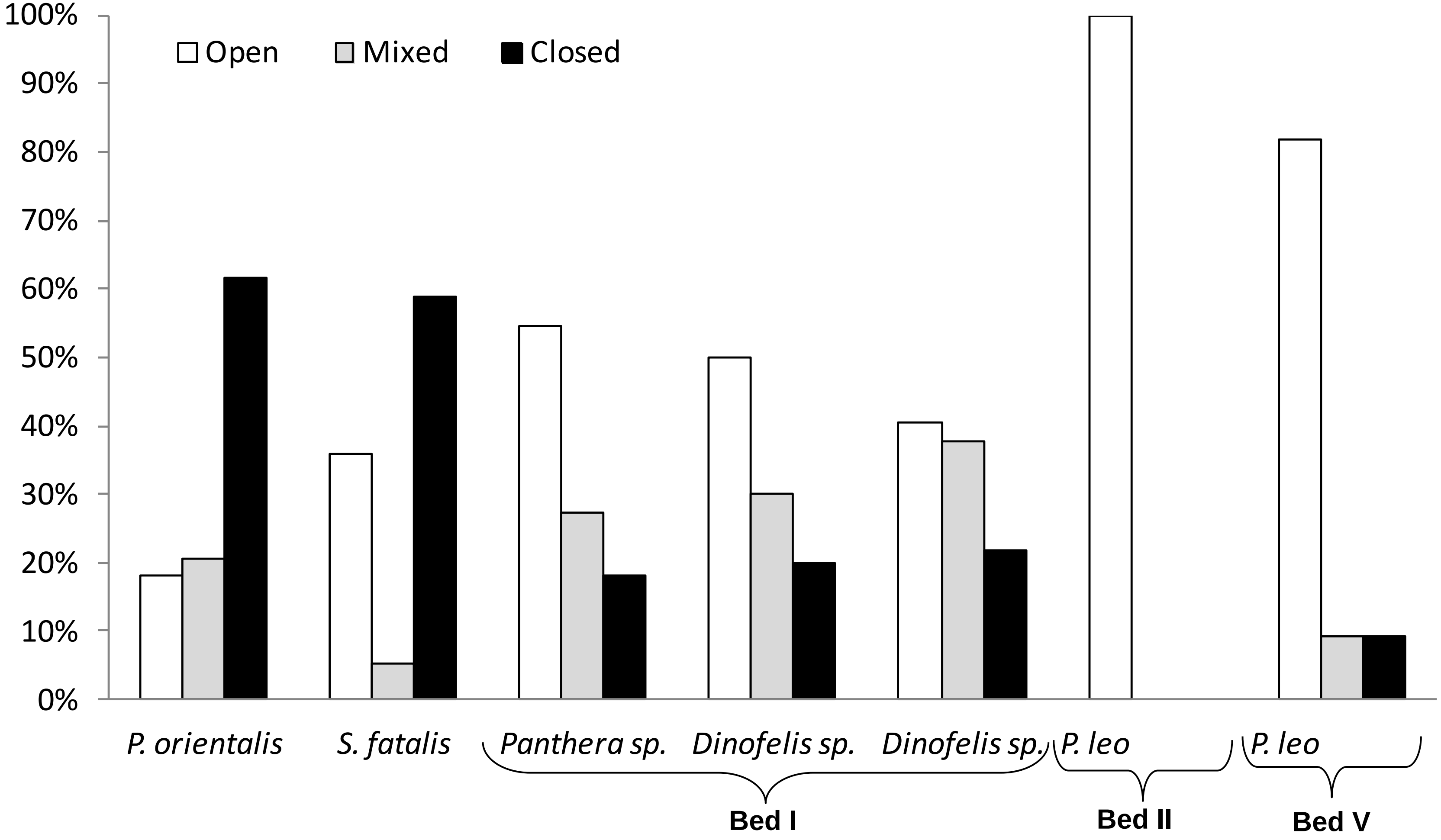

A
% Correctly Classified Cases
0
20
40
60
80
100
Open
Mixed
Closed
DistalBig
DistalRatio
DistalRaw
ProximalBig
ProxRatio
ProxRaw
Ratio
Raw
RawBig
Residual
B
Open
Closed
0
0
0
0
0
0
Habitat 1
Habitat 2
Habitat 3
Habitat 4
C
Distance of % Correct Cases
0.0
2.5
5.0
7.5
10.0
Prox_RAW_Big
Dist_RAW
DIST_RATIO
RESIDUALS
Dist_RAW_Big
RATIO
Prox_RAW
Prox_RATIO
RAW
RAW_Big
D
Distance of % Correct Cases
0
2
4
Meth_D
Meth_B
Meth_A
Meth_C

FIGURE 6



ONE COLUMN (72 mm)

FIGURE 7



ONE COLUMN (72 mm)