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RESEARCH ARTICLE

REVISED The ecomorphology of Caribou (*Rangifer tarandus*): a geometric morphometric study.

[version 2; peer review: 2 approved, 1 approved with reservations, 1 not approved]

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Abstract

Paleolithic reindeer (*Rangifer tarandus*) was a key species for human populations in western and central Europe during much of the Paleolithic period. In Southwestern France, and in particular during the Magdalenian, reindeer frequently figures among the privileged prey of hunter-gatherer groups. However, and despite numerous attempts to reconstruct the migratory behaviour of Paleolithic reindeer, there is no agreement on the degree of mobility of this prey. Modern ethological data indicate that reindeer herds adopt different mobility strategies depending on the type of habitat and the topography of the environment. Through metapodial bones and phalanges cross-sections, our project 'Reconstructing habitat type and mobility patterns of Rangifer tarandus during the Late Pleistocene in Southwestern France: an ecomorphological study' (Emorph) quantifies the link between habitat type, mobility, bone density and morphology using computer tomography (CT) and geometric morphometry (GMM). Based initially on the study of extant caribou populations with distinct migratory behaviours, the results obtained could be applied to several Magdalenian assemblages from southwestern France in the future, with the aim of reconstructing the mobility of these tardiglacial reindeer.

Keywords

Magdalenian, ecomorphology, migration, reindeer, geometric morphometrics.

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REVISED **Amendments from Version 1**

Please note that this version of the article includes minor revisions aimed at enhancing clarity and precision. These updates involve the refinement of certain concepts, the reduction of word repetition for improved flow, and the inclusion of specific dates where relevant to provide clearer chronological context. These adjustments are intended to improve the overall quality and accessibility of the presented information, contributing to a more insightful reading experience.

Any further responses from the reviewers can be found at the end of the article

Introduction

The study of reindeer and its role in Upper Palaeolithic subsistence systems (especially during the Magdalenian period) has produced a vast literature (Aaris-Sørensen *et al.,* 2007; Bahn, 1977; Banks *et al*., 2008; Bouchud, 1954; Bouchud, 1966; Bouchud *et al*., 1953; Costamagno *et al*., 2016; Delpech, 1983; Delpech, 1987; Deplano, 1994; Enloe, 2001; Fontana, 2000; Gordon, 1988a; Gordon, 1988b; Gordon, 1990; Kuntz, 2011; Kuntz & Costamagno, 2011; Lacorre, 1956; Morin, 2008; Spiess, 1979; Weinstock, 2000a; Weinstock, 2000b; Weladji *et al*., 2002; White, 1980). According to several authors (e.g., Driver, 1990; Heard, 1997; Kuntz, 2011; Kuntz & Costamagno, 2011) reindeer mobility patterns are essential to understanding the hunting strategies and mobility of human groups during the Late Pleistocene.

Because of the high frequency of reindeer remains in French sites, it is suggested that human populations were highly dependent on this animal resource (Kuntz & Costamagno, 2011). In the South of France (Costamagno, 1999), reindeer was exploited during the whole year. The Magdalenian (18,000–14,000 cal BP) has even been associated with the specialised hunting of reindeer (e.g., Mellars, 2004). But the predominance of reindeer remains in some archaeological sites could simply reflect their local abundance rather than selective hunting strategies (Costamagno, 1999; Costamagno & Mateos, 2007; Costamagno *et al*., 2016; Fontana & Chauvière, 2018; Grayson & Delpech, 2002).

During the past few decades, there have been several largely unsuccessful attempts to reconstruct the mobility patterns of reindeer. Different hypotheses have been proposed for the Magdalenian period (18,000–14,000 cal BP) in Southwestern France, for example. Early hypotheses proposed that reindeer migrated relatively long distances on a north-south axis, from winter ranges in the Perigord and the Quercy to summer ranges in the Pyrenees and were either followed or intercepted by human hunters along migration routes (Bahn, 1977; Lacorre, 1956; Gordon, 1988a; Gordon, 1988b; Gordon, 1990). Seasonal data (Kuntz, 2011) does not support the existence of large-scale migrations on a North-South axis, however. A second hypothesis, based on osteometric and dental data as well as seasonality studies, suggests relatively short-distance migrations, from the Perigord eastwards to the Massif Central (Delpech, 1983; Delpech, 1987; Kuntz & Costamagno, 2011). Other authors, using antler and tooth eruption evidence, propose that herds remained all year-round in the Perigord (Bouchud, 1954; Bouchud *et al.,* 1953; Deplano, 1994; Fontana, 2000; Fontana, 2017; Fontana & Chauvière, 2018). Moreover, it is necessary to consider the possibility that patterns of reindeer mobility evolved during the Late Glacial under the selective pressure of significant climatic changes (Costamagno *et al*., 2016; Delpech, 1983; Delpech, 1987).

In order to go beyond conventional archaeozoological analyses, we propose an actualistic approach from an ecomorphological perspective to address this question. Modern ethological data indicate that reindeer populations adopt different mobility strategies correlated to habitat type and to population density. Thus, long distance migrations tend to take place in tundra and steppe habitats (Goddard, 2009; Miller, 1990; Schaefer *et al.,* 2000; Seip & McLellan, 2010) while animals living in or near the forest tend to travel shorter distances comparatively with their tundra counterparts (Thomas & Gray, 2002) except when population densities increase, driving them to migrate further (Hinkes *et al.,* 2005). Ecomorphology studies the relationship between the functional design of organisms and the environment (Wainwright, 1991). Several studies have successfully demonstrated that it is possible to use ecomorphology to study past adaptations, even when the taxa involved are quite different from their modern descendants (Bignon *et al.,* 2005; Bishop, 1999; Curran, 2009; Curran, 2012; DeGusta & Vrba, 2003; DeGusta & Vrba, 2005a; DeGusta & Vrba, 2005b; Kappelman, 1988; Kappelman, 1991; Kappelman *et al.,* 1997; Plummer & Bishop, 1994; Plummer *et al.*, 2008; Scott *et al.,* 1999; Van Asperen, 2010).

Given the importance of reindeer for hunter-gatherer groups during the Last Glacial period in western and central Europe (Costamagno *et al.,* 2016), the knowledge of their mobility patterns is the key for a better understanding of Palaeolithic hunter-gather lifeways. The purpose of this study is to create a referential framework to study ecomorphological differences between animals from different biomes and with different mobility patterns with the aim of applying this knowledge towards the reconstruction of past reindeer mobility.

Extant Caribou in Canada: general description and origins

Caribou (*Rangifer tarandus*), or reindeer as they are known in Eurasia, are medium-sized members of the Cervidae family. In Canada, this species is distributed across boreal, montane, and arctic environments in most Canadian provinces and all territories. Over this broad area, caribou exhibit a huge variability in ecology, genetics, behaviour and morphology (COSEWIC, 2015). Antlers occur in both sexes, and they are well-adapted to cold environments with dense pelage, large fat stores, a counter-current heat exchange to reduce loss of heat in respiration, and an ability to reduce energy expenditure in the winter by decreasing metabolism. They rut in late autumn and calve in late spring and early summer, the exact timing varying with latitude and environmental and physical conditions (COSEWIC, 2015).

Caribou is a chionophile species. Their broad hooves and dew claws act as efficient paddles or as ice picks when navigating

steep, rocky, and icy mountainsides (Miller, 1990; Seip & McLellan, 2010) and make walking through the snow easier (Taillön, 2013). Peary caribou, in particular, have relatively large hooves, particularly useful for breaking up hard snow (Gunn, 2010). Caribou (specially mountain and tundra caribou) are excellent swimmers, able to cross rivers and lakes (Taillön, 2013) during their travels. They walk while feeding and moving between feeding areas. Fast walk often occurs during migration or periods of alertness. They can reach a speed of between three to 11km/h (Miller, 1990).

All caribou are considered to belong to the same species, but they are classified in several subspecies: *Rangifer tarandus groenlandicus* (Barren-Ground caribou), *Rangifer tarandus granti* (Alaskan Barren-Ground caribou), *Rangifer tarandus caribou* (Eastern caribou/Migratory woodland caribou, mountain caribou and boreal caribou/forest-dwelling caribou) and *Rangifer tarandus pearyi* (Peary caribou) (Miller, 1990). All of these species are present in this study.

The oldest caribou fossils are found in Eastern Beringia (present-day Alaska and the Yukon) and dated to 1.6 Ma (Harrington, 1999; Weckworth *et al.,* 2012), indicating a Berigian origin for the genus. Banfield´s taxonomy review (1961) and his morphological analyses indicated the existence of two distinct groups: tundra and forest caribou, with three extant subspecies in western North America. Genetic evaluations (Flagstad & Røed, 2003) have generally supported the ice age isolation and subsequent divergence of *Rangifer tarandus granti* and *Rangifer tarandus groenlandicus* from *Rangifer tarandus caribou.* This split is confirmed by McDevitt *et al.* (2009). In western Canada, federal classification of woodland caribou (*Rangifer tarandus caribou*) further divides them into four ecotypes (northern, central, southern and boreal) based upon geography and life history characteristics (Weckworth *et al.,* 2012).

According to mitochondrial DNA (mtDNA) sequences, caribou in North America evolved from two lineages that differentiated in isolation during the last glaciation: the Berigian-Eurasian and the North American lineages, each of which is named for their ancestral sources in two presumed and separate Pleistocene refugia (COSEWIC, 2015). Caribou from the southern refugium comprise the North American lineage (NAL). With the retreat of the ice sheets, they spread west across the boreal region and north into the Rocky Mountains. The caribou that were isolated north of the ice sheets comprise the Beringian-Eurasian Lineage (BEL). They spread south from the Beringian refugium in present-day Yukon, north into the Arctic Islands and eastwards. In this manner, those of the NAL are the ancestors of the current *Rangifer tarandus caribou* while BEL caribou are the ancestors of modern *Rangifer tarandus groenlandicus, Rangifer tarandus granti* and *Rangifer tarandus pearyi.* The southern clade supposedly evolved south of the continental ice sheet, while the northern clade was in a glacial refugium in Alaska and adjacent Arctic Canada. Caribou populations that contained unique southern gene types are found in Ontario and Newfoundland. In contrast, exclusively northern types occurred in some Yukon herds and in some forest-tundra and tundra populations of barren-ground caribou (*Rangifer tarandus groenlandicus*) in northern Canada. Most woodland caribou populations in the mountains of southern British Columbia, Alberta and in the boreal forest and taiga across Canada are a mixture of the two clades (Cavedon *et al.,* 2019; COSEWIC, 2002; McDevitt *et al.,* 2009).

Habitat, movement, and locomotion

Several classification systems have been proposed for different purposes (behaviour, morphological differences, ecology…). However, the 'ecotype' approach, whereby a population or group of populations is associated with a particular set of environmental conditions is adopted in conservation ecology (COSEWIC, 2011). Ecotypes classify caribou herds according to different life-history strategies and ecological conditions (COSEWIC, 2011). Although every provincial Government uses their own ecotype classification, three large ecotypes are recognized across Canada: migratory tundra, boreal forest, and mountain ecotypes (Seip & McLellan, 2010). Some ecologists consider Peary caribou as a fourth ecotype, separate from the migratory tundra ecotype (Taillön, 2013). Populations from these four ecotypes have been included in our study.

Migratory Tundra caribou include Barren Ground (*Rangifer tarandus groenlandicus)* and Grant's caribou (*Rangifer tarandus granti)*. Barren Ground caribou (*Rangifer tarandus groenlandicus*), are the caribou *par excellence* (Gunn, 2010), big herds containing hundreds of thousands of individuals migrate long distances across the tundra. Their range extends from Alaska to Western Greenland and is continuous across northern continental mainland Canada (COSEWIC, 2016) from Northwestern Yukon to Baffin Island. They differ in size, body proportions, pelage, and behaviour from other caribou subspecies. They undertake long distances in their annual migration, between 800 and 5055 km, depending on the herd and the year (COSEWIC, 2016; Fancy *et al.,* 1989; Ferguson & Messier, 2000; Joly *et al.*, 2019; Saher & Schmiegelow, 2005) and travel back and forth between northern tundra calving grounds and summer ranges, until fall when they move to winter ranges in the boreal forest. Their habitats are varied, therefore, from prostrate dwarf shrub tundra and upright shrub tundra in the summer to boreal forest in the winter. High Arctic caribou, however, remain on the tundra during all seasons (Hummel & Ray, 2010) Much of the area comprising the summer range is wet in summer, and lichens are often the most typical plant cover (Gunn, 2010), being the main source of fodder for caribou (Taillön, 2013).

Peary Caribou (*Rangifer tarandus pearyi*) is endemic to the Arctic Archipelago of Canada (except Baffin Island) and is genetically distinct from other caribou in Canada (COSEWIC, 2015). Their habitat is treeless arctic tundra across the entire annual range (Bergerud, 2000; Geist, 1998; Gunn, 2010; Taillön, 2013). Peary caribou herds are relatively small, ranging from tens to hundreds of individuals, very different from other tundra dwelling populations. Their seasonal migrations often occur between islands, involving crossing the sea ice or swimming (COSEWIC, 2011; Jenkins *et al.*, 2011; Miller, 1990; Miller, 2002; Miller & Gunn, 1978). During severe winters, they may make even longer movements to the mainland (COSEWIC, 2002; Miller, 1990) and erratic large-scale

movements among islands are sometimes recorded (COSEWIC, 2015). Peary caribou movements are shorter compared with Barren-Ground or Eastern Caribou (GRH/LRH), with seasonal migrations up to 500 km (Geist, 1998; Miller, 1991). They spend their annual cycle on one island or moving between two or more islands. For example, seasonal migrations within the Prince of Wales-Somerset-Boothia complex (Canadian Arctic Archipelago) range between 300–500 km, though longer movements have been recorded (COSEWIC, 2004).

Boreal forest caribou or woodland caribou (*Rangifer tarandus caribou*) are genetically, geographically, behaviourally, and morphologically distinct from their migratory tundra counterparts. Woodland caribou live year-round in small groups south of the treeline; they dwell in boreal and open taiga forests, with two main, well-defined seasons: a short summer, wet and slightly humid, followed by a long, cold, and dry winter (Taillön, 2013). Unlike Barren-ground (tundra) caribou, boreal forest caribou migrate short distances between calving, summer, and winter ranges (Miller, 2003; Nuttal, 2005), often between 80–100 km, (Schaefer, 2010; Seip & McLellan, 2010; Thomas & Gray, 2002) or 50–150 km, depending on the population (Mallory & Hillis, 1998). Boreal Forest (aka Woodland) caribou live all year round in northern coniferous forests and peatlands (Schaefer, 2010). When population density increases, they increase their range, migrating longer distances; they move across landscape seasonally foraging, and to avoid predators in the calving season (Thomas & Gray, 2002; Ferguson & Elike, 2004).

Eastern Migratory Caribou or Migratory Woodland caribou (*Rangifer tarandus caribou*) are divided into the George River Herd (GRH) and Leaf River Herd (LRH), which occur in open-tundra and boreal habitats in northern Labrador and Québec (Bergerud *et al.,* 2008; COSEWIC, 2017). Although they belong to the woodland caribou subspecies, they behave like Barren-Ground caribou and perform long migrations between northern Québec and Labrador, and the boreal forests of southern Québec in winter (COSEWIC, 2011; COSEWIC, 2017), with migration distances ranging between 1120 up to 1770 km on average per year (Leblond *et al.,* 2016)

Mountain caribou (*Rangifer tarandus caribou*) are both migratory and sedentary (COSEWIC, 2017). Mainly present in Alberta and British Columbia they inhabit a range of habitats including old-growth forests, lush alpine meadows, barren alpine tundra and glaciers and display a correspondingly broad diversity of habitat use patterns (Seip & McLellan, 2010). They undertake altitudinal migrations in spring and autumn and tend to calve at upper elevations (Cavedon *et al*., 2019; Edmonds, 1988; Hegel & Russel, 2013; Saher & Schmiegelow, 2005; Stuart-Smith *et al.,* 1997; Weaver, 2006), although some populations may make four migrations each year. Herds that calve at higher altitudes can move as much as 200 km between seasonal ranges or even more (COSEWIC, 2011). Other herds perform shorter movements, between 10 to 40 km to their calving grounds (Cumming & Beange, 1987; Saher & Schmiegelow, 2005; Weaver, 2006). Seasonal range shifts also occur in response to snowfall conditions affecting forage availability and to avoid predation (Heard & Vagt, 1998; Taillön, 2013). By undertaking altitudinal migrations, Mountain caribou experience a climatic and ecological change similar to that experienced by migratory tundra caribou moving north or south during their long migrations (Seip & McLellan, 2010). Mountain caribou use a variety of winter habitats, which include wind swept alpine ridges, subalpine forest, and low-elevation forest (Seip & McLellan, 2010).

Biologists generally distinguish between two mobility patterns for caribou: migratory and sedentary (Festa-Bianchet *et al.,* 2011). Migratory reindeer travel more than 200 km, often undertaking seasonal migrations in the order of thousands of kilometres, sedentary caribou travel distances of less than 200 km (Wittmer *et al.,* 2006). This means that Mountain and Woodland caribou are considered sedentary, whilst Peary, Barrenland, and Grant's caribou, and Eastern Woodland caribou, are considered migratory.

Methods

Sample

For this research we compiled a sample of 60 metacarpals, 70 metatarsals, and 117 proximal phalanges, from the four subspecies of caribou described above (Table 1). The samples come from caribou herds from mountain, boreal forest, and tundra habitats and includes both migratory and sedentary mobility patterns (all of them from British Columbia, Québec, Labrador, Alberta, Nunavut, and Alaska). Due to the fact that most sedentary populations are classified as "Endangered", the acquisition of samples from these populations was more difficult (since they are barely extant in museums, it was only possible to acquire them through samples sent by biologists acquired when a caribou died in a traffic accident or was found dead in the forest), resulting in uneven sample sizes.

Data about migration distances and habitat of the samples are based on sampling location and data from the literature (Cavedon *et al.,* 2019; COSEWIC, 2004; COSEWIC, 2011; COSEWIC, 2015; COSEWIC, 2016; COSEWIC, 2017; Cumming & Beange, 1987; Edmonds, 1988; Fancy *et al.,* 1989; Ferguson & Messier, 2000; Festa-Bianchet *et al.,* 2011; Geist, 1998; Gunn, 2010; Heard & Vagt, 1998; Hummel & Ray, 2010; Jenkins *et al.,* 2011; Joly *et al.,* 2019; Mallory & Hillis, 1998; Miller, 2003; Miller, 1990; Miller, 2002; Nuttal, 2005; Saher & Schmiegelow, 2005; Schaefer, 2010; Seip & McLellan, 2010; Stuart-Smith *et al.,* 1997; Taillön, 2013; Thomas & Gray, 2002; Weaver, 2006) and information provided by biologists. Biologists from the Ministry of Forests, Lands, Natural Resource Operations and Rural Development, British Columbia, provided mountain caribou samples and related information about herds (type of herd, sex, and location). Peary caribou, Barren-Ground, and Grant caribou specimens were collected from Canadian Museum of Nature (Ottawa), which houses one of the largest osteological collections in Canada. Eastern migratory and woodland caribou were obtained thanks to biologists from the Forest and Wildlife branch of the Québec Government, and from zooarchaeological labs at Laval University and the University of Montréal.

Metapodial bones and first phalanges are included in this study. Because artiodactyls have evolved to be efficient runners, using an unguligrade foot posture that minimizes the total

Table 1. Reference sample included in the present study and grouped according to subspecies, habitat, and mobility pattern.

	Subspecies		Habitat		Mobility pattern	
Metacarpal	*Rangifer tarandus caribou*	30	Mountain	12	Sedentary	14
	Rangifer tarandus groenlandicus	6	Boreal Forest	7		
	Rangifer tarandus granti	5	Tundra	41	Migratory	46
	Rangifer tarandus pearyi	19				
Metatarsal	*Rangifer tarandus caribou*	40	Mountain	17	Sedentary	11
	Rangifer tarandus groenlandicus	2	Boreal Forest	9		
	Rangifer tarandus granti	6	Tundra	44	Migratory	59
	Rangifer tarandus pearyi	22				
Proximal phalange	*Rangifer tarandus caribou*	82	Mountain	42	Sedentary	36
	Rangifer tarandus groenlandicus	13	Boreal Forest	21		
	Rangifer tarandus granti	11	Tundra	54	Migratory	81
	Rangifer tarandus pearyi	11				

area in contact with the substrate (Köhler, 1993; Reese, 2015) podial elements have been used in a number of morphometric studies assessing body size, locomotor behaviour, and habitat preference (Plummer & Bishop, 1994; Purdue, 1987; Reese, 2015; Scott, 1985; Scott, 2004). In addition, archaeological samples often include these elements, making this study relevant for archaeozoological analysis.

Regarding the methodology followed, bone samples were scanned at the Ecomorphology and Palaeontology lab (Université de Montréal) in order to obtain cross-sectional images using a peripheral quantitative computed tomograph, or CT-scanner (Stratec pQCT) (Galán López *et al.*, 2021). Both metacarpals and metatarsals were measured at pre-defined scan points corresponding to 20%, 35%, 50%, 65%, and 80% of the total bone length from distal to proximal (following Ruff, 2002). For proximal phalanges, the mid-section (50% section) was scanned. All of the bones were placed in anterior-posterior position and scanned from distal to proximal ends. The scan results were then subjected to a geometric morphological (GMM) analysis.

Measurement error was tested for each section. Ten images per section were digitalised one day and the same ten images the next day. A Procrustes ANOVA was carried out to test the error. Finally, the value of the mean squares of the Procrustes ANOVA of the error was in all the cases lower than the value of the mean squares of the individuals, therefore there is no measurement error in the data.

One-way permutational multivariate analysis of variance (PERMANOVA) and boxplots for cross-sectional geometry (CSG), individuals were also grouped by subspecies according to habitat and mobility pattern, e.g., *Rangifer tarandus caribou*-mountain-sedentary (Table 2).

Geometric Morphometric analysis

Geometric Morphometric Methods (GMM) use information captured in the form of homologous landmarks to describe each specimen separately. Once cross-sectional images were obtained, landmark data were collected as a curve, reflecting the round shape of the cross sections, using TpsDig2 2.31 (Rohlf, 2010) software and converted into landmarks with TpsUtil64 1.81 (Rohlf, 2013) software. Coordinate data were collected several times until an optimum number of landmarks was reached. Curves were resampled to have an equal number of evenly spaced coordinates in each specimen, starting at a homologous landmark (in the middle of the caudal face). Accordingly, in metacarpals 28 landmarks (LMs) were collected for the 20% and 35% sections, 32 LMs for the 50% section, and 35 LMs for the 65% and 80% sections. In metatarsals, we digitized 30 LMs for the 20% section, 32 LMs

Table 2. Codes used in the present study.

Code	Meaning
Rtcaribou_MS	Rangifer tarandus caribou Mountain Sedentary
Rtcaribou_BS	Rangifer tarandus caribou BorealForest Sedentary
Rtpeary_TM	Rangifer tarandus peary Tundra Migratory
Rtgroenlandicus_TM	Rangifer tarandus groenlandicus Tundra Migratory
Rtgranti_TM	Rangifer tarandus granti Tundra Migratory
Rtcaribou_MM	Rangifer tarandus caribou Mountain Migratory
Rtcaribou_TM	Rangifer tarandus caribou Tundra Migratory

for the 35% section, and 35 LMs for the 50%, 65%, and 80% sections. Finally, for proximal phalanges, both anterior and posterior, 22 LMs were collected from the mid-section.

As landmarks record shape and size information in the form of Cartesian coordinates, it is possible to compare different elements that are described in a homologous way (Klingenberg, 2008; ÓHiggins & Johnson, 1988).

Using MorphoJ (1.06d version) software (Klingenberg, 2011) landmark data per bone and section were analysed based on procrustes superimposition, known as generalized procrustes analysis (GPA). GPA normalizes shape information by the application of superimposition procedures: landmark configurations are translated, rotated, and scaled to remove all information unrelated to shape (Zelditch *et al.,* 2004).

After GPA, a principal component analysis (PCA) was performed using MorphoJ for data exploration and to reduce the dimensionality of the datasets for the later linear discriminant analysis (LDA). Principal Component scores (PCs) preserve much of the sample variation in a few variables, allowing us to properly represent morphological differences and avoid 'overfitting' the discriminant functions in the training set (Curran, 2012; Kovarovic *et al.,* 2011).

PC scores were then exported to PAST 3.24 software (Hammer *et al.,* 2001) to carry out further statistical analyses like the one-way Permutational Multivariate Analysis of Variance (PERMANOVA-sequencial Bonferroni correction). PERMANOVA is a geometric partitioning of variation across multivariate data, defined explicitly in the space of a chosen dissimilarity measure, in response to one or more factors in an analysis of variance design. The test performs a classical partitioning, as in analysis of variance (ANOVA), while simultaneously retaining important robust statistical properties of rank-based non-parametric methods. It is a useful statistical tool for the analysis of multivariate data on the basis of Euclidean distances or non-Euclidean embeddable dissimilarity measures (Anderson, 2017).

The relative weight of the three predictor variables, subspecies (*Rangifer tarandus granti, groenlandicus, pearyi,* and *caribou*), habitat (mountain, boreal forest, and tundra) and mobility pattern (migratory and sedentary), was statistically tested using a three-way PERMANOVA using the Vegan script in the Adonis package in R-Studio 1.3. 1093 (R Studio Team, 2020; r-project.org).

Linear discriminant analyses (LDA) were carried out (in PAST 3.24 as well) on the PC scores, per section, in order to discriminate between different mobility types. LDA is an ordination method that discriminates *a priori* established groups by calculating confusion matrices. The Jackknife test was used as a cross-validation method to assess the effectiveness of the resulting models (Webster & Sheets, 2010). According to Curran's methodology (2012) and because the aim of this study is to determine how well we can discriminate among groups, LDA's were performed iteratively, starting with the first two PCs (Table 4) as variables, and then adding each subsequent PC to compare cross-validations. To avoid overfitting the analyses, the maximum number of PCs used never exceeded a total cumulative variance of 99%.

LDA comparisons were performed in pairs and permutation tests were computed to test differences between group means. In some cases, when classification could be improved, Log Centroid Size was added as a variable (Franklin *et al.*, 2008).

Because of the uneven sample sizes across migratory and sedentary ecotypes (Table 1), which may lead to the largest sample dominating the pattern of variance in the data, the sensitivity of the LDA to the number of specimens in each group was tested using randomisation experiments (Evin *et al.,* 2013), creating balanced groups by a random selection of a number of specimens in the largest group (migratory) equal to the sample size of smallest group (sedentary).

Finally, in order to visualize shape changes and provide information on morphological changes in their immediate anatomical context, 'lollipop' graphs were produced. In this type of graph,

landmark positions of the starting shape are indicated by dots (the 'candy' of the lollipop) and the shifts of landmarks to the target shape are represented as lines (the 'lollipop' stick) (Klingenberg, 2013).

Cross-sectional geometry

The cross-sectional geometry of lower limb bone shafts is often analysed to infer physical activity levels (López & Castillo, 2014; Macintosh *et al.*, 2013). This is because of the capacity of bone shafts to adjust their morphology in response to mechanical loading. Using cross sectional images obtained from the CT-scanner, the Fiji 2.1.0 software (Schindelin *et al.,* 2012) and the BoneJ (v.1) Plugin (Doube *et al.,* 2010), it is possible to use the geometric properties of the cross section diaphysis to calculate resistance to mechanical stresses (Lambert *et al.,* 2014).

Here, we are interested in comparing shape results from two different methods (GMM and shape ratio), therefore only the shape variable from this analysis is included. The bending strength index is often considered one of the most informative variables, and it is calculated as the ratio of second moments of area about the orthogonal principal axes (Imax/Imin). Shafts with ratios greater than 1 are linked to greater mechanical stress and thus, physical activity (Ruff & Hayes, 1983) while scores closer to 1 imply a more sedentary pattern (Ruff & Hayes, 1983; Stock & Macintosh, 2016). Higher values for the bending strength index are expected in migratory groups of caribou, compared with sedentary groups.

The Shapiro-Wilk normality test was carried out for each numerical variable, and Bartlett and Levene´s tests were used to verify the homogeneity of variances prior to the analysis. Then, in order to test statistical differences between the two mobility groups (sedentary and migratory), t-tests and Wilcoxon's test (for non-normally distributed variables) were performed. Finally, a series of boxplots were made to see the distribution of significant categories and they were grouped according to subspecies, mobility and habitat. All the tests were performed using R Studio 1.3.1093 and the packages "dplyr" "ggplot2" and "devtools" (r-project.org).

Results

Geometric morphometrics

One-way PERMANOVA (by subspecies according to habitat and mobility pattern as group variable) was carried out on all the sections for both metacarpal and metatarsal PC scores (Table 3). In metacarpals, the 20% section for Rtpeary_TM (see Table 1 for codes) mainly showed differences with Rtcaribou_BS (p=0,01). Rtgroenlandicus_TM had statistical differences with Rtcaribou_MS (p=0,03), Rtcaribou_BS (p=0,006) and with Rtgranti_TM (p=0,01). Both Rtcaribou_MM and Rt caribou_TM have differences with Rtcaribou_MS (p=0,007 and p=0,01 respectively) and Rtcaribou_BS and Rtgranti_TM (p=0,001) as well. These two sedentary groups showed statistical differences with the rest of the migratory groups. In the 35% section, Rtpeary_TM had differences statistically significant with all the groups, which are especially important with Rtcaribou_MS (p=0,0002), Rtcaribou_MM (p=0,002), and Rtcaribou_TM (p=0,002). In the 50% section, there are no significant statistical differences for any group and in the 65% section we find these differences only between Rtcaribou_TM and Rtcaribou_MS (p=0,003), Rtpeary_TM and Rtcaribou_MM (p=0,02), and Rtgroenlandicus_TM and

Table 3. PERMANOVA per section according to mobility pattern as group variable.

Bone	Section	Mobility Pattern	*P- value*
Metacarpal	20%	Migratory----Sedentary	0,0002
Metacarpal	35%	Migratory----Sedentary	0,0054
Metacarpal	50%	Migratory---Sedentary	0,0396
Metacarpal	65%	Migratory----Sedentary	0,0369
Metacarpal	80%	Migratory----Sedentary	0,2481
Metatarsal	20%	Migratory----Sedentary	0,0154
Metatarsal	35%	Migratory----Sedentary	0,0023
Metatarsal	50%	Migratory----Sedentary	0,0207
Metatarsal	65%	Migratory----Sedentary	0,0289
Metatarsal	80%	Migratory----Sedentary	0,1966
Prox. Phalanges-anterior-	50%	Migratory----Sedentary	0,0004
Prox. Phalanges-Posterior.	50%	Migratory----Sedentary	0,5396

Table 4. Number of principal components (PCs) used in linear discriminant analysis (LDA), per section and bone.

Bone	Section	PCs	PC variance % (accumulated)	% Resubstitution	% Cross-validation
Metacarpal	20%	5	92,52	90%	88,33
Metacarpal	35%	8	95,69	87,93	84,48
Metacarpal	50%	7	95,40	85	83,33
Metacarpal	65%	14	98,36	95,05	81,97
Metacarpal	80%	15	97,79	90,16	75,41
Metatarsal	20%	3	81,85	78,37	75,71
Metatarsal	35%	6	93,42	84,29	81,43
Metatarsal	50%	15	98,81	86,36	77,27
Metatarsal	65%	14	98,81	84,85	74,24
Metatarsal	80%	8	99	86,57	77,61
Proximal. Phalanges-anterior-	50%	18	98,62	88,68	77,36
Proximal. Phalanges-Posterior.	50%	3	66,74	60,94	57,58

Rtcaribou_TM (p=0,02). In the 80% section, Rtpeary_TM had differences with all the other groups except Rtcaribou_BS. Rtcaribou_TM, and Rtcaribou_MS (p=0,07) which had significant values.

For metatarsals, in the 20% section, differences between groups are less obvious. Major differences with the rest of the groups are shown by Rtpeary_TM and Rtgranti_TM (p=0,002). In the 35% section, the main differences are between Rtcaribou_TM and the rest of the groups (except Rtpeary_TM), and between Rtpeary_TM and the other populations. The 50% section presented mainly statistically significant differences between Rtpeary_TM and Rtcarbou_MM (p=0,08), and Rtcaribou_BS(p=0,0007), Rtcaribou_TM, and Rtgranti_TM (p=0,03). In the 65% section, the major differences are between Rtcaribou_BS and Rtcaribou_MM (p=0,04), Rtpeary_TM and Rtgranti_TM (p=0,03), and between Rtpeary_TM and all the groups except Rtcaribou_MS and Rtgroenlandicus_TM. Finally, in the 80% sections all the groups except Rtcaribou_MS had significant differences with Rtpeary_TM.

Then, a three-way PERMANOVA was performed in all the sections for both metapodial bones and phalanges on PC scores as well, in order to assess the three group variables and explore the interaction between them. The subspecies variable got significant values on the 35% (p=0,002) and 80% (p=0,003) metacarpal sections, and all metatarsals and phalanges sections. However, a larger sample is needed to include that variable in further analyses. Habitat was significant (p=0,003) on the 35% and 80% (p=0,03) metatarsal section, 35% metacarpal section (p=0,01) and posterior first phalange section (p=0,005). Mobility pattern was statistically significant on the following sections in metacarpal: 20% (p=0,001), 35% (p=0,007), 65% (p=0,02); in metatarsal: 20% (p=0,01), 35% (p=0,003), 50% (p=0,02) 65% (p=0,03) and in anterior first phalanx (p=0, 001).

Finally, once the dependent variables were tested, mobility pattern emerged as a good predictor and, due to the size of the reference sample, we considered it a suitable predictor for discriminant analyses.

Then, a one-way PERMANOVA was done only on the mobility pattern variable. The results obtained with the one-way PERMANOVA test indicate statistically significant differences between sedentary and migratory groups per almost every bone section, with the exception of the anterior proximal phalanges (Table 3) and on the proximal (80%) sections in both metacarpals and metatarsals. These differences are greater on distal ends.

Considering all these results, although all the analyses were carried out on all the sections (Galán López *et al.*, 2021), given the best outcomes were produced for distal sections (20%), we are going to focus mainly on this section (for both metacarpals and metatarsals).

Regarding randomization experiments, taking only five PCs for the metacarpals 20% section, the result was very similar to the unbalanced sample: 96,15% (cross-validated 88,46%) of the specimens were well classified (uneven sample: 93,33%-90%). When Log Centroid Size is added, the accuracy

is 96,15% (including cross-validation) (uneven sample: 96,67%-93,33%). Randomization experiments were performed in every section, and the results, like in the metacarpals 20% section were very similar between balanced/unbalanced samples. Therefore, sample size did not affect LDA results.

Referring to LDA, when Log Centroid size is incorporated to the analysis, the 35% section on metatarsals showed an improvement in classification accuracy on mobility pattern.

Metacarpals

When lollipop graphs are examined in 20% section on metacarpals (Figure 1) on Principal Component 1 (PC1) showed the biggest differences on the anterior side: migratory individuals have a deeper anterior canal than sedentary ones.

The LDA results (Table 4) for the 20% section are as follows (including LOOCV values that estimate model performance): five principal components (PC) summarized 92,52% of the total variation (Table 4 and Table 5). In the first case, 90% of the individuals (leave one out cross-validation, 88,33%) are successfully classified in migratory and sedentary groups. For the 35% section, mobility pattern accounted for 95,69% of the variance (eight PCs) and had a correct classification of 87,93% (leave one out cross-validation 84,48%). The 50% section summarized 95,40% of the variance in first seven PCs for mobility patterns and 85% (83,33% leave one out) of specimens are correctly classified.

For the 65% section, 14 principal components accounted 98,36% of the total sample variance. The LDA was able to classify 95,05% of the specimens (leave one out cross-validation 81,97%) correctly according to mobility pattern (migratory/sedentary).

The 80% section showed the lowest classification rates. With 15 principal components that summarized 97,79% of the variance and correctly classifying 90,16% of the specimens (leave one out cross-validation 75,71%) according to mobility pattern.

In view of the results of the PERMANOVA, and in order to test the impact of habitat independently of mobility, a separate LDA was conducted using the 20% section dataset leaving out the sedentary groups (both mountain and boreal forest) individuals and preserving mountain migratory (n= 7) and tundra (n= 41) migratory groups. A new GPA and covariance matrix were carried out to perform a PCA. Then, PCA scores were exported to PAST and LDA was performed iteratively (without exceeding the cumulative 99% variance to avoid overfitting) until obtaining 89,58% (81,25% leave one out cross-validation) of correctly classified cases using 95,53% of the total variance (eight PC scores). However, it should be pointed out that the sample was very unbalanced, with only seven individuals in the mountain migratory group (versus 41 for migratory tundra).

Metatarsals

For the 20% section, Figure 2 shows how differences are distributed homogeneously along the whole section. Migratory individuals have a wider section on their medial-lateral axis than sedentary ones, with the former slenderer than the latter.

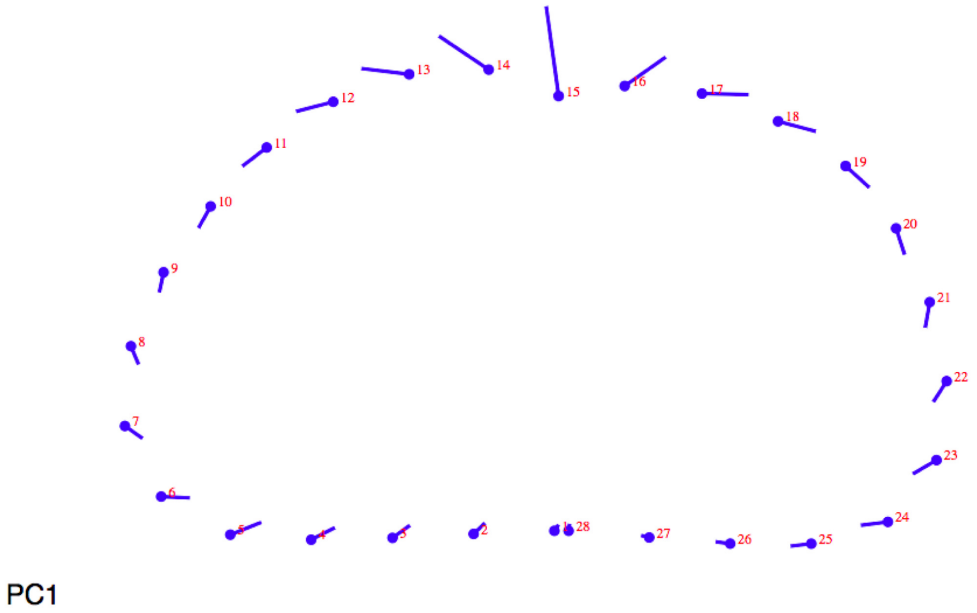


Figure 1. Lollipop graph (20% metacarpal section) visualizing cross-section changes on Principal Component 1 (PC1).

The LDA (Table 4), for the 20% section, used three principal components that accounted 81,85% of the total sample variance; 78,37% (leave one out cross-validation, 75,71%) of the specimens were correctly classified according to mobility pattern.

Table 5. T-tests for each section according to mobility pattern for shape ratio.

	t-Test		
	t	**Df**	***p***
Metacarpus			
20%	2.58	54	0.012
35%	0.82	54	0.413
50%	2.23	54	0.029
Metatarsus			
20%	0.19	15	0.849
35%	1.77	63	0.079
50%	1.66	63	0.114
65%	0.98	63	0.326
80%	1.47	63	0.143

In the 35% section, six principal components summarized 93,42% of the variance, and the LDA returned a correct classification of 84,29% (leave one out cross-validation, 81,43%) of the specimens into migratory and sedentary groups. For the 50% section using 15 PCs accounting for 98,81% of the total sample variance, 86,36% (leave one out cross-validation, 77,27%) of the specimens are successfully predicted as migratory or sedentary. For the 65% section, using 14 principal components (98,81% of the variance), the LDA successfully classifies 84,85% (leave one out cross-validation, 74,24%) of the specimens by mobility pattern. Finally, for 80% section, using eight PCs accounting for 99% of accumulated total sample variance to the LDA classifies 86,57% (leave one out cross-validation, 77,61%) correctly.

As before, a LDA was performed on the 20% section dataset of metatarsals in MorphoJ leaving out sedentary (mountain and boreal forest) individuals and preserving mountain migratory (n=15) and tundra (n=42) migratory groups. A new GPA and covariance matrix were carried out to perform a PCA. Then, PCA scores were exported to PAST and LDA was performed iteratively. Using a 98,88% of the total variance (17 PC scores), a total of 92,98% (87,72% leave one out cross-validation) were correctly classified.

Proximal phalanges

It is possible to segregate the anterior proximal phalanges according to mobility pattern (sedentary and migratory) with 18 PCs that summarize 98,62% of the total variance with an

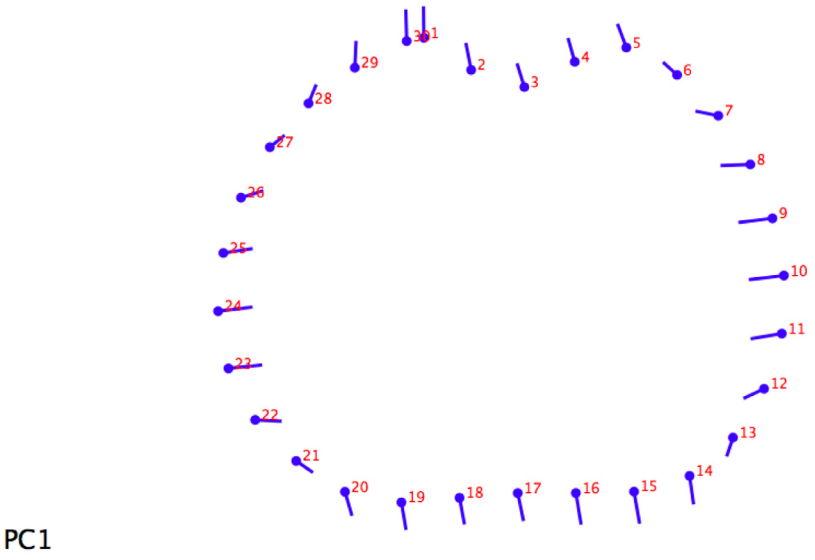


Figure 2. Lollipop graph (20% metatarsal section) visualizing cross-section changes on principal component 1 (PC1).

accuracy of 88,68% (leave one out 77,36%). Posterior phalanges have low overall classification rates, ranging between 60–50% (including cross-validation rates) (Table 4).

Cross-sectional geometry

Finally, a cross-sectional analysis was carried out to analyse geometrical properties. Here, we are going to focus on the shape ratio (Imax/Imin) results, which we suggest are directly linked to mobility and in this case, are also related to our geometric morphometric study. Normality tests (Shapiro-Wilks) showed normal distributions ($p>0.05$) on metatarsal shape variables and on metacarpals for the 20%, 35%, and 50% sections. The variables from the remaining sections were non-normally distributed. Homogeneity of variances was observed ($p>0.05$) in all sections of both metacarpals and metatarsals except for 20% ($p=0.04$) section of metatarsal (Welch test instead of t-test was used because of that).

The t-tests on metacarpals (Table 5) shows significant differences according to mobility pattern only in the 20% ($p=0.01$) and 50% ($p=0.02$) sections. The Wilcoxon test (Table 6) was also significant on the 65% section ($p=0.006$). However, t-tests and the Welch test performed on metatarsals produced non-significant values for all sections (Table 5).

Since mobility pattern was only significant on the 20%, 50%, and 65% metacarpal sections (Table 5), only these were retained for further analysis.

According to Imax/Imin distribution plots, higher values in the 20% section (Figure 3) correspond to migratory populations. Rtcaribou_borealforest_sedentary and Rtcaribou_mountain_sedentary show a complete overlap. Rtcaribou_tundra_migratory stands out among the rest of the groups. In the

Table 6. Wilcoxon tests for metacarpal 65% and 80% sections (non-normal distribution) according to mobility pattern for shape variable.

Wilcoxon-Metacarpus		
	W	***p***
65%	419.5	0.006
80%	370	0.080

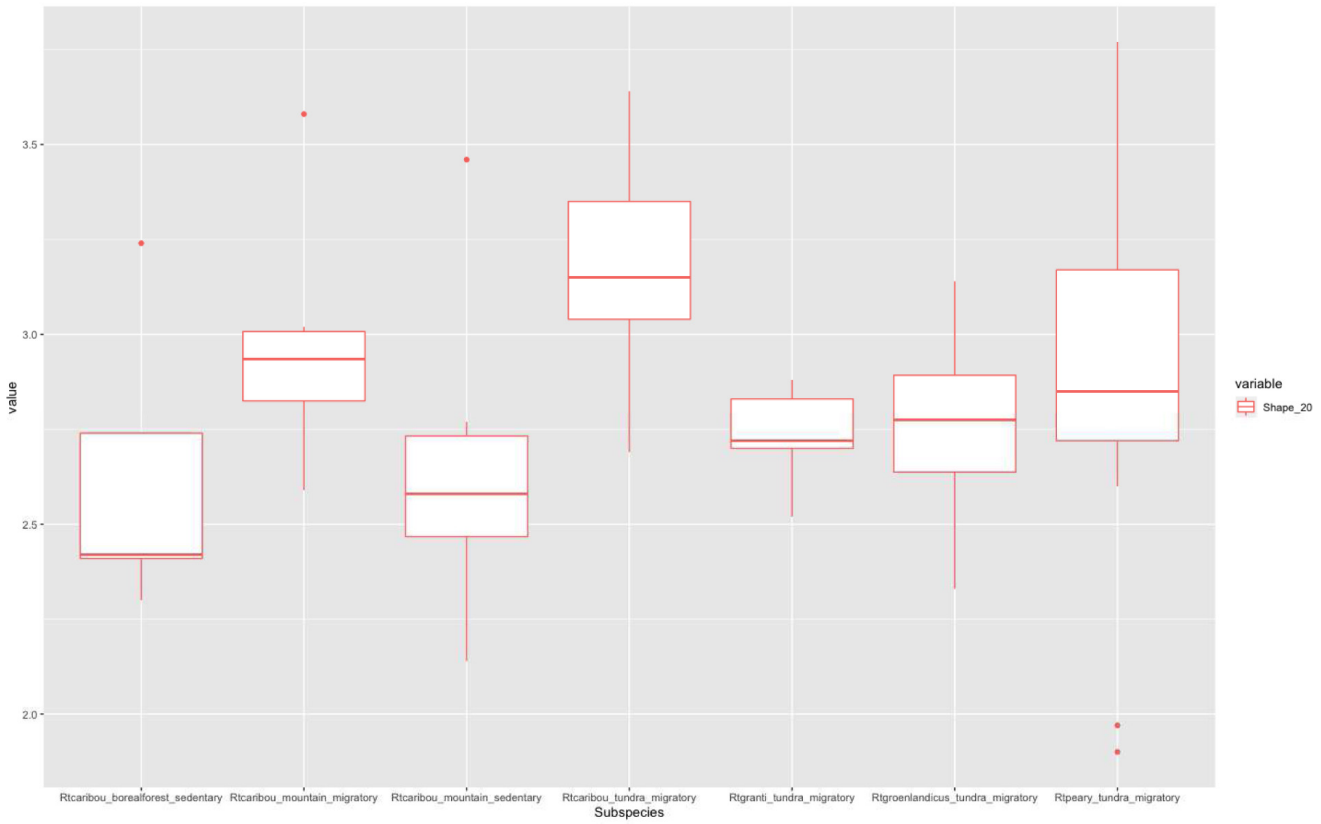


Figure 3. Shape ratio variable (metacarpal 20% section) according to subspecies, habitat, and mobility pattern.

50% section (Figure 4), the values between the groups are homogeneously distributed, except for R.t.caribou_mountain_migratory, which stands out, and R.t.caribou_boreal forest_sedentary, with the lowest values. In the 65% section (Figure 5), Rtpeary_tundra_migratory and Rtcaribou_mountain_migratory clearly feature over the rest, with a slight overlap, while Rtcaribou_mountain_sedentary, Rtcaribou_tundra_migratory, Rtgranti_tundra_migratory, and Rtgroenlandicus_tundra_migratory overlap. Rtcaribou_borealforest_sedentary again shows the lowest values.

Thus, if we consider only mobility pattern (Figure 6) in these three sections, in the 20% section, the migratory group is separated from the sedentary one, although with some overlap of some individuals. However, this separation is less evident for the other two sections.

Discussion

First of all, it is important to notice that the definition of 'sedentary' reindeer used in the present study, which is consistent with the biological literature (Wittmer *et al.,* 2006) is very far from what is meant in an archaeological context. Here, sedentary caribou refers to herds that travel less than 200 km (Wittmer *et al.,* 2006). For some authors and archaeologists, however, (Bouchud, 1966; Bouchud *et al.,* 1953; Deplano, 1994; Fontana, 2000; Fontana, 2012; Fontana, 2017), sedentary reindeer behaviour is defined as an annual presence of reindeer in the Périgord area, e.g., at La Madeleine (Bonnisent, 1993) and layer IX of the Flageolet II (Deplano, 1994), linked to environmental characteristics (Fontana, 2000). However, some Woodland caribou and Mountain caribou herds travel very short distances within their annual range (Hummel & Ray, 2010) and would probably be good proxies for the archaeological model.

The results of the present study (both from geometric morphometrics and shape ratio), show that mobility, which is linked to habitat, affects lower limb bone shape and makes it possible to distinguish between migratory tundra dwellers and sedentary woodland and mountain herds. More sampling and further analyses will be required to test whether or not woodland and mountain populations can be distinguished from one another using these methods.

For the GMM analysis, successful results are produced using distal sections both in metacarpals and metatarsals, especially the 20% section in the metacarpal. The anterior and posterior first phalanges are not suitable for distinguishing mobility patterns according to the low classification rates obtained in this analysis.

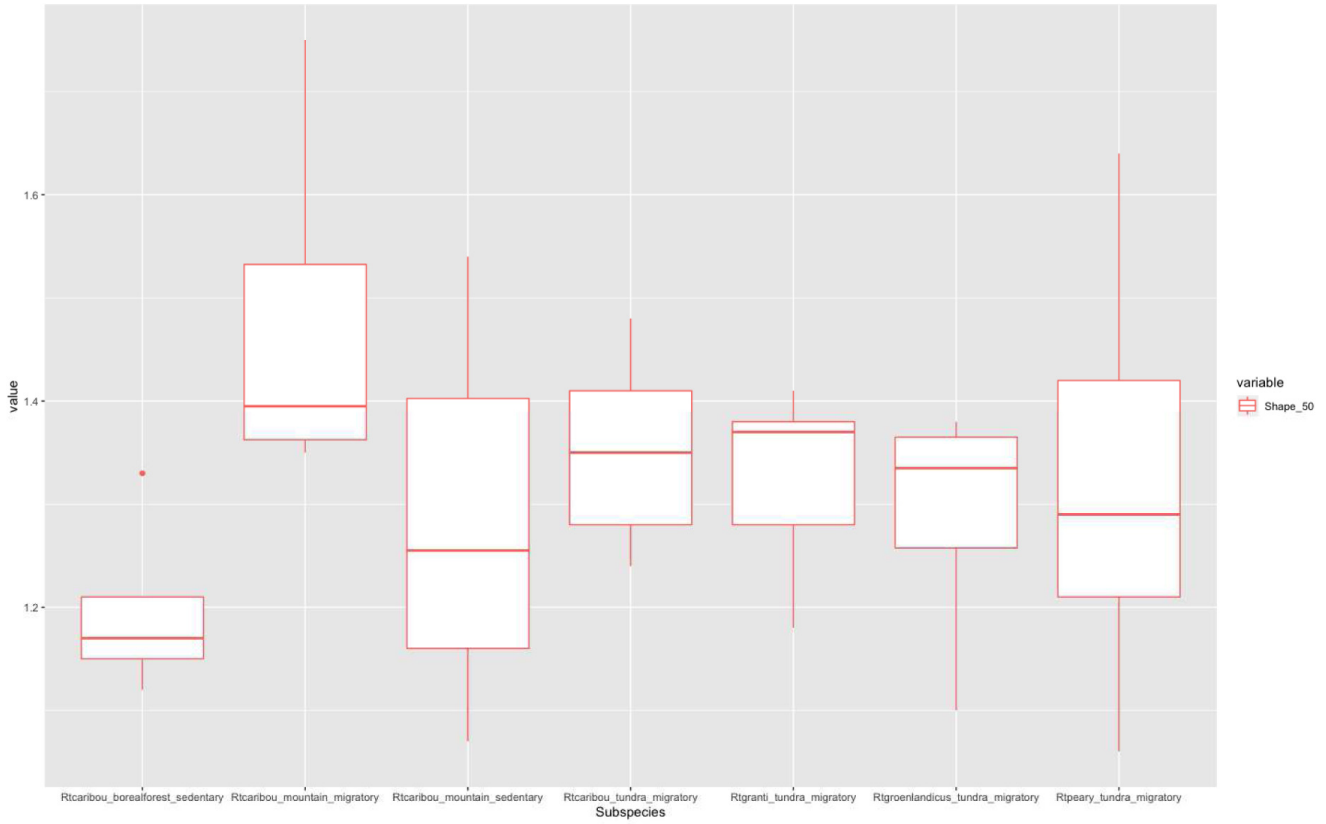


Figure 4. Shape ratio variable (metacarpal 50% section) according to subspecies, habitat, and mobility pattern.

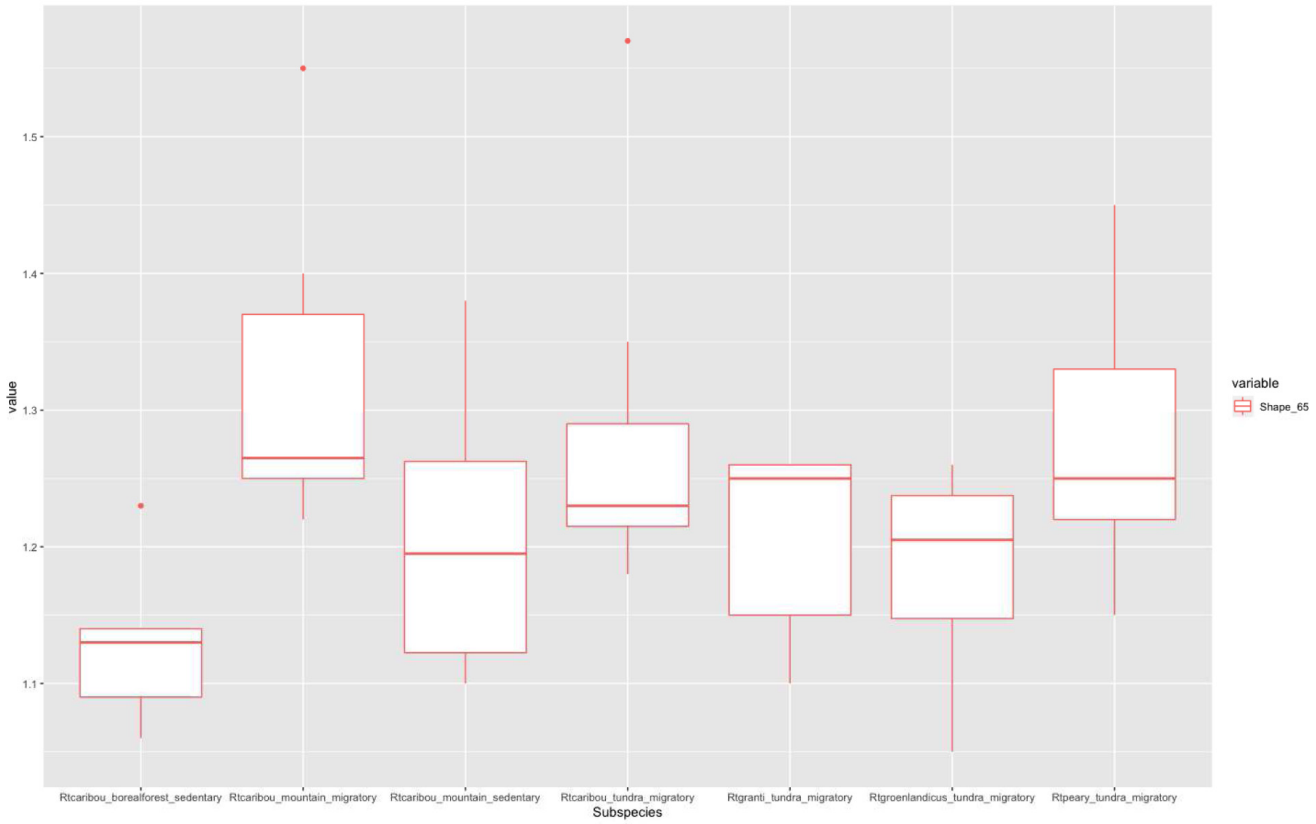


Figure 5. **Shape ratio variable (metacarpal 65% section) according to subspecies, habitat, and mobility pattern.**

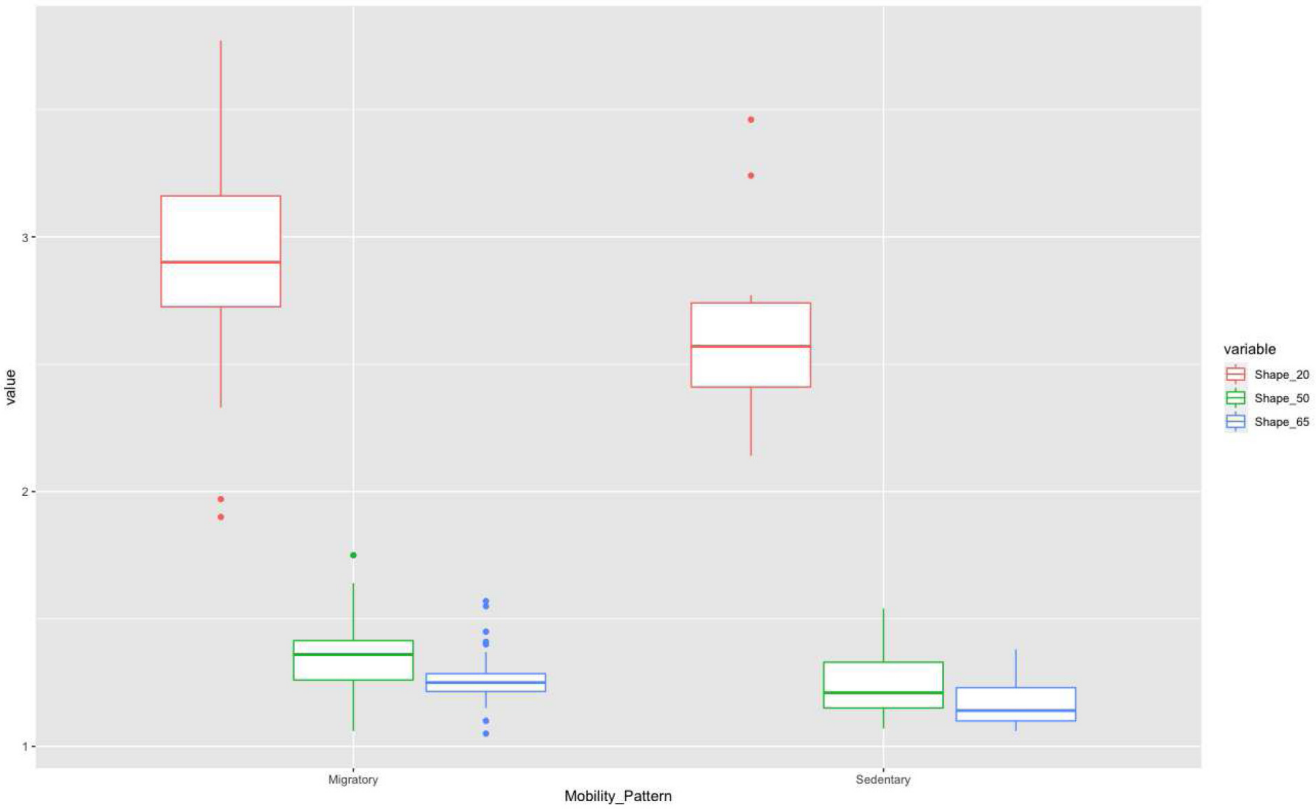


Figure 6. **Shape ratio variable (metacarpal 20%, 50%, and 65% sections) according to mobility pattern.**

Thus, we observe that the best section to apply further analyses on archaeological material is the metacarpal 20% section (higher resubstitution and cross-validation percentages). Differences in shape stand out on the metacarpal (20% section) as well. The main shape differences are found on the anterior face, which is slightly more circular on sedentary individuals and oval (with more of a cranial groove) on migratory ones. Furthermore, migratory individuals have a wider section on their medial-lateral axis than sedentary ones.

Regarding cross-sectional geometry, the only significant differences are in the metacarpal bones, on the 20%, 50% and 65% sections, with the best performance on the 20% section. In this sense, the forelimbs produce better results than the hindlimbs. This makes sense if we consider the fact that thoracic limbs carry 60% of an animal's static body weight and absorb ground impact as the body is thrown forward by the pelvic structure (Fletcher, 2019; Zhang *et al.,* 2020). Forelimbs are designed to adopt different locomotor strategies to improve locomotor performance and save energy (Zhang *et al.,* 2020). Therefore, it is not surprising to find the best evidence of performances on thoracic limbs.

In metacarpals, the transversal section allows us to discriminate migratory and sedentary patterns, with at least a 90% success rate using the distal 20% cross-section. The effectiveness of the 20% section is very important because this part of the bone is often relatively well preserved in archaeological record. In contrast, differences in metatarsals are less pronounced among groups, and they are not as good as metacarpals as indicators of shape variation. However, the metatarsal 20% section showed good results to discriminate among migratory populations. It produced a successful indicator to distinguish between mountain and tundra migratory groups, excluding sedentary individuals from the analysis.

There is correspondence between shape analysis performed using GMM and cross-sectional geometry using shape ratio (Imax/Imin) on the distal 20% section in metacarpals: migratory populations have greater shape ratio values which appear to be linked to higher mobility, and sedentary groups have the lowest scores, which means lower activity patterns. Thus, changes in shape related to mobility and the forces that affect bone are linked to the engineering principle known as "beam theory" (Ruff & Hayes, 1983). Mobility patterns affect the loads placed on the limb bones during locomotion and influence variation in diaphysis robustness and shape.

On the 20% metacarpal section, greater shape values correspond to Rtcarbou_tundra migratory specimens. However, on the 50% Rtcaribou_mountain_migratory stands out (and also on the 65% section together to Rtpeary_tundra_migratory) over the rest of the groups, probably because of a combination of the altitudinal movement performed by this caribou and differences in the substrate between mountain and tundra populations. The mountain caribou range includes a great habitat variety (Seip & McLellan, 2010), combining open and close environments: high forest of old-growth cedar and hemlock, vast extensions of pine, spruce and fir forests, alpine meadows, barren alpine tundra, and glaciers which probably creates subtle differences in bone shape or the way that forces or stresses (Ruff & Hayes, 1983) are affecting the bone, and for that reason we can observe higher values for these mountain individuals.

Sedentary populations that inhabit closed environments, one from Québec and the other from British Columbia, exhibit the same bone morphology, more circular than in their tundra counterparts. The same applies for migratory groups (which all live in open habitats) although some of them belong to different subspecies and migration distances can be variable, all these groups present a common oval shape morphology. Furthermore, considering Imax/Imin ratio results of the 20%, 50%, and 65% sections in metacarpals, there are subtle differences that enable us to identify altitudinal migration (performed by migratory mountain caribou), possibly due to the more varied types of substrate in mountain habitats (as stated above) in contrast to the Peary caribou, which migrate in an open tundra habitat all year round, or Barren Ground and Eastern Migratory Woodland caribou, which move most of the year on open tundra. The 50% and 65% sections reflect that they are more affected by mountain movements which are more altitudinal than longitudinal, which implies greater locomotive effort (reflected in higher values of cross-sectional analyses) than tundra caribou populations which make longitudinal migrations involving longer distances and thousands of kilometres.

Conclusion

Geometric morphometrics allows us to distinguish subtle morphological differences and helps us understand the causes of morphological variation in vertebrate species. The present study provides a new and actualistic framework to assess reindeer migration patterns, which are linked to habitat, according to bone shape, discriminating between migratory and sedentary herds.

As Pleistocene environments are not analogous to Holocene ones, it is not possible to infer reindeer mobility patterns from palaeoenvironmental reconstructions. Contemporary caribou herds are found in different environmental settings today and this has allowed us to create a referential framework to study ecomorphological differences between animals from different biomes and mobility patterns. We can also infer habitat type, since those animals which move medium and long distances inhabit mainly open habitats, while those which migrate shorter distances are closed habitat dwellers overall.

Thus, the practical application of this methodology will allow us to reconstruct reindeer movements in future and study how they affected human hunting strategies and understand the precise role of reindeer in their economy during the Magdalenian period.

South-western France is well known for its high density of Upper Palaeolithic archaeological sites (Castel *et al.,* 2013). The Magdalenian culture (18.000-14.000 cal BP) appears in the region during the Tardiglacial, and the paleoclimatic and

environmental variations of the period provide insights into the changes in hunter-gatherer technology, mobility patterns and hunting strategies that occurred during this timeframe (Langlais *et al.,* 2012). Magdalenian faunal assemblages are frequently dominated by reindeer, one of the best represented taxa in the different climate stages (61% in Late Pleniglacial, 69% in ancient Dryas, 67% in Bølling-Allerød) whose predominance stands out in areas such as the Perigord, Quercy, and Bassin de l'Aude. Mobility patterns of reindeer will have affected the hunting strategies and the mobility of the hunter-gatherer groups that depended upon them. The question of the seasonal behaviour of reindeer remains open (Kuntz, 2011) and it cannot be solved if we are not able to develop new approaches to this issue.

In a follow-up study, we propose to use the distal 20% section of the metacarpal to perform this task. In order to establish the degree of mobility of reindeer herds, it is necessary more data provided by a larger sample. So, this is the first step to further analyses. This referential sample and its application to an archaeological record, through the scan of metacarpal 20% distal section and later landmark information, will allow us to be able to infer these two main mobility patterns that have been identified on extant reindeer (caribou), through the use of mainly geometric morphometrics analysis, that have been proven more useful than cross sectional analysis to classify both mobility types.

Data availability

Underlying data

Zenodo. EmorphProject: Reconstructing habitat type and mobility patterns of Rangifer tarandus during the Late Pleistocene in Southwestern France: an ecomorphological study

https://doi.org/10.5281/zenodo.5105714. (Galán Lopez *et al.,* 2021)

This project contains the following underlying data:

- CT SCAN EMORPHPROJECT.zip. (Cross-sectional images from metatarsal, metacarpal and first phalanges according to Rangifer tarandus populations.)
- One-way PERMANOVAS performed in PAST and R respectively.
- Three-way PERMANOVAS performed in PAST and R respectively.

Data are available under the terms of the Creative Commons Attribution 4.0 International license (CC-BY 4.0).

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✗ **Andrew Orkney**
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Summary:
The submitting authors wish to develop tools that will help them determine whether Magdalenian remains of Reindeer in France belong to populations that were sedentary or migratory in their behavior. They hence need a morphological proxy from commonly preserved skeletal components that reflects mobility behavior in Reindeer.
The authors identify contemporary North American Caribou as a suitably closely related lineage that has not been subject to serious changes from domestication, and exhibits a full range of mobility behaviors. The authors collect an expansive set of morphometric measurements from a variety of distal limb bones, although their efforts to do this are partly frustrated by the fact that some populations are endangered.
The authors undertake Permutation-based ANOVA analyses with a sequential interactive model structure, with mobility tested for first, then habitat and finally subspecies- and report that mobility is frequently associated with a significant difference across populations, and further identity that the distal fifth of the metacarpal is a candidate osteological proxy for mobility, based on a leave-out-out cross validation approach.
Sexual differences between samples were not apparent in tables, nor was age structure mentioned, which may confound analyses (for example, if migratory populations tend to experience more mortality and the samples are not fully grown, or if random chance means that one population has more males than females and there may be sexual differences in shape.) A previous reviewer identified this potential problem.
My personal source of doubt originates from the fact that mobility behaviour is highly correlated with Caribou subspecies that are the result of admixture between a Euro-Beringian and Canadian population that are deeply divergent. Differences in osteology may therefore be more likely to reflect differences in ancestry between populations, rather than differences in adaptive responses to mobility. Even if they did reflect adaptation, if those adaptations are specific to a deeply divergent Canadian lineage, analogous adaptations may not have existed in any Magdalenian French population that derives no ancestry from this lineage. The authors' PERMANOVA results recurrently show that subspecies explains a larger portion of the sum of squares variation in osteological properties than either mobility or habitat. I suspect that if the model structure was re-

ordered to 'subspecies + habitat + mobility', (which is a more conservative test of the hypothesis), that subspecies would explain a greater portion of the variance and may actually show that mobility does not uniquely explain variance in osteology among North American Caribou populations.

Is the work clearly and accurately presented and does it engage with the current literature?
Response: Partly
A previous reviewer pointed out that the data and analysis in the study is focused on osteological differences among North American Caribou populations, while the stated aims are to improve knowledge of behaviors in Magdalenian populations of southern France. I understand why this may confuse some readers, who might expect Reindeer remains from France to be included in at least some capacity.
I do, however, believe that the authors explain well that western and northern North American Caribou populations and Eurasian ice age Reindeer derive from a hypothesized Euro-Beringian population, while European populations have experienced widespread domestic influences, which means that some North American specimens may be more appropriate representations of ice age Europe than are contemporary Eurasian populations. There are some reasons that this might not be true, due to existing population structure and admixture in the North American Caribou population, but I have reserved this discussion for my comments on study design, statistical analyses and conclusions.
I note that the authors discuss the semantic differences between migratory and sedentary behaviors described in literature about the ice age and contemporary Caribou populations, and that a migratory-sedentary dichotomy is not absolute- populations switch strategies as needed. I think it is useful that this is mentioned early in the authors' discussion, but it would be even better if this were mentioned more explicitly in the introduction or methods in order to justify the authors' choice of study design.
I discovered two examples of text which appears to have been copied and pasted from previous work by Anderson 2014 and Anderson 2017. The clause 'while simultaneously retaining important robust statistical properties of rank-based nonparametric multivariate methods,' was identical to a sentence in Anderson 2014 [Ref:4], implying that the larger statement it was a part of had been copied and pasted, with a subsequent rearrangement to produce 'original' text. I wish to discourage this style of writing. If the authors believe Anderson 2014's explanation was complete and should not be expressed in new language, then they should set it within quote marks and include a citation. Similarly, text from Anderson 2017 was repeated verbatim. While this text was correctly cited, the text should have been set in quote marks to reflect the fact that this is a quote and not the submitting authors' original language. This of course, does not mean the results necessarily need to be questioned, but it made me feel uneasy.
In general, I think that the study would benefit from a greater number of citations from more recent works. Examples the authors may wish to add include Catz et al., 2020, a dental microwear study in ice age Reindeer Ref:1. Some greater degree of citation and discussion of the Younger Dryas climate instability (mentioned by name only once in the submitting authors' conclusion) is appropriate, especially given climate instability might cause plastic behavioral responses that decouple a hypothesized form-functional relationship between reindeer foot bones and mobility behaviors. Yannic et al., 2020 Ref:2 could be cited with respect to population structure and admixture in North American Caribou populations, while Martino et al., 2024 Ref:3 is an example of a recent morphometric study of metapodial bones in giraffidae. In particular, citing Martino could help demonstrate why foot bones in are especially interesting and why the chosen study approach should be expected to be informative and help clarify the submitting authors' ambitions.

Is the study design appropriate and the work technically sound?
Response: Partly
I mentioned earlier that substantial population structure exists in North American Caribou. The eastern-Canadian and the Beringian lineages have a deep divergence and this may have provided them with the opportunity to adapt over a relatively long time scale to distinct environments which require different mobility behaviors. Morphological differences might have accumulated as a result of selection, but could have also emerged as a result of random drift or because of lurking variables that have not been investigated. Contemporary North American Caribou populations' differences in mobility are strongly associated with their lineage, and there is admixture between the two populations in the western Canadian population. It is therefore conceivable that morphological differences between migratory and sedentary North American Caribou populations result from their different ancestries and that, even if there is a mechanistic role for morphological differences, that European ice age reindeer may not have evolved analogues of these adaptations because their gene pool did not contain admixture from the eastern Canadian population. Moreover, there is an acknowledged semantic difference between observed mobility behaviors in North America and the types of nomadic behavior that other researchers describe in Magdalenian France. So the study design is unable to promise that differences between North American Caribou depend mechanistically on morphology and that those morphological differences should exist in ice age European populations. Rather, an additional study is necessary to determine if this is true.
That said, if all of this is made clear, the authors can present the case that their study is a good attempt to assess form-functional relationships with the data currently available to them, and identify the above questions as avenues of future study.

Are sufficient details of methods and analysis provided to allow replication by others?
Response: Partly
See my detailed comments in response to methods.

Are all the source data and materials underlying the results available?
Response: Yes
I checked the submitting authors' Zenodo deposition and the original images, environmental and behavioral classifications are available there. The authors have hence met the criteria. The image files are large (0.725 GB), and it would benefit other researchers if the derived landmark data, which would be much easier to download, were also available (I hope that I did not overlook them if they were present and apologize if I did). I found at least some of the original code and scripts in the PERMANOVA pdf deposits, and it appears these were introduced at the request of a previous reviewer. I personally believe these results better support alternative interpretations to those advocated by the submitting authors, but reserve these comments for my appraisal of their conclusions.

If applicable, is the statistical analysis and its interpretation appropriate?
Response: Partly
The authors justify limitations in sample collection from endangered populations, and I am satisfied by that.
The submitting authors' statement that there is 'no measurement error in the data' is not credible, and it is unclear what is meant by the statement 'a Procrustes ANOVA was carried out to test the

error'. I think what they meant to state is that a partial Generalized Least Squares model found that individual specimen identity was a strong predictor of cross section geometry and that the day of measurement was not, implying a strong reproducibility of measurements. This is not equivalent to zero error; even a scenario where measurements were invariant would not show that. Imagine if I incorrectly measured a bone to have a length of 0 centimeters twice. The fact that my measurements are exactly concordant is not ipso facto a demonstration that I made no mistake. I agree with the authors that it suggests their data probably are not seriously contaminated by error, but suggesting there 'is no error' belies the meaning of their analysis.
With regard to the authors' methods, using a PERMANOVA approach to explore differences in cross-sectional geometry:
The authors could have stacked the cross sections into a 3-dimensional matrix for these analyses, to assess full bone shape simultaneously. This approach would have reduced the probability of false positives, because fewer repeated tests are carried out (if we had carried out tests on 20 different cross sections, we would expect one of them would probably yield a significant result at an alpha value of 0.05 for instance), and would have accommodated the possibility that subtle shape changes distinguish migratory or sedentary behaviors that are only evident in full 3-dimensional shape.
Approaches exist to accommodate this kind of statistical test in the R geomorph package, for example the ProcD.lm() function.
I note in Table 1 that Caribou subspecies in the geometric study are associated solely with a single mobility pattern and with a single habitat type, and habitat is strongly correlated with mobility pattern. PERMANOVA models may therefore struggle to distinguish whether Caribou ancestry or habitat type have independent contributions to structure. The impression I get is that the dominant signal in the dataset is actually going to be the degree of Euro-Beringian ancestry subspecies possess (indeed, subspecies was found to almost always explain more variety between specimens than mobility type), and that this is strongly regressed upon mobility pattern because mountain and boreal forest populations are almost all described as sedentary and have all experienced genetic admixture from a divergent eastern Canadian population. I do not understand why only PERMANOVA results for mobility group are tabulated in the manuscript body, the three-way PERMANOVA in the Zenodo deposition was essential to complete my review.
The sentence 'Finally, once the dependent variables were tested, mobility pattern emerged as a good predictor and, due to the size of the reference sample, we considered it a suitable predictor for discriminant analyses.' is opaque and needs to be explained in more detail.
I note that there is some subjective language such as 'best' to describe retrieved patterns in PERMANOVA; it is sufficient to state that the p-values were lowest.
I am confused that explained variances were not presented alongside p-values in the manuscript body. A variable that explains a greater degree of variance might be preferred over a variable that explains very little variance even if the p-value for the second variable is lower, for example (indeed this is the case with ancestry, which is almost universally a superior description of variety, even though it was included as the last sequential term in the PERMANOVA models).
Where the authors describe their implementation of PERMANOVA: 'three-way PERMANOVA using the Vegan script in the Adonis package in R-Studio 1.3', I think this should read 'adonis function of the Vegan Package'. The documentation of the adonis function shows that it is designed to process distance matrices as input, and was written with the expectation that these would represent species abundances. This may not affect the authors' results, but procD.lm() of geomorph would have been a more appropriate choice of statistical method, because it is directly designed for 3D landmark data. ProcD.lm performs a partial Generalized Least Squares fit explaining the differences between landmark constellations (or any matrix of continuous data) as

a function of independent variables represented in a design matrix, and can be specified to explore sequential, hierarchical or sum of squares methods. Marginal sum of squares would be the most conservative choice, because it would directly test whether the differences between landmark constellations are uniquely explained by mobility in a way that neither habitat or subspecies identity explains. My suspicion is that subspecies identity would explain the majority of morphological difference and that it may not be possible to discern an effect of mobility, when this structure is implemented.
I am not directly familiar with the syntax for adonis PERMANOVA models, but the structure in the submitting authors' script implies that they specified their model as interactions between all terms. Most reported model results do not include an interaction. Interpreting Table 1 and 2, I think this is because it is rare that habitat and mobility pattern cross in the heterogeneous sampling across bones. I note that it appears pattern and subspecies never cross, which means that pattern is entirely a proxy of subspecies.
I note that a previous author requested that sex be investigated. Can the submitting authors justify the omission of sex in their PERMANOVA analyses? I am assuming that all specimens were from mature adult animals, but found no statement to this effect in the manuscript. I apologize if I failed to find such a statement.

Are the conclusions drawn adequately supported by the results?
Response: No
Having read the submitting authors' manuscript in detail, I believe that it is possible that their conclusions could be supported by their analysis. However, I think they actually presented stronger evidence that patterns of admixture between two deeply divergent Caribou source populations are associated with minor skeletal differences between populations with different ancestral affinities.
When I reviewed the original 3-way PERMANOVA results, which are available with reported R-squared values in full in a supporting PDF on the dedicated Zenodo deposition, I found that the variable which explained the greatest variety in the dependent dataset was subspecies identity, and that this was on the order of twice the value that mobility pattern explained.
Moreover, terms were added sequentially; mobility pattern was added first while subspecies was added last. The reverse would have been more logical if the authors sought to determine whether mobility explained any variety in osteology that cannot be explained by subsepecies identity or local habitat properties.
I therefore do not yet personally believe that mobility explains morphological variety in North American Caribou distal limb bone cross-section or that there is a strong reason provided here to justify that the differences found between different North American subspecies should be analogous to any mobility-dependent osteological differences in Reindeer of the European Magdalenian.
I have therefore concluded that a re-ordered model specification, or use of marginal probabilities is necessary before it can be concluded that a unique morphometric signal of mobility has been identified with scientific validity. Previous reviewer comments about sex and population age structure must be addressed to confirm they do not confound the results.

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genetic data to predict intraspecific genetic structure.*Evol Appl*. 2020; **13** (6): 1526-1542 PubMed Abstract | Publisher Full Text
3. Martino R, Sianis P, Estraviz-López D, Rotatori F, et al.: Disentangling morphological variation in metapodials of giraffids: Modern and traditional approaches. *Organisms Diversity & Evolution*. 2024; **24** (2): 201-213 Publisher Full Text
4. Anderson M: Permutational Multivariate Analysis of Variance (PERMANOVA). 2014. 1-15 Publisher Full Text

Is the work clearly and accurately presented and does it engage with the current literature?
Partly

Is the study design appropriate and is the work technically sound?
Partly

Are sufficient details of methods and analysis provided to allow replication by others?
Partly

Are all the source data and materials underlying the results available?
Yes

If applicable, is the statistical analysis and its interpretation appropriate?
Partly

Are the conclusions drawn adequately supported by the results?
No

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: Vertebrate evolution, geometric morphometrics, statistical methods in phylogenetic comparative analyses

I confirm that I have read this submission and believe that I have an appropriate level of expertise to state that I do not consider it to be of an acceptable scientific standard, for reasons outlined above.

Reviewer Report 24 April 2025

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María Isabel Borao-Álvarez
University of Valencia, Valencia, Valencian Community, Spain

I would like to express my sincere gratitude to the editorial team of *Open Research Europe* and to the authors for the opportunity to review the manuscript entitled *"The ecomorphology of Caribou (Rangifer tarandus): a geometric morphometric study."*
This study sets out to establish a robust reference framework of morphometric data based on metacarpals, metatarsals, and phalanges from Canadian caribou populations inhabiting distinct biomes. These populations display varying mobility patterns—either migratory or sedentary—correlated with their ecological settings (boreal forest, mountainous regions, or Arctic tundra).
The morphometric differences identified between high-mobility populations (typically associated with tundra and mountainous habitats) and those with restricted movement (inhabiting more closed environments) hold significant potential for reconstructing caribou mobility patterns during the Upper Palaeolithic. Such reconstructions offer valuable insights into human subsistence strategies, particularly in regions where caribou/reindeer played a central role in hunter-gatherer economies.
The authors demonstrate a thorough command of caribou ecology, genetics, behaviour, and morphology. The study employs a rigorous and up-to-date methodological framework, incorporating geometric morphometrics and statistical analysis implemented in the R programming language.
The digital acquisition and processing of bone scans are appropriately conducted and validated, ensuring the reliability of the landmark-based morphometric data. The statistical procedures are correctly applied and thoughtfully interpreted.
Moreover, the manuscript is clearly written and logically structured, facilitating a smooth and coherent reading experience.
In conclusion, I find this to be a well-executed and scientifically valuable contribution. I recommend the manuscript for indexing without reservation and commend the authors for their exemplary work, which represents a significant advancement in the study of prehistoric reindeer hunting strategies.

Is the work clearly and accurately presented and does it engage with the current literature?
Yes

Is the study design appropriate and is the work technically sound?
Yes

Are sufficient details of methods and analysis provided to allow replication by others?
Yes

Are all the source data and materials underlying the results available?
Yes

If applicable, is the statistical analysis and its interpretation appropriate?
Yes

Are the conclusions drawn adequately supported by the results?
Yes

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: My research focuses on reindeer and red deer osseous technology, with particular attention to the acquisition of raw materials and its relation to hunting strategies.

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

Version 1

Reviewer Report 17 October 2024

https://doi.org/10.21956/openreseurope.14861.r44843

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Iván Rey-Rodríguez
Centro de Investigación Mariña (CIM), MAPAS lab, University of Vigo (Ringgold ID: 16784), Vigo, Galicia, Spain

In my review of the article, I offer several points of feedback to enhance its clarity and focus. Below is a summary of my suggestions and observations regarding different sections of the paper:
In the abstract I recommend providing a chronological range for the Paleolithic period to help readers unfamiliar with *Rangifer tarandus* better understand the timeframe. Specifically, it would be helpful to clarify whether the study focuses. This would provide important context for readers who may not be specialists in this.
It is also important to clarify which species the ethological data is based on and whether human influence is considered. This will help frame the study within a relevant biological context, especially for readers interested in how human interactions with reindeer or caribou might have influenced their mobility and bone structure.
In the title of the project, “Reconstructing habitat type and mobility patterns of *Rangifer tarandus* during the Late Pleistocene in Southwestern France: an ecomorphological study,” the quotation marks should be properly closed, and the species name *Rangifer tarandus* should be italicized to follow standard scientific conventions.
In Table 1, it would be very useful to include the provenance of the sample and to indicate from which museum the samples were obtained. Additionally, I suggest incorporating a map that shows the current distribution of the caribou populations studied. This would provide a valuable visual aid and help readers better understand the geographic context of the data.
Clarification is needed on why only specific bone sections were analyzed rather than the complete bone. This methodological decision should be justified, especially considering the potential importance of analyzing the whole structure in morphological studies.
One question is whether there are any differences between the species in terms of age and sex. Were these factors considered in the study? Furthermore, the Zenodo repository differentiates between right and left bones. Was laterality considered in the analysis?

The PCA and LDA analyses are well executed, but it would be very interesting to see a visualization of the different morphologies. Plotting these morphologies would make it easier to see the distinctions between the species and the groups being analyzed. This would also strengthen the presentation of the results and make the differences between migratory and sedentary herds more apparent.
The results are particularly compelling, as they show that mobility, which is linked to habitat, affects the shape of the lower limb bones. This relationship allows for the distinction between migratory and sedentary species. However, since the study is focused on extant species, the archaeological inferences are limited in this article.
One commendable aspect of the study is the sharing of the CT scans, which adds transparency to the research process. However, it would be ideal if the authors could also include the R script used for their analysis (they indicate them, but it would be better to have them at zenodo), making it easier for other researchers to replicate the study and build upon its findings.
In summary, with a few adjustments and clarifications, this study has the potential to make a significant contribution to understanding the relationship between habitat, mobility, and bone morphology in *Rangifer tarandus*. I would like to congratulate the authors on this insightful and valuable contribution. Given that this article was published in 2021, and considering the authors' impressive scientific track record, it is clear that this study lays the groundwork for future research in this field. The methodologies and findings presented here establish a solid foundation for continued exploration into the relationship between mobility, habitat, and bone morphology in *Rangifer tarandus*, and I look forward to seeing how this research evolves and expands in the coming years

Is the work clearly and accurately presented and does it engage with the current literature?
Yes

Is the study design appropriate and is the work technically sound?
Yes

Are sufficient details of methods and analysis provided to allow replication by others?
Yes

Are all the source data and materials underlying the results available?
Yes

If applicable, is the statistical analysis and its interpretation appropriate?
Yes

Are the conclusions drawn adequately supported by the results?
Yes

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: paleontology, paleoclimate, geometric morphometrics, rodents, prehistory,

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

Reviewer Report 22 March 2022

https://doi.org/10.21956/openreseurope.14861.r28842

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Pamela Groves
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I am a little confused by this article as the Abstract and Introduction focus on paleo reindeer in France, but the bulk of the rest is about Canadian caribou and distinguishing between migratory and sedentary herds based on analysis of scanned bones. I understand this paper is setting the groundwork for more research on paleo-French caribou, but that should be in the discussion and the first part of this paper should focus on what it is really about.

The background on Canadian caribou is possibly more detailed than is needed for this study. That said, it would be useful to have some maps showing the ranges of the populations studied with their migration routes indicated. I would also like earlier in the paper some indication of what is meant by long and short migration distances.
I don't feel qualified to assess the statistical methods used in this study and trust there are others with those capabilities. I do wonder though about the bones that were sampled. Is the sex and age of the animals known? Presumably, the bones of an older animal would show more evidence of long migrations or lack there-of. Do larger males put more stress on bones that would contribute to changes? Along those lines, it would be useful to include a brief physiological description of the processes that would contribute to changes in bones based on activity. Finally, are the bones all from the same time period? In the actual text, it would be useful to include an image of at least one scanned bone cross-section.

When time periods are mentioned, such as Magdalenian or Late Glacial, the timeframe in years should be included. There are a few places with some awkward wording that should be corrected.

I think if this article is re-framed as a morphometric study of Canadian caribou, it would be a worthwhile contribution to the field. The ability to distinguish between migratory and non-migratory animals within a species does have significant implications for wildlife management and conservation.

Is the work clearly and accurately presented and does it engage with the current literature?
Partly

Is the study design appropriate and is the work technically sound?
Partly

Are sufficient details of methods and analysis provided to allow replication by others?
Yes

Are all the source data and materials underlying the results available?
Yes

If applicable, is the statistical analysis and its interpretation appropriate?
Yes

Are the conclusions drawn adequately supported by the results?
Partly

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: History of paleo megafauna in Alaska. DNA studies of Alaskan caribou and muskoxen.

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.