

1 Ecomorphology of the cervid calcaneus as a proxy for palaeoenvironmental reconstruction

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8 Running title: Ecomorphology of the cervid calcaneus

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29 Abstract:

30 This study presents new ecomorphological models for the cervid calcaneus that can be used to
31 make predictions about the nature of ancient environments. Using geometric morphometrics
32 to quantitatively assess the length of the articular surface supporting the malleolus, the length
33 and orientation of the tuber calcanei, and the position of the articular facets, we aimed to
34 establish correlations between morphological traits, locomotor behavior and environmental
35 parameters in extant cervids. The morphology of the calcaneus was found to primarily vary with
36 locomotor strategy and habitat, along a continuum from habitats with an open vegetation
37 structure to habitats with a closed vegetation structure. Confounding factors, including sexual
38 dimorphism, allometry and phylogeny were accounted for using Principal Component Analysis,
39 regressions and phylogenetic comparative methods. The results of our analyses suggested that
40 these factors did not substantially obscure habitat predictions. As such, the calcaneus provides
41 a valuable proxy for palaeoenvironmental reconstruction that is broadly applicable to
42 Quaternary fossil assemblages with a sufficiently large sample of cervids.

43 Keywords: Cervidae, palaeoecology, ecomorphology, morphometrics, locomotion

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49 1. Introduction

50 Accurate palaeoenvironmental reconstructions are important components of the testing and
51 refinement of hypotheses regarding patterns in mammalian evolution, including that of our
52 own species (Reed, 1997; Potts, 1998; Degusta and Vrba, 2003; Curran, 2012). In order to
53 construct high resolution environmental frameworks, it is imperative to use a combination of
54 different proxies in contrast with each other (Bishop et al., 2006). Although taphonomic factors
55 dictate the availability of specific palaeoenvironmental proxies at palaeontological and
56 archaeological sites, the study of vertebrate remains often plays an important role in habitat
57 reconstructions (e.g. Geraards et al., 1986; Bobe et al., 2007; Blain et al., 2014). This is often
58 accomplished by looking at the presence or absence of certain taxa in the fossil record that are
59 indicative of specific ecological conditions (e.g. Vrba, 1975; Shipman and Harris, 1988). A
60 potential weakness of this approach, however, is that it assumes that the ecological
61 preferences of extinct species were similar to those of their closest living relatives (Andrews,
62 1995). This is not necessarily a valid assumption (Dodd and Stanton, 1990).

63 Ecomorphology can circumvent this problem by examining the functional morphology of
64 skeletal elements in a vertebrate group as it relates to ecological variables (Andrews and Hixon,
65 2014). Comparing morphological patterns in recent species with those observed in extinct
66 forms, allows us to make inferences about probable adaptations in fossils (Degusta and Vrba,
67 2003; Andrews and Hixon, 2014). Although not uncriticized (Klein et al., 2010), ecomorphology
68 is often considered a taxon-free method, as it can be applied on mammalian remains that have
69 not been identified beyond the family level (Kovarovic and Andrews, 2007). As a method it can

70 therefore provide a more direct reconstruction of past habitats, as it considers how animals
71 functioned in their ecosystem instead of simply which taxa were present at a site (Curran,
72 2009).

73 Palaeoecologically focussed ecomorphological studies have been conducted on a number of
74 mammalian groups, including canids (Meloro and Louys, 2011), ursids (Figuerido et al., 2009),
75 rodents (Fernandez and Campomanes, 2003), bats (Stimpson, 2010), equids (Scott, 2004;
76 Schellhorn, 2009), suids (Bishop, 1994; Bishop et al., 2006), and –especially relevant to this
77 study- ruminants (e.g. Kappelman, 1988; Kappelman et al., 1997; Plummer and Bishop, 1994;
78 Scott, 2004; Plummer et al., 2008; Schellhorn, 2009; Barr, 2017). Within the latter group the
79 focus has been mostly on the Bovidae. Outside the work by Curran (2009, 2012, 2015, 2018),
80 the Cervidae have received comparatively little attention, despite their ecological similarity and
81 phylogenetic relatedness to the Bovidae (Geist, 1998; Janis, 2007). Although the capacity of
82 deer to cope with more extreme environments is not of the same magnitude as that of bovids
83 (Geist, 1998; Janis, 2007), this family is characterized by high species diversity and adapted to a
84 range of environments (Putman and Fluek, 2011). As cervids are a common taxonomic group in
85 European and Asian Pleistocene assemblages (Kurten, 1968), they have the potential to serve
86 as valuable palaeoecological proxies in the same way as bovids have for African sites (e.g.
87 Plummer and Bishop, 1994; Forrest et al., 2018).

88 This paper presents newly developed ecomorphological models for the cervid calcaneus. This
89 element was not only selected because of its high chance of survival in the fossil record
90 (Borerro, 1990), but also because it represents an important component of the locomotor

91 apparatus, and because its morphology is thought to be primarily constrained by environmental
92 factors (Köhler, 1993; Polly, 2007; Curran, 2012). Although the latter assumption is further
93 explored in section 1.1, it suggests that the calcaneus can be used to predict habitat preference
94 in extinct species. By adding fossil specimens of unknown ecological affinity to a training set of
95 extant specimens, it should be possible to make inferences about the nature of Pleistocene
96 cervid environments.

97 1.1 Theoretical basis and functional framework

98 The connection between cervid morphology and the environment, finds its basis in the idea
99 that predator evasion strategy is the main selective constraint on the locomotor system in
100 artiodactyls (Geist, 1998; Curran, 2009). Ruminants especially have a range of methods to
101 overcome encounters with predators (Ralls, 1974; Geist, 1998), but once detected, flight is the
102 chief anti-predatory counter measure (Geist, 1998). Consequently, such animals have evolved
103 several modes of locomotion, employed during flight. Despite limited data on how locomotion
104 is precisely related to evasion tactics, there are five principal locomotor behaviors linked to
105 predator evasion in ruminants: leaping (vertical jump), bounding (long horizontal jump),
106 stotting (a bouncing gait), prancing (type of pronounced and exaggerated high step) and tacking
107 or zig-zag running (sharp turn that suddenly changes course) (Caro, 1986, 1994; Caro et al.,
108 2004). Prancing and stotting act more as signals to wrongfoot the predator than as true
109 locomotor adaptations for flight (Caro, 1994, Caro et al., 2004), but tacking is the preferred
110 flight mode amongst species living in open habitats (Caro, 2004). Leaping is more prevalent

111 when fleeing animals have to deal with rugged topography or elaborate vegetation (Caro,
112 1994).

113 These observations support the idea that predator evasion and locomotor strategy are strongly
114 connected to the characteristics of ruminant habitats (Jenkins and Camazine, 1977; Kappelman,
115 1988; Scott, 2004; Barr, 2014a). Because each locomotor strategy has certain biomechanic
116 requirements, differences in habitat structure are predicted to be reflected in the morphology
117 of the limb bones (e.g. Degusta and Vrba, 2003, 2005a, 2005b; Kovarovic and Andrews, 2007;
118 Schellhorn, 2009; Barr, 2018). Ruminants under predation pressure in dense vegetation have
119 limb bones adapted for saltatorial evasion, allowing them to optimally jump over obstacles in
120 the landscape, to maximize the distance between themselves and their pursuer (Leinders,
121 1979; Kappelman, 1988; Köhler, 1993; Curran, 2009). Ruminants that evade predators in open
122 vegetation, are thought to have limb bones adapted for cursoriality, allowing them to quickly
123 generate speed and accommodate for the forces associated with quick tacking movements
124 (Leinders, 1979; Kappelman, 1988; Köhler, 1993). Although most of this ecomorphological
125 groundwork is based on bovids, it is thought that these principles also apply to cervids
126 (Kovarovic, 2004; Curran, 2009, 2012, 2015).

127 There are multiple ways in which these adaptations are thought to be expressed in the
128 morphology of the cervid calcaneus. The calcaneus, which together with the astragalus
129 functions as a hinge point between the tibia and the metatarsus (the hock joint) (Barr, 2014b),
130 acts as a lever for the triceps surae muscles that insert into the tuber calcanei via the achilles
131 tendon (Galvez-Lopez and Casinos, 2012). Being mostly restricted to movement in the sagittal

132 plane (Schaeffer, 1947), the calcaneus pushes the limb against the ground and causes the
133 animal to advance by acting as a moment arm of the triceps surae muscles (Alexander, 1983;
134 Galvez-Lopez and Casinos, 2012; Curran, 2012; Barr, 2018). As part of this mechanism; the
135 length of the lever arm of this muscle group (the tuber calcanei) to a large degree determines
136 the force produced by the posterior limbs during locomotion. Increasing its length increases
137 power but will make the joint move slower, a trait considered adaptive in saltatorial species
138 (Curran, 2009, 2012) (Fig. 1). A shorter tuber will lack power, but allows for quicker movement
139 and acceleration, a trait optimal for cursoriality (Curran, 2009).

140 The rest position of the calcaneus is also thought to differ between cursorial and saltatorial
141 forms. If the tuber calcanei is positioned more vertically relative to the astragalus and the
142 cubonavicular, the distance covered by the lever arm is shorter, but less powerful (Polly, 2008;
143 Curran, 2012). This adaptation is associated with cursorial animals of open environments that
144 strongly increase their number of paces when accelerating (Gambardyan, 1974; Geist, 1998;
145 Curran, 2012). When the tuber has a more horizontal position, more power is generated when
146 the muscles contract, a trait advantageous in saltatorial species (Curran, 2009, 2012).
147 Morphologically this is thought to be expressed in a more oblique orientation of the tuber
148 relative to the articular surfaces of the calcaneus in cursorial species (Curran, 2012).
149 Additionally, there are indications that in cursorial forms the calcaneus is more tightly locked to
150 the astragalus, due to a higher relief in the ridges and grooves on the articular surfaces
151 between the calcaneus and astragalus and because the articular facet supporting the malleolus
152 is thought to be larger and more developed (Polly, 2007; Scarborough et al., 2016). This way

153 movement is minimized in the parasagittal plane, so as to provide optimal stabilization when
154 running (Polly, 2007).

155 To translate this functional framework into an ecomorphological model, our study builds on
156 earlier studies conducted by Curran (2009, 2012, 2015, 2018), who found correlations between
157 the morphology of the calcaneus and habitat type, using a Geometric Morphometrics (GMM)
158 model based on ten landmarks. In her work, Curran (2012) saw evidence that cervids associated
159 with open vegetation have calcanei adapted for more cursorial movement and vice versa.
160 Although Curran (2009, 2012) observed some variation in mobility of the hock joint elements,
161 with closed environment species having a wider sustentaculum than open adapted species, the
162 primary morphological variation noted between open and closed environment specimens was a
163 difference in the rest position of the calcaneus. More horizontally oriented calcanei were found
164 in closed-adapted cervids and more vertically positioned calcanei in open environment forms
165 (Curran, 2012). The models presented in our paper are an extension of those pioneered by
166 Curran (2009, 2012, 2015). Using an alternative methodology (i.e. a different data acquisition
167 protocol, alternative habitat/functional group categorization, an altered set of landmarks, an
168 extant dataset less skewed towards North and South American species, and different methods
169 of analysis) this study aims to evaluate some of the ecomorphological correlations found by
170 Curran (2009, 2012, 2015) and potentially establish new ones.

171 Based on the ecomorphological models and theoretical framework outlined above, we have
172 summarized three functional hypotheses related to the calcaneus (Table 1). The viability of
173 these hypotheses and the extent to which specific morphotypes can be correlated with
174 locomotor behaviors and environmental parameters, are addressed in this paper.

175

176 2. Materials

177 Our models were mainly tested using extant cervid data collected by the authors at several
178 European and American institutes (see supplementary data). In addition, 3D data from a small
179 number of specimens was shared by the Max Planck Institute of Evolutionary Anthropology
180 (Niven et al., 2009) and the Virtual Zooarchaeology of the Arctic project (Maschner et al., 2011;
181 Betts et al., 2011). In total 129 calcanei of extant individuals were studied, belonging to 26
182 species and 6 tribes (Table 2). The composition of the dataset was to an extent a function of the
183 availability of species at the different institutes and sample sizes were in the same range as
184 many similar studies (e.g. Weinand, 2005; Curran, 2009; Schellhorn, 2009). A maximum of 16
185 specimens were scanned per element for each species, to prevent the dataset from becoming
186 skewed towards more common taxa. Although captivity is recognized to affect morphology in
187 certain mammals (O'Regan and Kitchener, 2005), a number (n=23) of known captive specimens
188 were included to maximize diversity and sample size. The sample of captive individuals per
189 species was too small for a robust analysis of the potentially confounding effects of this factor,
190 but preliminary tests (not included here) conducted on six *Axis axis* specimens and six *Rangifer*
191 *tarandus* specimens, suggested that at least for these species the effects are limited.

192 Both sexes were included in the sample and only adult, non-pathological, specimens were
193 analyzed. Skeletons were considered adult if all epiphyses were fused and all teeth erupted.
194 When possible, the left calcaneus was selected, but in some cases scanned specimens had to be
195 virtually mirrored using Meshlab 2.0. (Cignoni et al., 2008).

196

197 3. Methods and statistical analyses

198 To emphasize the fact that different morphotypes vary as a result of functional differences
199 related to locomotion (Barr, 2014a, 2014b), we used a combined functional/ecological category
200 system, rather than a purely ecological one (e.g. Degusta and Vrba, 2003; Kovarovic and
201 Andrews, 2007; Curran, 2012). Although this difference in categorization was mainly
202 theoretical, in cases where species had an atypical locomotor strategy to cope with certain
203 environments (e.g. species of large body size lacking a capacity for saltatorial locomotion) this
204 had a potential effect on how taxa were categorized. Our approach should be considered an
205 attempt to take the complex interactions between habitat and locomotion into account, but
206 what is ultimately needed for a more complete understanding of the relationship between
207 locomotion and ecology is a series of experimental studies on living specimens (e.g.
208 Wainwright, 1991). In the absence of such data we assigned the cervid calcanei into five
209 habitat/locomotor types based on different sources from the literature (see Table 2), a number
210 chosen to avoid oversimplifying actual habitat variation, but maximize the ability of our
211 statistical models to classify specimens into the correct category (Curran, 2009).

212 Type A animals (57 specimens) were characterized by a cursorial locomotor strategy, and
213 preference for open environments. However, as cervids are rarely found in truly open,
214 coverless environments (Geist, 1998), this category united taxa adapted to open woodland and
215 the few species found in open plains. Open woodland was defined as an area of trees with an
216 open canopy of 40% or less closure (Thomas and Packham, 2007). Type B species (35

217 specimens) were saltatorial forms, adapted to closed environments. This included animals of
218 forest types, ranging from closed woodland (defined as an area of trees with more than 40%
219 canopy closure (Thomas and Packham, 2007)) to tropical rainforest. Type C species (eight
220 specimens) were intermediate between type A and type B species and generalists adapted to
221 open- or closed environments. Although some of the species in this group may be behaviorally
222 closer to either the type A or type B forms, they lack the endurance of real cursorial species but
223 are also less adept at leaping than saltatorial species. Because of this reason, and because of
224 the limited number of specimens in this group, it was neither appropriate to add them to one of
225 the other categories, nor to split them into multiple sub-categories.

226 There were two additional types, that had either a more cursorial or saltatorial strategy, but
227 merited their own separate categories for being associated with very specific environmental
228 conditions. The type D group (eight specimens) included high altitude species from
229 mountainous environments and may require a combination of saltatorial and cursorial traits
230 (Geist, 1998). Type E cervids (21 specimens) were defined as species of open wetlands. They are
231 generally considered cursorial forms, but the unusual structure of these habitat types may also
232 favor certain saltatorial traits (Curran, 2009).

233 Although many authors have made use of linear measurements to quantify osteomorphological
234 traits in ecomorphology (e.g. Kappelman, 1988; Bishop et al., 2006; Scott, 2004; Kovarovic and
235 Andrews, 2007), recent studies (e.g. Cucchi et al., 2009, 2011; Brophy et al., 2014; Forrest et al.,
236 2018) have demonstrated that Geometric Morphometrics (GMM) have advantages over linear
237 measurement when applied on artiodactyl morphology. We therefore followed Curran (2009,

238 2012) and opted for a landmark based three-dimensional GMM approach to quantify shape.
239 This allowed for an efficient control of isometric size effects (Zelditch et al., 2004; Viscosi and
240 Cardini, 2011) through the application of Generalized Procrustes Analysis (GPA) on the raw
241 coordinate data (see Bookstein, 1991; Zelditch et al., 2004). It also permitted for a better
242 preservation of object geometry in the measured data (Rohlf and Marcus, 1993; Slice, 2005;
243 Baab et al., 2012), a distinct advantage when quantifying subtle shape differences inherent to
244 the morphologically conservative cervids (Kurten, 1968; Strand Vidarsdottir et al., 2002; Perez
245 et al., 2007). And thirdly, GMM allowed us to visualize shape differences using thin plate spline
246 transformation grids that describe morphological variation as distortions in a grid (Bookstein,
247 1991; Zelditch et al., 2004).

248 We collected raw data on skeletal elements in the form of 3D surface scans generated with a
249 NextEngine 2020i laser scanner. Using the associated software Scanstudio HD 1.3.2, individual
250 scan divisions were cleaned and fused into 3D-objects, after which landmarks were virtually
251 placed on the objects with Landmark editor 3.0 (Wiley et al., 2005). Six landmarks were placed
252 at discrete anatomical loci on the calcaneus (Fig. 2). The positioning of the landmarks was
253 inspired by earlier ecomorphological models (Kovarovic and Andrews, 2007; Curran, 2009,
254 2012, 2015), but also chosen because of their relevance to the functional hypotheses. The
255 resulting coordinate data were then exported from Landmark editor and uploaded in
256 Morphologika 2.5 (O'Higgins and Jones, 2006), where a GPA was conducted on the data. From
257 this software we generated an output-file with procrustes residuals and (log) centroid size as a
258 size measure, for further statistical analysis in PAST 2.17 (Hammer et al., 2001).

259 Following earlier ecomorphological studies (e.g. Bignon et al., 2005; Figueirido et al., 2009;
260 Forrest et al., 2018) we made use of Principal Components Analysis (PCA) to simplify
261 descriptions of variation between specimens and groups and as a primary method to explore
262 morphological variation (Dryden and Mardia, 1998; Zelditch et al., 2004). This reduced the
263 chances of an over-fitted the model, a problem that can arise when e.g. Linear Discriminant
264 Analyses are conducted on smaller datasets with unequally balanced samples (Kovarovic et al.,
265 2011). Nevertheless, to emphasize between group differences we made use of between groups
266 PCA (bgPCA), where eigenvectors are derived from the variance-covariance matrix of the group
267 means instead of all the data-points (Seetah et al., 2012). PCA was in a first instance also used
268 to assess intra-observer error. To test the repeatability of the digitization procedure we used an
269 adjusted version of a protocol by Adriaens (2007), that consisted of randomly selecting and
270 scanning five specimens and landmarking each specimen five separate times using our
271 landmarking procedure. If the replicated specimens clustered tightly together on the first two
272 axes of a PCA conducted on the dataset, the digitization error was considered low (Adriaens,
273 2007). The same procedure (but without re-scanning the specimens) was repeated on another
274 five specimens, to explore for potential error in repeating the landmarking protocol.

275 To assess statistical significance ($p < 0.05$) of cluster separations in the PCA's, an approach was
276 taken that involved conducting a non parametric MANOVA (npMANOVA) on the relevant PC-
277 scores (Schutz et al., 2009; Polly et al., 2013; Marramà and Kriwet, 2017; Hou et al., 2021). We
278 opted for a permutational test, as assumptions required for parametric testing -including
279 across-group homogeneity of variance-covariance matrices and normal distribution- are not
280 necessarily met by highly dimensional data resulting from GMM (Cardini et al., 2015; Lopez-

281 Lazaro et al., 2018). NpMANOVA tests were run on a data matrix including all relevant principal
282 component scores, as indicated by a scree plot of the eigenvalue distribution (Jackson, 1993).
283 When between-group differences were significant, the overall npMANOVA was followed by a
284 post-hoc test in the form of pairwise npMANOVAs between all pairs of groups, to assess which
285 groups differed significantly. Bonferroni corrected probabilities were reported to adequately
286 control for Type I errors (Dunn, 1961, 1964).

287 In addition we accounted for a number of potentially confounding factors. To assess the effect
288 of allometry, we regressed PC-scores against the natural log of centroid size (e.g. Cucchi et al.,
289 2011; Owen, 2013), using the ordinary least squares algorithm (following Kilmer and Rodriguez,
290 2016). If significant correlations between size and shape were found in the regressions, this was
291 considered indicative of an allometric effect (Zelditch et al., 2004). A regression was also
292 computed of the average centroid size per species against the natural log of average body mass
293 for each species, to test if centroid size could be considered a good proxy for total body size. As
294 no specific mass was known for the individual studied skeletons, we relied on species averages
295 from the literature (see Table 2 for references).

296 To visually assess the confounding effects of a phylogenetic signal, mean shapes per species
297 were calculated and projected on the PCA scatterplots derived from the variance-covariance
298 matrix of the habitat/locomotion group means. Minimal spanning trees were calculated to
299 estimate the minimal total lengths connecting all datapoints as an aid in grouping together taxa
300 (Hammer et al., 2001). Furthermore, we made use of several quantitative approaches to
301 evaluate the influence of phylogeny on patterns of morphological variation in the dataset. We

302 first used Caper 1.0 in R (Orme et al., 2018) to conduct phylogenetic generalized least squares
303 (PGLS) regressions (Martins and Hansen, 1997) and regressed the relevant PC-scores on our
304 functional/habitat groups (Meloro, 2007, 2008; Walmsley et al., 2012; Barr, 2014a, 2014b;
305 Curran, 2015). In this weighed regression, phylogeny was incorporated as an error term during
306 regression of the shape variables on ecological/locomotor categories transformed into dummy
307 variables (Martins and Hansen, 1997; Walmsley et al., 2012). Using tree branch lengths to
308 estimate phylogenetic covariance, the covariance for two given species was proportional to the
309 sum of branch lengths from the root to the last common ancestor (Monteiro, 2013). It was
310 assumed that cervid traits evolved according to a simple Brownian motion model (see
311 Felsenstein, 1985; Monteiro, 2013; Barr and Scott, 2014). Habitat/locomotion groups were
312 transformed into dummy variables and regressed against the mean shape coordinates for each
313 species (Walmsley et al., 2012). Phylogenetic tree distances were downloaded from the
314 10KTrees website (Arnold et al., 2010) and topologies checked for accuracy against Heckeberg's
315 (2020) cervid phylogenetic framework. Two species present in the main analyses (*Cervus*
316 *marianus* and *Cervus alfredi*), were excluded from the PGLS regressions, as they were absent
317 from the phylogenetic tree. *Cervus elaphus* and *Cervus canadensis* were considered conspecific
318 in the phylogenetic tree and consequently lumped together in the PGLS regressions. Pagel's λ
319 was used as a measure of phylogenetic dependence (Pagel, 1999). In this approach, a maximum
320 likelihood estimate is used to find the value that best explains variation between species at the
321 tips of a phylogeny (Edwards and Cavalli-Sforza, 1964; Kamlar and Cooper, 2013). More
322 specifically, this measure was derived by multiplying all off-diagonal elements (or the
323 covariances between species pairs in the phylogenetic variance-covariance matrix) by λ (Pagel,

324 1999; Harmon, 2019). Values close to 0 indicate a weak phylogenetic signal, and values close to
325 1 indicate that related species were morphologically more similar (Molina-Venegas and
326 Rodriguez, 2017).

327 In addition, we used the phylogenetic tree from 10KTrees (Arnold et al., 2010) to calculate
328 Blomberg's K -statistic (Blomberg et al., 2003) for the relevant principal components. This
329 statistic gives the magnitude of phylogenetic signal as a ratio of the mean squared error in
330 phylogenetic tip data measured from the phylogenetic corrected mean and the variance as
331 expected under a Brownian motion model (Blomberg et al., 2003; Münkemüller et al., 2012).
332 Values below 1 indicate that related species resemble each other less than expected under a
333 Brownian motion model, while values above 1 suggest that related species have more similar
334 traits (Diniz-Filho et al., 2012). This analysis was conducted in the Picante package for R (Kembel
335 et al., 2010). Statistical significance ($p < 0.05$) of K was tested with permutation tests using 9999
336 replications (Alvarez et al., 2011).

337 Although earlier work on cervids (Curran, 2009) already indicated that the effect of sexual
338 dimorphism is small on the shape of the calcaneus, an exploratory analysis was performed on a
339 subset of 31 calcanei of *Dama dama* (five females and six males), *Axis axis* (five females and
340 four males) and *Capreolus capreolus* (six females and five males). To examine if separations
341 were confounded by sex differences, a PCA was conducted on the dataset, followed by an
342 npMANOVA on the first four principal components.

343 4. Results

344 The results of our repeatability tests revealed a close clustering together of replicates (Fig.3).
345 This indicated that the error due to variation caused by the data acquisition and digitization
346 protocols was minimal. Furthermore, a PCA on 31 *Dama dama*, *Axis axis* and *Capreolus*
347 *capreolus* calcanei of known sex (Fig. 4) revealed no clear visual separation between males and
348 females, despite clear inter-specific differences. This was confirmed by an npMANOVA on the
349 first four principal components ($F=4.68$, $p<0.001$), with pairwise comparisons indicating
350 significant differences between the three species (all $p<0.001$), but non-significant differences
351 between males and females (*Axis axis*: $p=0.786$, *Dama dama*: $p=0.694$, *Capreolus capreolus*:
352 $p=0.585$).

353 The results of a PCA on all calcanei gave visual separation along the axes of the first four –and
354 especially the first two- principal components (Fig. 5). Based on a scree plot of the eigenvalues,
355 PC1 to PC4 (summarizing 99.8% of the total variance) were retained for further analysis. The
356 npMANOVA on the relevant PC-scores indicated highly significant overall differences between
357 the habitat/locomotor groups ($F=4.35$, $p=0.0001$). Pairwise comparisons (Table 3) showed that
358 all but one relationship exhibited significant differences. The exception was the type C group,
359 that did not differ significantly from the type B group ($p=0.2276$), suggesting the intermediate
360 specimens were similar in morphology to the type B specimens, as far as the shape differences
361 described by the first four axes were concerned.

362 Visual assessment of the thin plate spline transformations associated with PC1 –and
363 representing the minimum and maximum scores along that axis- revealed two main shape
364 changes (Fig. 6 and Table 4). A first shape change was a difference in angle of the tuber calcanei

365 relative to the articular surfaces of the element. Specimens with a more positive score had
366 tuber calcanei that were positioned more perpendicular relative to the anterior part of the
367 bone with the articular surfaces. Specimens with a negative score had tuber calcanei
368 positioned less perpendicular relative to the anterior part of the calcaneus. In addition, the first
369 axis also appeared to summarize variation in the relative length of the tuber calcanei.
370 Specimens with a high positive score tended to have calcanei with a relatively shorter tuber
371 than specimens with a low score.

372 Shape differences noted along PC2 were mostly expressed in the articular surface that supports
373 the malleolus, which tended to be longer in the antero-posterior direction in specimens with a
374 high score (Fig. 6 and Table 4). In specimens with a low score this articular surface was shorter
375 in the antero-posterior direction. The variation in shape summarized by PC3 seemed to be
376 mainly expressed in a difference in infero-superior length of the posterior talar articular surface
377 and in the distance between the articular surface of the malleolus and the posterior talar
378 articular surface (Fig. 6 and Table 4). The main variation observed along PC4 was a difference in
379 position of the anterior end of the articular surface supporting the cubonavicular relative to the
380 landmarks on the posterior talar articular surface (Fig. 6 and Table 4). In specimens with a
381 lower negative score the anterior end of this facet was placed at a more superior height relative
382 to the most infero-lateral point of the posterior talar articular surface.

383 Although the thin plate spline visualizations suggested that a substantial shape variation was
384 explained by the (first two) principal components, it remained to be evaluated how these
385 patterns were reflected in specimen and group distributions in the scatterplots. Despite

386 substantial overlap, type A specimens gave a high score on the first axis, while type B specimens
387 gave a lower score (Fig. 5). In light of the shape variation explained by this axis, this implied that
388 the type A and type B groups had substantially different morphological characteristics. As
389 expected, the intermediate type C specimens gave intermediate scores on PC1. In other words,
390 there was a continuum from saltatorial specimens of closed environments, over intermediate
391 specimens, to cursorial specimens of open environments. This continuum was also observed
392 along the second axis. It should, however, be mentioned that on both axes the intermediate
393 type C group showed more visual overlap with the type B group than with the type A group.
394 This was in line with the results of the npMANOVA, which indicated that the differences
395 between the type C and the type B group were non-significant.

396 The type D specimens (high altitude) gave high scores on the first axis, most similar to the type
397 A group. On the second axis, the mountain group was less well separated from the other
398 groups, but generally gave a higher positive score than the type B specimens. This indicated
399 that the calcaneus of the type D species was at least morphologically different from the
400 saltatorial type B species of closed environment. The type E group (cursorial/open wetland) was
401 relatively well separated from the other specimens when PC1 was plotted against PC2. On PC1
402 this group produced predominantly negative scores, similar to the type C and type B groups.
403 Somewhat unexpected, it suggested that the specimens were morphologically more similar to
404 the intermediate- and saltatorial (closed habitat) species. On the second axis, however, this
405 group gave a high score more similar to the cursorial type A group. Specimen distributions
406 along PC3 and PC4 did not show good visual separation between the groups (Fig. 5). The

407 morphological variation along these axes did not appear to be expressed in any discernable
408 patters.

409 To test if the observed morphological variation was confounded by allometric size effects, we
410 first regressed centroid size against log transformed average body mass per species. The results
411 indicated that there was a highly significant correlation ($R^2=0.875$, $p<0.001$) between the size of
412 the calcaneus and the average body mass of the species. Assuming that cervid body mass is a
413 good indicator of total body size (Curran, 2009), this suggested that centroid size could be
414 considered a good proxy for body size. Then we assessed the results of the regressions of shape
415 against log centroid size (Fig. 7). When PC1 ($R^2=0.0414$, $p=0.0202$) and PC2 ($R^2=0.0306$,
416 $p=0.0462$) were regressed against log centroid size a significant, but weak, correlation was
417 found. The regression of the third component against log centroid size ($R^2=0.005$, $p=0.4199$)
418 indicated no significant correlation between size and shape. This implied that only a small
419 amount of the shape variance explained by the first three components could be attributed to
420 allometry. In PC4 the allometric effect was potentially somewhat stronger, with a -still relatively
421 weak- correlation with centroid size ($R^2=0.0975$, $p<0.001$).

422 A PGLS regression of habitat/locomotion dummy variables on PC1 to PC4 ($R^2=0.283$, overall
423 $p=0.236$) resulted in a high Pagel's λ (0.906), but one that was not significantly different from 1
424 ($p(H_0:\lambda=1)=0.2902$) or from 0 ($p(H_0:\lambda=0)=0.3227$). The λ value was high in PC1 ($\lambda=0.86$,
425 $p(H_0:\lambda=1)=0.0106$, $p(H_0:\lambda=0)=0.0217$) and PC4 ($\lambda=0.949$, $p(H_0:\lambda=1)=0.632$, $p(H_0:\lambda=0)=0.102$),
426 but lower in PC3 ($\lambda=0.683$, $p(H_0:\lambda=1)=0.034$), $p(H_0:\lambda=0)=0.0217$), and especially in PC2 ($\lambda=0.33$,
427 $p(H_0:\lambda=1)<0.001$), $p(H_0:\lambda=0)=0.348$). These results indicated that there was a phylogenetic

428 signal present in PC1, PC3 and PC4, but as p -values were not significantly different from the
429 upper (1) and lower bound (0) for PC1, and both significantly different from the lower and
430 upper bound for PC3 and PC4, it was implied that phylogeny was only partially responsible for
431 the morphological differences summarized by the PCA. For PC2 the values showed that the
432 phylogenetic signal was limited. Our calculations of Blomberg's K -values for the relevant
433 principal components (PC1 to PC4) confirmed this relatively limited phylogenetic signal. PC1
434 ($K=0.356$, $p=0.032$), PC2 ($K=0.407$, $p=0.02$), PC3 ($K=0.367$, $p=0.014$) and PC4 ($K=0.404$, $p=0.015$)
435 gave significant results substantially below 1, indicating traits did not evolve as expected under
436 a Brownian motion model (Blomberg et al., 2003).

437 To further explore the magnitude of this effect along the first two axes, giving the best
438 separation (PC1 and PC2), we re-assessed the PCA scatterplot after calculating mean shapes per
439 species (Fig. 8). In several cases some closely related taxa clustered together. Several members
440 of the Cervini tribe (*Cervus elaphus*, *Cervus canadensis*, *Cervus unicolor*, *Cervus timorensis* and
441 *Axis axis*) plotted relatively close together. On the other hand, type E members of the Cervini
442 tribe gave lower scores on PC1, similar to other, unrelated type E taxa, such as *Hydropotes*
443 *inermis*.

444 The members of the genus *Muntiacus* also clustered together. When PC1 was plotted against
445 PC2, *Muntiacus muntjak* was close to *Muntiacus reevesi*, but nevertheless closer to some other,
446 unrelated taxa such as *Capreolus capreolus* and *Cervus mariannus*. Moreover, the *Elaphodus*-
447 members of the tribe gave different scores despite their relatedness to *Muntiacus* and plotted
448 out with other species of similar habitat/locomotor strategy. A similar pattern was noted for

449 the Rangiferini. Despite being most closely related to the Odocoileini, they were positioned
450 near the main group of type A species. The Alceini tribe, consisting of *Alces alces* only, was
451 positioned near the somewhat related Rangiferini. It was, nevertheless, also close to the other
452 cursorial type A species. The Capreolini, with the genera *Capreolus* and *Hydropotes*, gave very
453 different results on the first two axes of the PCA. *Capreolus* gave slightly negative scores on
454 PC1, close to *Axis kuhlii* and *Muntiacus muntjak*. *Hydropotes* gave scores similar to the type E
455 Cervini.

456 5. Discussion

457 Although our dataset did not allow us to fully test the effects of sexual dimorphism for all
458 species, the analysis of a sub-sample of specimens of known sex suggested that shape related
459 differences between males and females were probably limited for the calcaneus and did not
460 substantially obscure phylogenetic and functional patterns. Similarly, our regressions of the
461 shape variables on centroid size indicated that allometric size effects played a limited role as a
462 confounding factor.

463 Overall, it appeared that morphological variation along the first two axes of the PCA was mainly
464 driven by function, and in the case of PC1, perhaps to some extent by phylogeny. Along the first
465 axis we noted a variation in angle of the tuber calcanei, that appeared to be linked to
466 hypothesis 2 that in cursorial forms of open environment the calcaneus is expected to be more
467 vertically placed relative to the hock joint, while a more horizontally placed tuber calcanei was
468 related to saltatorial species of closed environment (Fig. 6). Furthermore, the variation in length
469 of the tuber calcanei explained by PC1 could most likely be related to hypothesis 1, that tuber is

470 more elongated in saltatorial forms than in cursorial species. The third functional hypothesis
471 proposed for the calcaneus appeared to be expressed in the shape differences summarized by
472 PC2. Here it was theorized that cursorial species have a more developed articular surface for
473 the malleolus than saltatorial species. Overall the type A, B and C groups were in line with a
474 functional explanation. The fact that the group of mountain specimens (Type D) gave results
475 similar to the cursorial type A group was not unexpected in this light, as mountain cervids are
476 probably less well adapted to such environments than mountain bovids (Geist, 1998) -and
477 according to some authors (Flueck and Flueck, 2017) prefer flat terrain when found at high
478 altitude - they may retain some cursorial traits. It should be noted that in bovid
479 ecomorphological studies, mountain species were also often “misclassified” into different
480 habitat categories and substantially overlapped with other groups (Kovarovic, 2004; Weinand,
481 2005, 2007). This may indicate that vegetation type, and not altitude, could be primarily driving
482 the morphology of the calcaneus in ruminants.

483 The position of the type E group was apparently somewhat contradictory as it was closer to the
484 type A group along the first axis, but closer to the type B group on the second axis. This pattern
485 may be related to the fact that the wetlands inhabited by type E forms, are usually dominated
486 by tall grasses and reeds that provide more cover than the open landscapes inhabited by more
487 truly cursorial cervids (Curran, 2009). Possibly this group retains both cursorial traits as well as a
488 significant amount of saltatorial traits. Overall, the patterns described by the
489 habitat/locomotion groups along the first two axes appeared to indicate the presence of a
490 functional signal.

491 Although it could not be excluded that some functional signal was contained in PC3 and PC4
492 (Fig. 6), the weak separations between the pre-assigned groups and the lack of a clear
493 connection between the observed shape variation and our hypotheses, would suggest that this
494 signal was too obscured by other confounding effects, to act as a reliable predictor of
495 locomotion or habitat preference.

496 Phylogeny may also have played a limited role in driving the shape differences along the axes of
497 the PCA. Our high –albeit non significant- Pagel's λ indicated that there was a phylogenetic
498 signal present, perhaps primarily in the traits summarized by the first and fourth axis.
499 Blomberg's K -values, nevertheless, indicated that the phylogenetic signal was low and that the
500 traits did not depend heavily on heritability. The PCA on the species averages (Fig. 8) showed
501 that some closely related taxa had the tendency to cluster together. Nevertheless, it seemed
502 clear that most of the major patterns were functionally driven. Many taxa of similar locomotor
503 and ecological affinity clustered together, despite being distantly related. This was exemplified
504 in a number of cases. The fact that *Cervus unicolor* and *Cervus timorensis* –despite their
505 different ecological preferences- exhibited similar scores, might be due to phylogenetic
506 relatedness. However, the observation that the type E members of the Cervini tribe gave
507 negative scores on the first axis, similar to unrelated species of the same locomotor strategy
508 and ecology (e.g. *Hydropotes inermis*) should probably be interpreted as functional. *Muntiacus*
509 *muntyak* and *Muntiacus reevesi* were not only close to each other in PC space, but also to other
510 unrelated taxa of similar locomotor/ecological affinity (*Capreolus capreolus* and *Cervus*
511 *mariannus*), which would at least in part imply a functional pattern. This was corroborated by
512 *Elaphodus cephalopus* –also of the Muntiacini tribe- taking a different position, closer to other

513 species of similar habitat/locomotor strategy. The position of the Rangiferini, being highly
514 cursorial, and plotting close to the other type A species, could also indicate a functional pattern,
515 especially as the related Odocoileini gave different scores. The position of the Alceini might be
516 partially confounded by a phylogenetic signal, as they are positioned close to the related
517 Rangiferini. Its position was, nevertheless, also close to the type A species of similar
518 locomotion/ecological preference, suggesting function may also play a role. In the Capreolini
519 tribe, the division between the genera *Capreolus* and *Hydropotes* may also be functional, as the
520 members of the former plotted close to the unrelated, but ecologically more similar *Muntiacus*
521 *muntjak*, and the latter to the ecologically similar type E Cervini.

522 Taking these findings into consideration we found support for the first two hypotheses
523 proposed for the calcaneus (see table 1). The shape variation along the first component
524 reflected a gradient from saltatorial species of closed environment with long, horizontally
525 positioned tuber calcanei to cursorial species of open environments, with short, vertically
526 positioned tuber calcanei. Using these traits, the model effectively differentiated between the
527 groups. Although the intermediate group had a transitional shape, overlap with the saltatorial
528 specimens was more substantial, and the model did not discriminate as well from this group.
529 Assuming that the type D deer (mountain) prefer flat terrain at high altitudes (Flueck and
530 Flueck, 2017; Geist, 1998) or are morphologically more driven by vegetation structure, and that
531 type E deer (wetland) retain some cursorial and saltatorial traits due to the specific vegetation
532 structure of such open wetlands, these two groups corroborated the validity of hypotheses 1
533 and 2.

534 The third functional hypothesis (Table 1) was supported by specimen patterns along the second
535 component in the PCA and by the associated deformation grids. Again, a gradient was observed
536 from cursorial, open habitat species (type A) with long articular surfaces for the malleolus, to
537 saltatorial, closed habitat species (type B) with short articular surfaces (Fig. 5). The model could
538 effectively use this trait to differentiate between species of open environments and closed
539 environments. Intermediate specimens (type C) were morphologically more similar to the
540 closed environment group. Similar to the length and orientation of the tuber, the articular
541 surface supporting the malleolus in mountain species, was analogous to that of cursorial
542 species of open environment, further confirming the interpretation that the morphology of the
543 calcaneus in such species is driven primarily by vegetation structure. Unlike the shape of the
544 tuber calcanei, the shape of the articular surface supporting the malleolus in type E species was
545 similar to that of dry, open environment species (Type A). The reason for this discrepancy was
546 unclear, but it may again reflect the notion that cervids of open wetlands retain a combination
547 of saltatorial and cursorial traits.

548 As a range of different methods have been reported in the artiodactyl ecomorphological
549 literature (see e.g. Degusta and Vrba, 2003, 2005a, 2005b; Scott, 2004; Plummer et al., 2008;
550 Schellhorn, 2009; Curran, 2009, 2012, 2015), it is difficult to compare the results of our models
551 to those of other studies. This is also the case for the npMANOVA approach we used, that,
552 despite its advantages, did not provide a measure of reclassification accuracy, as is sometimes
553 seen in studies that make use of discriminant analyses (e.g. Kovarovic and Andrews, 2007;
554 Curran, 2009, 2012). That said, the results were in line with those of earlier GMM-based models
555 where the cervid calcaneus performed well as a habitat predictor (Curran, 2009, 2012, 2015). In

556 contrast, studies of bovid ecomorphology have been less unanimous in their estimation of the
557 calcaneus as a good habitat predictor (Kovarovic, 2004; Schellhorn, 2009; Schellhorn and
558 Pfretzschner, 2015; Barr, 2018). Some researchers considered it a useful habitat predictor, but
559 also warned for the potentially confounding effects of allometry and phylogeny in this element
560 (Kovarovic, 2004; Barr, 2018). Despite these reservations, in our model allometric and
561 phylogenetic effects did not seem to substantially obscure the functional signal. This could
562 suggest a discrepancy between cervids and bovids, but could also be the consequence of
563 methodological differences. In this context it is worth noting that in Barr's (2018) bovid
564 analyses many of the shape variations measured in the calcaneus were similar to those in the
565 model presented here: variation in the length of the tuber calcanei and variation in the articular
566 surface supporting the astragalus. Where the latter trait was considered mainly functional by
567 Barr (2018), it was purported that the length of the tuber was more confounded by body size
568 and phylogenetic relatedness (Barr, 2018). One possible explanation is that in bovids the larger
569 species are driving the allometric signal. In bovids many larger forms exist (e.g. *Syncerus*, *Bos*,
570 *Taurotragus*) that may require additional morphological accommodations to support their
571 weight (Scott, 1979), and are probably too heavy to support the saltatorial or cursorial
572 adaptations typically seen in smaller forms (Geist, 1998; Plummer et al., 2008). This could
573 obscure the functional signal (Geist, 1998). Although some ecomorphological studies (Scott,
574 1979; Plummer and Bishop, 2008) have *a priori* excluded species of very large body size from
575 their analyses for precisely these reasons, most that have focused on the calcaneus, have not
576 done so (Kovarovic, 2004; Kovarovic and Andrews, 2007; Schellhorn, 2009; Schellhorn and
577 Pfretzschner, 2015; Barr, 2018).

578 Another explanation for the discrepancy between cervid and bovid studies of the calcaneus,
579 could be that the GMM methods, used in cervid studies so far (Curran, 2009, 2012, 2015, this
580 study), more efficiently exclude size differences from the dataset than the linear size
581 corrections often used in bovid studies (e.g. Kovarovic and Andrews, 2007; Barr, 2018).
582 Although it should be noted that the GPA procedure, used here and in Curran's (2009, 2012,
583 2015) work, only accounts for size differences in the measured object itself, it does so in a more
584 efficient way than traditional morphometrics (Viscosi and Cardini, 2011). If we accept that the
585 size of the calcaneus is a good indicator for total body size, an assumption that appears to be
586 confirmed by the correlation we found between calcaneus centroid size and total body mass, it
587 is likely that our GMM approach more efficiently accounted for total body size differences as
588 well.

589 The above explanations may account for the absence of an allometric effect in the cervid
590 calcaneus, but they do perhaps not fully explain that only a limited phylogenetic signal was found
591 in our study, in comparison with certain bovid studies (Kovarovic, 2004; Kovarovic and
592 Andrews, 2007; Barr, 2018). Our results suggested that many of the larger patterns observed in
593 our analyses were functionally driven, and that there was only limited phylogenetic effect for
594 the calcaneus in our model. These limited effects can possibly be seen in some related taxa
595 clustering together in the scatterplot of PC1 and PC2 (Fig. 8). This was not unexpected, because
596 some cervid tribes have an evolutionary history of adaptation to certain habitats (e.g. muntjacs
597 to closed habitats) (Geist, 1998).

598 Degusta and Vrba (2003) argued that phylogenetic effects can be easily excluded from
599 morphometric datasets, by selecting those anatomic features that co-vary with locomotion and
600 habitat. While this is true to some extent, the underlying assumption is that a specific feature is
601 either driven by phylogeny *or* by function. Although it should be remembered that our
602 phylogenetic analyses were based on a limited number of species, what appeared from our
603 results is that for most shape traits, this is not entirely possible. Features such as the length of
604 the tuber calcanei are not driven by *either* phylogenetic relatedness *or* functional aspects, but
605 most likely by a combination of both (Elton et al., 2016). That being said, when considering the
606 major patterns observed between the large and diverse habitat/locomotion groups in our PCA,
607 the effects of phylogeny were probably not strong enough to substantially confound the
608 functional signal. This would suggest that our models are useful at predicting ecological and
609 locomotor affinity in fossil samples.

610 Nevertheless, our method also had its limitations. First of all, it is important to keep in mind
611 that, despite the significant overall differences observed between cervids of different
612 habitat/locomotor strategy, there was still substantial overlap between the groups. For a robust
613 analysis of a group of fossil specimens, it would therefore be advisable to test this on a sample
614 of sufficient size. The results of such an analysis would also be limited in scope, in the sense
615 that they are only informative about one aspect of the cervids' ecology: the vegetation
616 structure of the habitat in which the animals evade predators. Depending on their behavioral
617 repertoire, some deer can make use of different habitats for feeding, sleeping or reproduction
618 (Geist, 1998). Looking at other parts of the skeleton as well -including the masticatory
619 apparatus for feeding behavior- can lead to a more precise reconstruction of a species' ecology

620 (Bishop et al., 2006). Ecomorphology is also but one approach in palaeoecology. The results of
621 ecomorphological studies are best considered in concert with other proxies for a robust
622 palaeoenvironmental reconstruction (Degusta and Vrba, 2003).

623 Finally, it should be noted that the functional framework on which our predictive models were
624 based, relied on the assumption that similar selection pressures (i.e. predator evasion strategy)
625 drove the morphology of the extinct deer species on which our models are ultimately intended
626 to be applied. If we accept the notion that phylogeny played a limited role in driving the traits
627 of the calcaneus we studied, this was a reasonable assumption, as the underlying biomechanics
628 that drive functional morphology are constant (Degusta and Vrba, 2003). It should, however, be
629 taken into account that in certain insular ecosystems with an impoverished carnivore fauna,
630 predation pressure can be reduced (Bouteaux, 2005, McClain et al., 2006). The morphology of
631 deer living in such isolated conditions may therefore be driven by different factors than that of
632 species from continental ecosystems.

633 6. Conclusions

634 In this paper we demonstrated that the morphology of the cervid calcaneus can be used to
635 predict the habitat preferences of taxa of unknown ecological affinity. The shape of this bone
636 was found to be primarily a good predictor of vegetation structure. In addition, we improved
637 the way ecomorphological studies are conducted, by the use of GMM and by relying more
638 heavily on the underlying functional aspects driving shape. Applying the methods presented
639 here, could contribute to a better understanding of Pleistocene environments.

640 Acknowledgements:

641 The authors would like to thank the following researchers, collection managers and curators
642 who have facilitated our access to cervid collections: Pepijn Kamminga, Valentin Fisher, Julien
643 Denayer, Henry van der Es, Joséphine Lesur, George Lenglet, Sebastien Bruaux, Jason Nadell,
644 Briana Pobiner and Bobby Kaplan. Our gratitude also goes to Sarah Elton and Una Strand
645 Vidarsdottir for their guidance and to John de Vos and Tarek Oueslati for their advice and
646 insights. In addition, we wish to acknowledge the anonymous reviewers for their constructive
647 comments and suggestions to help improve this paper. The Department of Anthropology
648 (Durham University) is thanked for the financial assistance and logistical support that went into
649 this project.

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1138 Tables:

1139 Table 1. Functional hypotheses for the calcaneus.

1140 Table 2. Extant species used in the dataset, with total sample of studied calcanei (N),

1141 locomotor/habitat group (L/H), average species body mass (\bar{x} kg) and justification.

1142 Table 3. *p*-values of pairwise comparisons of an npMANOVA on the first four principal

1143 component scores of a between groups PCA on the calcaneus dataset, with significant values

1144 ($p < 0.05$) in bold.

1145 Table 4. Summary of the shape variation explained by the individual axes of a PCA on all

1146 specimens.

1147 Figures:

1148 Figure 1. Parts of the calcaneus (a (yellow): tuber calcanei; b (green): articular surface for the

1149 malleolus; c (red): articular facet between calcaneus and astragalus; d (orange): articular facet

1150 between calcaneus and cubonavicular).

1151 Figure 2. Landmarks recorded on the calcaneus (with a description of their location and type

1152 [following Bookstein, 1991] in parenthesis).

1153 Figure 3. Results of repeatability tests (I: scatterplot of a PCA conducted on four re-scanned and
1154 landmarked replicates of five calcanei, with eigenvalues given in parenthesis, II: scatterplot of a
1155 PCA conducted on four re-landmarked replicates of five calcanei, with eigenvalues given in
1156 parenthesis).

1157 Figure 4. Results PCA on group of 31 *Dama dama* (DDA), *Axis axis* (AXA) and *Capreolus*
1158 *capreolus* (CAC) calcanei to assess sexual dimorphism, with eigenvalues in parenthesis (m=male,
1159 f=female).

1160 Figure 5. PCA scatterplots of a bg- PCA of all calcanei with 50% confidence intervals
1161 (eigenvalues in parenthesis and large symbols representing group averages), thin plate spline
1162 deformation grids, and a scree plot of the eigenvalue distribution per axis.

1163 Figure 6. Shape changes observed along the first four components of a bg-PCA on all calcanei,
1164 shown from the medial side (I: PC1; variation in length and angle of the tuber calcanei, II: PC2;
1165 variation in the size of the articular surface supporting the malleolus, III: PC3; variation in size of
1166 the posterior talar articular surface and in the distance between the posterior talar articular
1167 surface and the articular surface supporting the malleolus, IV: PC4; variation in the height of the
1168 anterior end of the articular surface with the cubonavicular).

1169 Figure 7. Results of ordinary least squares regressions of the first four principal components
1170 against log centroid size for all extant calcanei.

1171 Figure 8. Scatterplot of mean shapes per species as described by PC1 and PC2 of a bg-PCA on all
1172 calcanei with minimal spanning tree representing shortest possible distance between data
1173 points.

Hypothesis 1:	The relative length of the tuber calcanei is predicted to be greater in species adapted to closed environments and shorter in species adapted to open environments.
Hypothesis 2	The orientation of the tuber and articular facets between calcaneus and astragalus are predicted to be more oblique in species adapted to more open environments and less oblique in species of closed environments.
Hypothesis 3	The articular surface supporting the malleolus is predicted to be larger and more developed in species adapted to open environments and shorter in species adapted to closed environments.

Table 1. Functional hypotheses for the calcaneus.

Tribe	Species	N	L/H	\bar{x} kg	Justification
Cervini	<i>Axis axis</i>	11	A	86	(Eisenberg and Seidensticker, 1976; Geist, 1998)
	<i>Axis (Hyelaphus) kuhlii</i>	2	C	43	(Blouch and Atmosoedirdjo, 1987; Kurt, 1990; Geist, 1998)
	<i>Axis (Hyelaphus) porcinus</i>	4	E	68	(Blandford, 1888; Geist, 1998; Bhowmik et al., 1999)
	<i>Cervus (Elaphurus) davidianus</i>	3	E	214.5	(Geist, 1998; Hu and Jiang, 2002)
	<i>Cervus (Panolia) eldii</i>	2	E	105	(Geist, 1998; Tordoff et al., 2005)
	<i>Cervus (Rusa) timorensis</i>	2	A	155	(Geist, 1998; Nur Alizati, 2020)
	<i>Cervus (Rusa) alfredi</i>	1	C	-	(Rabor, 1977)
	<i>Cervus (Rusa) marianna</i>	1	C	50	(Taylor, 1934; Geist, 1998; Nur Alizati, 2020)
	<i>Cervus (Rusa) unicolor</i>	3	B	276	(Blandford, 1888; Schaller, 1967)
	<i>Cervus canadensis</i>	4	A	230	(Geist, 1998)
	<i>Cervus elaphus</i>	10	A	230	(Geist, 1998; Koubek and Zima, 1999)
	<i>Cervus nippon</i>	2	C	128.5	(Geist, 1998; Smith and Xie, 2008)
	<i>Dama dama</i>	11	A	75.1	(Janis and Wilhelm, 1993; Apollonio et al., 1998; Geist, 1998)
Muntiacini	<i>Elaphodus cephalopus</i>	3	D	33.5	(Ohtaishi and Gao, 1990; Geist, 1998)
	<i>Muntiacus reevesi</i>	3	B	14	(Geist, 1998; Chiang, 2007)
	<i>Muntiacus muntjak</i>	4	B	16	(Geist, 1998; Ekwal et al., 2012)
Capreolini	<i>Capreolus capreolus</i>	16	B	23	(Geist, 1998; Stubbe, 1999)
	<i>Hydropotes inermis</i>	11	E	12.5	(Geist, 1998; Zhang et al., 2006)
Rangiferini	<i>Rangifer tarandus</i>	12	A	153.5	(Baskin, 1986; Geist, 1998)
	<i>Mazama americana</i>	2	B	20	(Bodmer, 1997; Geist, 1998)
	<i>Odocoileus virginianus</i>	3	C	85	(Geist, 1998; Potapov et al., 2014)
	<i>Odocoileus hemionus</i>	2	D	84	(Olson, 1992; Geist, 1998)
	<i>Ozotoceros bezoarticus</i>	1	A	40	(Geist, 1998; Merino and Semeniuk, 2011)
	<i>Pudu mephistophiles</i>	2	D	5.9	(Geist, 1998; Escamilo et al., 2010)
	<i>Pudu puda</i>	5	B	10	(Hershkovitz, 1982 ; Geist, 1998)
Alceini	<i>Alces alces</i>	5	A	557	(Geist, 1998 ; Bauer and Nygrén, 1999)

Table 2. Extant species used in the dataset, with total sample of studied calcanei (N), locomotor/habitat group (L/H), average species body mass (\bar{x} kg) and justification.

	Type A	Type B	Type C	Type D
Type B	0.0001	-	-	-
Type C	0.0031	0.2276	-	-
Type D	0.0002	0.0007	0.0017	-
Type E	0.0001	0.0001	0.0021	0.0001

Table 3. p -values of pairwise comparisons of an npMANOVA on the first four principal component scores of a between groups PCA on the calcaneus dataset, with significant values ($p < 0.05$) in bold.

PCA axes	Observed shape variation
PC1	Variation in relative length of the tuber calcanei and orientation of the tuber relative to the anterior part of the bone with the articular surfaces.
PC2	Variation in antero-posterior length of the articular surface supporting the malleolus.
PC3	Variation in infero-superior length of the posterior talar articular surface and in the distance between the articular surface of the malleolus and the posterior talar articular surface.
PC4	Variation in position of the anterior end of the articular surface supporting the cubonavicular relative to the landmarks on the posterior talar articular surface.

Table 4. Summary of the shape variation explained by the individual axes of a PCA on all specimens.

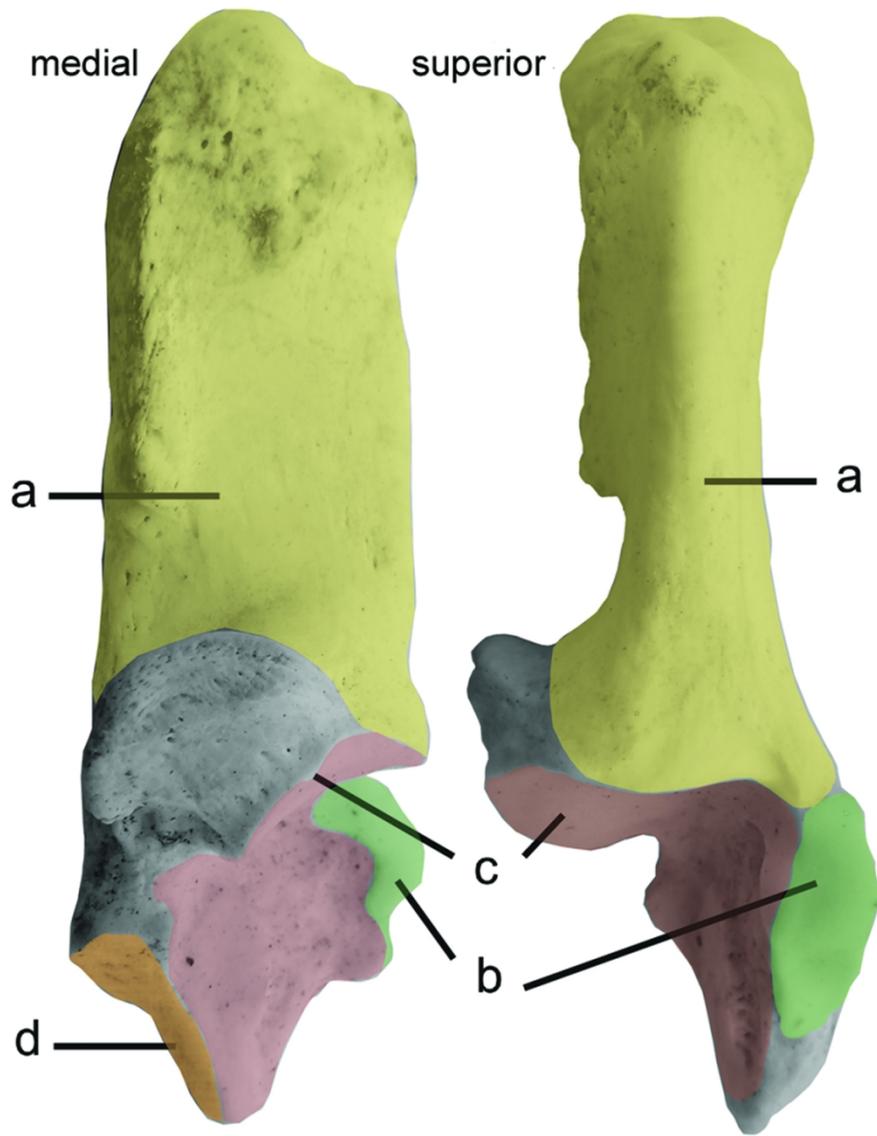


Figure 1. Parts of the calcaneus (a (yellow): tuber calcanei; b (green): articular surface for the malleolus; c (red): articular facet between calcaneus and astragalus; d (orange): articular facet between calcaneus and cubonavicular).

112x131mm (300 x 300 DPI)

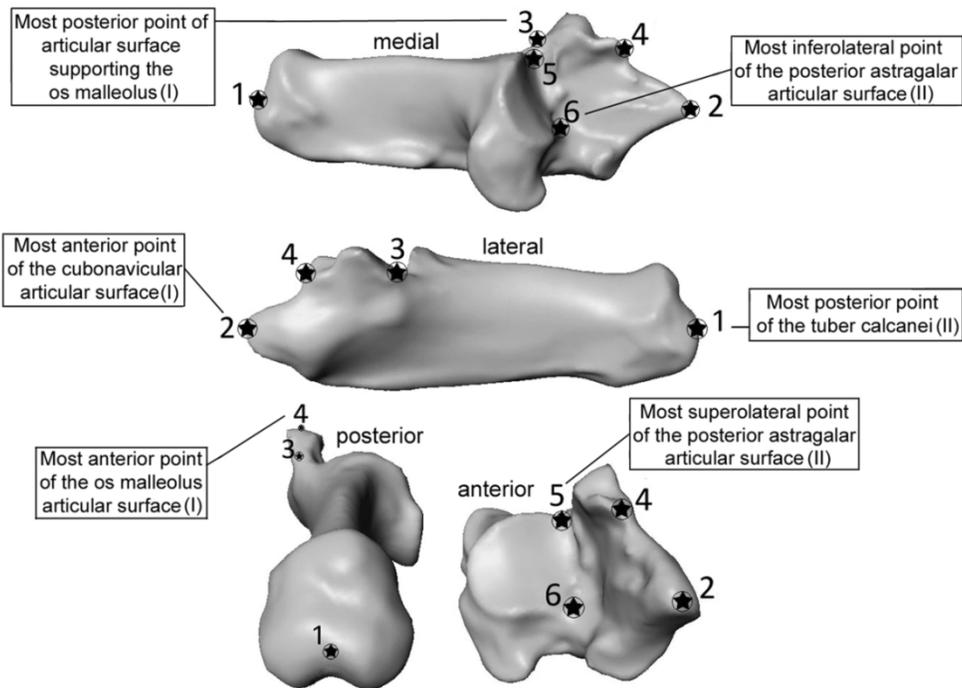


Figure 2. Landmarks recorded on the calcaneus (with a description of their location and type [following Bookstein, 1991] in parenthesis).

105x75mm (300 x 300 DPI)

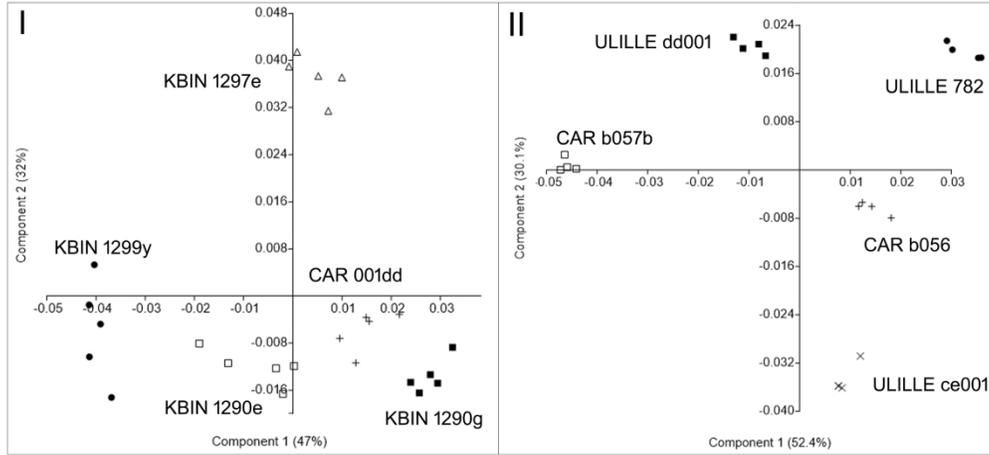


Figure 3. Results of repeatability tests (I: scatterplot of a PCA conducted on four re-scanned and landmarked replicates of five calcanei, with eigenvalues given in parenthesis, II: scatterplot of a PCA conducted on four re-landmarked replicates of five calcanei, with eigenvalues given in parenthesis).

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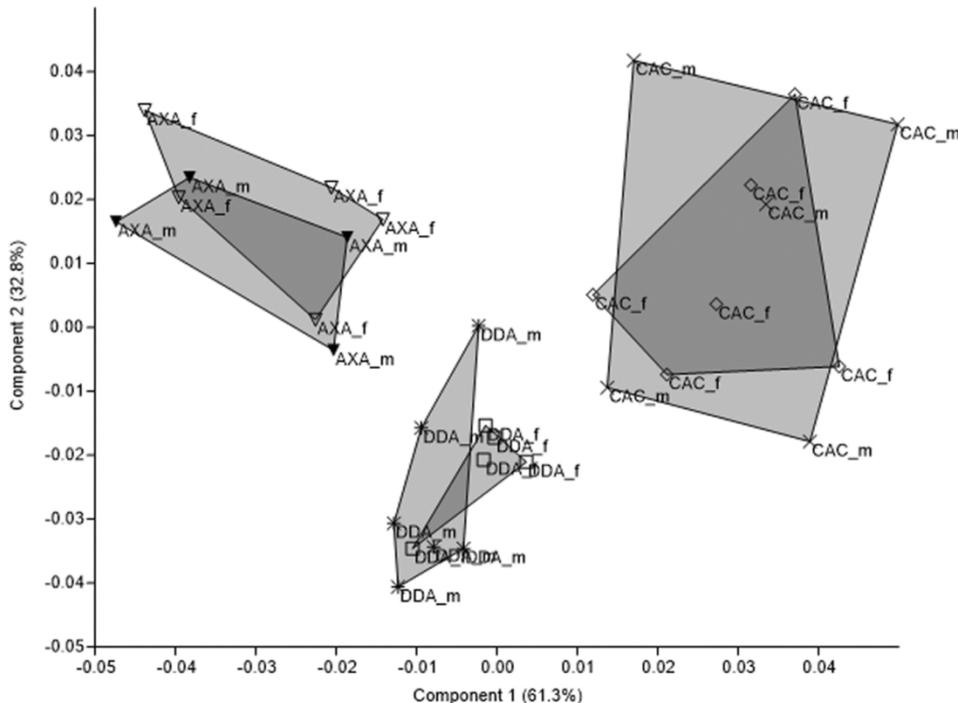


Figure 4. Results PCA on group of 31 Dama dama (DDA), Axis axis (AXA) and Capreolus capreolus (CAC) calcanei to assess sexual dimorphism, with eigenvalues in parenthesis (m=male, f=female).

63x54mm (600 x 600 DPI)

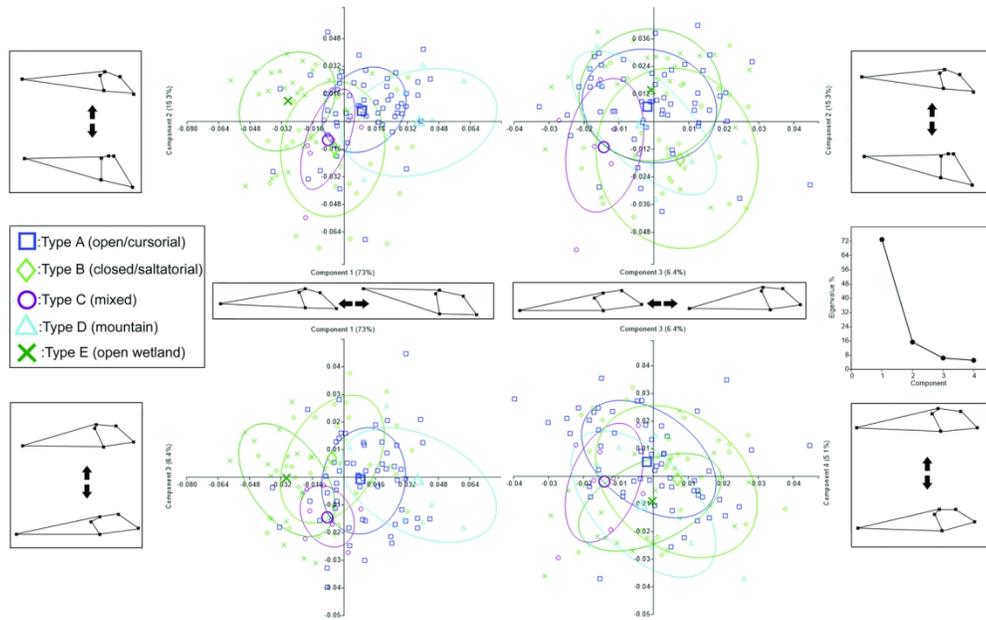


Figure 5. PCA scatterplots of a bg- PCA of all calcanei with 50% confidence intervals (eigenvalues in parenthesis and large symbols representing group averages), thin plate spline deformation grids, and a scree plot of the eigenvalue distribution per axis.

139x90mm (300 x 300 DPI)

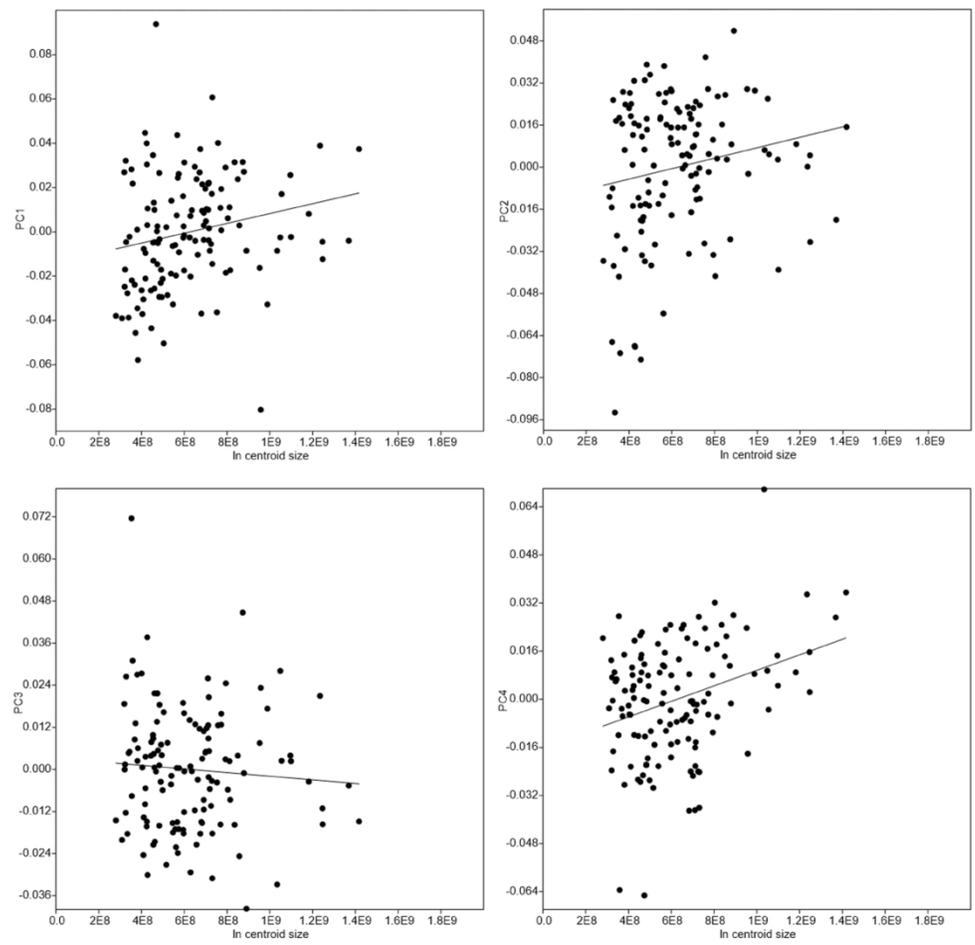


Figure 7. Results of ordinary least squares regressions of the first four principal components against log centroid size for all extant calcanei.

84x80mm (600 x 600 DPI)

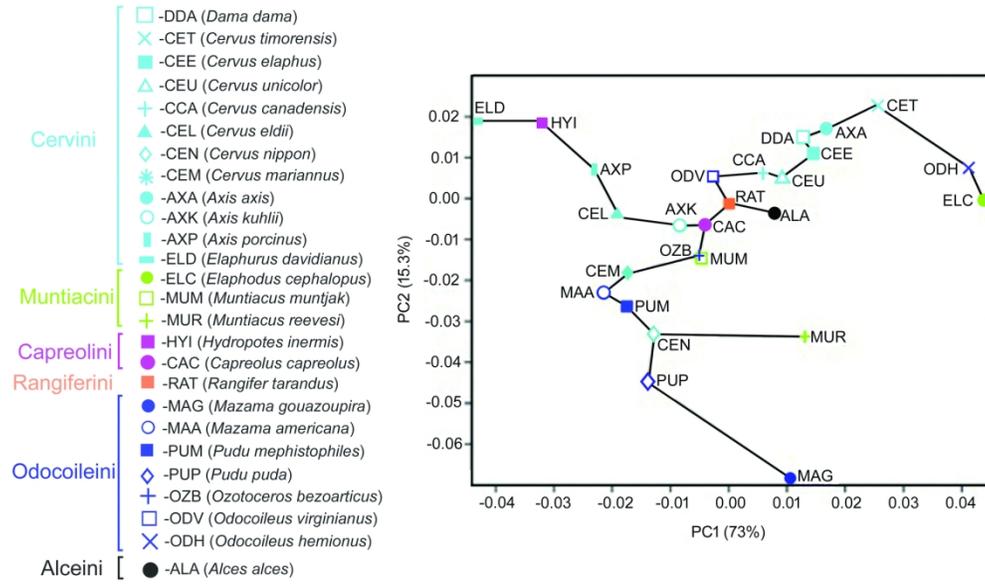


Figure 8. Scatterplot of mean shapes per species as described by PC1 and PC2 of a bg-PCA on all calcanei with minimal spanning tree representing shortest possible distance between data points.

169x104mm (300 x 300 DPI)