Influence of captivity and selection on limb long bone cross-sectional morphology of reindeer

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Abstract
The emergence of pastoralism and animal husbandry has been a critical point in the history of human evolution. Beyond profound behavioural changes in domesticated animals compared to wild ones, characterising the morphological changes associated with domestication process remains challenging. Because reindeer (Rangifer tarandus) can be considered to still be in the early phases of the domestication process, the study of modern populations provides a unique opportunity to examine the impact of captivity and selective breeding on skeletal changes. In this work, we investigated the morphological changes in long limb bone cross-sections using 137 wild and domestic reindeer individuals bred in free-range, in captivity or used for racing and pulling. The shape and shaft cortical thickness of the six long limb bones (i.e., humerus, radioulna, metacarpal, femur, tibia and metatarsal) were measured using a 2D-geometric morphometrics approach taking into account subspecies, sex, body mass and lifestyle differences. These bones are important to understanding functional morphological changes because they can provide information on feeding and locomotor behaviours, as well as on body propulsion and weight bearing. Apart from the effects of taxonomy, etho-ecology and sex, we have found that captivity and selection induced important variations in the size and body mass of modern reindeer. Our results also showed that patterns of variation in cortical bone thickness of long limb bone cross-sections were strongly impacted by body mass and human-imposed restrictions in roaming. This demonstrates that bone cross-sections can provide information on changes in locomotor, reproductive and feeding behaviours induced by the domestication process. These results are valuable not only for (paleo) biologists studying the impact of captivity and selection in ungulates but also for archaeologists exploring the origins of domestication and early herding strategies.

Keywords
bone cross-section, domestication signal, geometric morphometrics, morpho-functional adaptation, Rangifer tarandus
1 | INTRODUCTION

The process of domestication has been a key stage in the evolution of interactions between humans, animals and their environment. Throughout history, animal domestication has often been initiated by controlling wild species outside their natural habitats with the aim of using them as production or working animals (Price, 2002; Vigne, 2015; Zeder, 2015). Thus, these animals are subjected to new selective pressures and to different environmental stimuli, inducing significant phenotypic and genotypic changes (Vigne et al., 2005). Amongst morphological changes, the retention of paedomorphic traits or a general reduction in body size are traditionally used to document domestication (e.g., Albarella, 2002; Evin et al., 2013, 2017; Morey, 1992; Trut et al., 2009). However, these changes are often considered to not reflect the early stages of the process, but occur later (Arbuckle, 2005). Thus, most of the morphological changes associated with the early stages of human-induced artificial selection on wild populations remain unrecognised and need to be identified.

One of the means of apprehending the direct impact of these initial processes could be to explore the plastic responses of the skeleton induced specifically by captivity and the performance of domestic tasks by comparing modern wild and domestic populations. Towards this end, we were specifically interested in Eurasian reindeer (Rangifer tarandus Linnaeus, 1758) which is a circumpolar ungulate species extending from Eastern Siberia and Northern Mongolia to Northern Fennoscandia (Geist, 1998). Reindeer herding appears to have developed in Siberia around the turn of the last millennium or even earlier (Anderson et al., 2019; Losey et al., 2021; Murashkin et al., 2016), whereas in Northern Fennoscandia, the first evidence of reindeer herding dates to the Late Iron Age (ca. 800–900 AD; Hansen & Olsen, 2014; Helskog & Indrelid, 2011; Ingold, 1980; Salmi et al., 2014, 2018, 2021; Salmi, Fjellström, et al., 2020). Since then, most reindeer populations in Northern Eurasia are now considered domestic or semi-domestic (Baskin, 2005; Syroechkovskii, 1995). However, there is such a high degree of complexity and variability in reindeer husbandry methods and practices, significantly different from industrial stockbreeding in bovines, caprines or suids, that many scholars consider it to still be in the early stages of the domestication process (Baskin, 2000; Reimers & Colman, 2006). This therefore offers a unique opportunity to analyse the direct effects of artificial selection on domestic and wild reindeer morphotypes, which could also potentially serve as an excellent model species for understanding how morphological changes take place during the first stage of the herding process.

Interactions between humans and reindeer have led to major behavioural and activity changes in animals in terms of locomotion, feeding and even reproduction. Wild reindeer are well known as a gregarious and migratory animal of the tundra and taiga. Although there is no historical evidence that (domesticated) reindeer have been kept in total captivity from the Iron Age, their mobility has at least been reduced or controlled. Thus, our aim is to study the direct impact of environmental and activity changes (i.e., mobility reduction in captivity or use as draft animals) on the structure of the limb’s long bones in modern reindeer populations whose genotypes and phenotypes are well known. Indeed, changes in the patterns of physical activity in an animal, particularly due to sustained interaction with humans, induce significant phenotypic plasticity in the skeleton and affect the mechanical properties of the long bones (Flensborg & Kaufmann, 2012; Harbers et al., 2020; Niinimäki & Salmi, 2016; Niinimäki et al., in press; Salmi & Niinimäki, 2016; Pelletier et al., 2020, 2021; Salmi, Niinimäki, & Pudas, 2020; Shackelford et al., 2013). As the environmental and locomotor parameters influence the evolution of bone properties (e.g., Kilbourne & Hutchison, 2019; Parsi-Pour & Kilbourne, 2020; Scheidt et al., 2019), the increase in habitual loading (e.g., in working reindeer) or decrease (e.g., in captive reindeer), as well as changes in foraging patterns, can potentially alter the cortical bone along the shaft. The amount of cortical bone in long bone cross-sections is correlated with the strength of the shaft to weight constraints, whilst the shape of the cross-sections provides information about the direction of the forces acting on the bone, indicating the function of the considered bone during locomotion (Harbers et al., 2020; Niinimäki et al., in press; Pearson & Lieberman, 2004; Shackelford et al., 2013).

Thus, these changes in bone cortical form and thickness were quantified using 2D-geometric morphometrics (2D GMM) on a large set of long limb bones (i.e., humerus, radioulna, metacarpal, femur, tibia and metatarsal). Although changes in bone cross-sectional properties are often studied for the humerus or femur, no study has simultaneously investigated changes in the bone structure of all fore- and hind limb long bones related to domestication and control induced by humans. Similar works have recently been conducted on the morphology of the long bones of the fore- and hind limb in reindeer and have shown that they could provide information on changes in feeding and locomotor behaviour induced by captivity and domestication (Pelletier et al., 2020, 2021). However, these works only concerned external morphological changes on articular surfaces, trochanters or condyles, as well as on muscle and ligament insertions to explain the functional changes in reindeer, but they did not study the effects on the internal structure of these bones, nor their relationship to body mass. Yet, studies of bone shaft shape and cortical thickness based on landmarks (LM) are commonly performed to explore the adaptation of long bones in response to loading in all species, with a view to understanding the impact of locomotion, physical activity and body mass on internal bone structure (e.g., Profico et al. 2021 and references therein). In addition to quantitative analyses of shaft form and cortical bone thickness, 2D GMM allows the rapid visual comparison of size, shape and allometry between different groups of individuals. Thus, the purpose of our study was to evaluate the effects of different parameters (i.e., size, body mass, subspecies, sex and lifestyle) on bone cross-sectional morphology. This provides valuable information on the relationship between changes in reindeer behaviour induced by human control and changes in bone cross-sectional properties. It also contributes to a better understanding of the relationship between physical activity and morphological changes. Ultimately, this methodology and these results are valuable for enhancing our understanding of animal domestication and early herding practises.
2 | MATERIAL AND METHODS

2.1 | Modern reindeer sample

In this study, we mainly relied on a modern reindeer sample from central Finland in order to minimise the biases due to the genetic diversity and environment and to better focus on the anthropogenic impact. Indeed, this choice was motivated by the fact that it has been demonstrated that several intrinsic and extrinsic factors could influence the body size and/or morphology of reindeer (e.g., Thomas & Everson, 1981; Weinstock, 1997, 2002; Weladji & Holand, 2006). The sample included the complete or partial skeletons of 137 reindeer. The individuals are represented by the two subspecies currently living in Finland: the mountain reindeer (R. t. tarandus, n = 74) and the wild Finnish forest reindeer (R. t. fennicus, n = 53), as well as hybrids resulting from the crossing of these two subspecies (n = 10). All specimens were adults whose sex (males, ♂ = 75 and females, ♀ = 62) and lifestyle (free ranging, n = 28; captive, n = 28) were known. Body mass was known for 42 of the reindeer and could also be estimated for 81 reindeer based on regression equations from Puputti and Niskanen (2008). In order to limit potential sources of error in the calculations, the body mass estimation is a mean of estimation based on measurements of the trochlear height of the humerus, proximal breadth of the humerus, proximal breadth of the metacarpal and distal breadth of the metacarpal. These measurements were selected because they were all relatively accurate in estimating the body mass of the reindeer (Puputti & Niskanen, 2008). Captive and free-ranging individuals are part of the collection of the Biodiversity Unit of the University of Oulu. Working reindeer are archived at the Archaeology Laboratory of the University of Oulu. Working reindeer are part of the collection of the Biodiversity Unit of the University of Oulu. Working reindeer are archived at the Archaeology Laboratory of the University of Oulu. However, not all the skeletons are complete (i.e., not all bone elements are present for most of the individuals). The details of samples used for each bone are given in Table 1.

2.2 | 2D-geometric morphometrics

Cross-sections of the limb long bones (i.e., humerus, radioulna, metacarpal, femur, tibia and metatarsal) were obtained using a peripheral quantitative computed tomography (pQCT) scanner (Stratec XCT Research SA+, Stratec Medizintechnik GmbH, Pforzheim, Germany). All bones were scanned at 50% of inter-articular length, according to the acquisition protocol proposed by Niinimäki et al. (in press), in order to obtain one digital image of each cross-section. Only left bones were selected for scanning but when left sides were not available, right bones were selected instead and mirrored before analysis.

The bone cross-section forms were analysed using a 2D-geometric morphometrics (GMM) approach, which allows the comparison of bone shapes and the visualisation of significant morphological changes between groups of specimens by means of spatial coordinates of points called LM (Adams et al., 2004; Zelditch et al., 2012). This widely used method can be extended to the study of the cross-section shape (López-Aguirre et al., 2021; Profico et al., 2021; Wilson & Humphrey, 2015). As it was difficult to quantify the rather circular shape of the shafts of the limb long bones using traditional LM, as well as the lack of homologous anatomical structures, semi-LM were included on outline curves helping to better capture bone shape (Bookstein, 1997). Thus, on each bone cross-section (except for the radioulna), one anatomical LM was placed on the point of maximum curvature of the peristeum and one LM was placed on the point of maximum curvature of the endosteum. At 50% of the total inter-articular length, the point of maximum curvature on the cross-section represents the deltoid crest of the humerus, the linea aspera of the femur, the prominent lateral edge of the tibia and the central trough of the metacarpal and metatarsal (Figure 1). For the radioulna, the methodology was adapted by positioning two LMs on the periosteum to exclude the radioulnar groove and the lateral edge of the ulna from the analyses because they were often found to be damaged on most the specimens. Outlines of the peristeum and endosteum were defined by curves, each comprising 50 and 30 equidistant semilandmarks (CSLM), respectively (Figure 1, Table 2). The advantage of our protocol is that the anatomical orientation of the LM is retained, which allows us to examine the directionality of the shape change.

The LM and semi-LM coordinates were derived from digital images of cross-sections using tpsDig2 v.2.16 software (Rohl, 2010). Unlike LM, semi-LM do not have an exact anatomical correspondence on the outline of the shaft and were instead allowed to slide along the curves between adjacent points to minimise the sum of the Procrustes distances between each individual and the average shape (Bookstein, 1997; Gunz et al., 2005; Gunz & Mitteroecker, 2013). After sliding, all specimen coordinates were aligned using a Generalised Procrustes Analysis (GPA, Bookstein, 1991, 1996; Rohlf & Slice, 1990) obtained with tpsRelw v.1.49 software (Rohl, 2010). All configurations were translated and rotated to minimise the overall sum of the squared distances between the corresponding LM and semi-LM. To remove the effects of scale, GPA also computes a unit centroid size as the square root of the summed squared distances from all LM to their centroid (Bookstein, 1996; Dryden & Mardia, 1998).

2.3 | Statistical analyses

Differences in log-transformed centroid sizes and body mass were evaluated using Kruskal-Wallis tests with an error threshold set at α = 0.05, by pooling the specimens according to (1) subspecies, (2) sex, (3) lifestyle, (4) “subspecies + sex” and (5) “subspecies + sex + lifestyle”. Pairwise comparisons of the populations were performed using multiple Wilcoxon rank tests according to these different categories. To control for the false discovery rate, a multi-comparison correction was applied to the p-values using the “Benjamini-Hochberg” method (Benjamini & Hochberg, 1995). It has been previously demonstrated that centroid size could be a good approximation of the body mass of the specimen, amongst many taxa (Berner, 2011; Cassini et al., 2012; Ercoli & Prevosti, 2011; Iskjaer et al., 1989; MacLaren et al., 2018; Mallet et al., 2019). Thus, in order to test whether size is related to...
TABLE 1  Detail of specimens studied from the zoological Museum of Oulu according to the subspecies (R.t. tarandus, R.t. fennicus and hybrids), sex (male = ♂ and female = ♀) and lifestyle (free-ranging, captive and working)

|                | Free-ranging | Captive | Working | Total |
|----------------|--------------|---------|---------|-------|
| Humerus        |              |         |         |       |
| R.t. tarandus  | 8 ♂/11 ♀    | 2 ♂/8 ♀ | 9 ♂/0 ♀ | 19 ♂/19 ♀ |
| R.t. fennicus  | 22 ♂/20 ♀   | 1 ♂/5 ♀ | 0 ♂/0 ♀ | 23 ♂/25 ♀ |
| Hybrids        | 0 ♂/0 ♀     | 6 ♂/4 ♀ | 0 ♂/0 ♀ | 6 ♂/4 ♀ |
| Total          | 30 ♂/31 ♀   | 9 ♂/17 ♀ | 9 ♂/0 ♀ | 48 ♂/48 ♀ |
| Radioulna      |              |         |         |       |
| R.t. tarandus  | 8 ♂/11 ♀    | 2 ♂/8 ♀ | 9 ♂/0 ♀ | 19 ♂/19 ♀ |
| R.t. fennicus  | 23 ♂/21 ♀   | 0 ♂/5 ♀ | 0 ♂/0 ♀ | 23 ♂/26 ♀ |
| Hybrids        | 0 ♂/0 ♀     | 6 ♂/4 ♀ | 0 ♂/0 ♀ | 6 ♂/4 ♀ |
| Total          | 31 ♂/32 ♀   | 8 ♂/17 ♀ | 9 ♂/0 ♀ | 48 ♂/49 ♀ |
| Metacarpal      |              |         |         |       |
| R.t. tarandus  | 22 ♂/16 ♀   | 2 ♂/9 ♀ | 15 ♂/0 ♀ | 39 ♂/25 ♀ |
| R.t. fennicus  | 21 ♂/21 ♀   | 0 ♂/5 ♀ | 0 ♂/0 ♀ | 21 ♂/26 ♀ |
| Hybrids        | 0 ♂/0 ♀     | 6 ♂/4 ♀ | 0 ♂/0 ♀ | 6 ♂/4 ♀ |
| Total          | 43 ♂/37 ♀   | 8 ♂/18 ♀ | 15 ♂/0 ♀ | 66 ♂/55 ♀ |
| Femur          |              |         |         |       |
| R.t. tarandus  | 7 ♂/8 ♀     | 2 ♂/9 ♀ | 9 ♂/0 ♀ | 18 ♂/17 ♀ |
| R.t. fennicus  | 20 ♂/20 ♀   | 1 ♂/4 ♀ | 0 ♂/0 ♀ | 21 ♂/24 ♀ |
| Hybrids        | 0 ♂/0 ♀     | 6 ♂/4 ♀ | 0 ♂/0 ♀ | 6 ♂/4 ♀ |
| Total          | 27 ♂/28 ♀   | 9 ♂/17 ♀ | 9 ♂/0 ♀ | 45 ♂/45 ♀ |
| Tibia          |              |         |         |       |
| R.t. tarandus  | 8 ♂/8 ♀     | 2 ♂/8 ♀ | 9 ♂/0 ♀ | 19 ♂/16 ♀ |
| R.t. fennicus  | 20 ♂/21 ♀   | 1 ♂/5 ♀ | 0 ♂/0 ♀ | 21 ♂/26 ♀ |
| Hybrids        | 0 ♂/0 ♀     | 6 ♂/4 ♀ | 0 ♂/0 ♀ | 6 ♂/4 ♀ |
| Total          | 28 ♂/29 ♀   | 9 ♂/17 ♀ | 9 ♂/0 ♀ | 46 ♂/46 ♀ |
| Metatarsal      |              |         |         |       |
| R.t. tarandus  | 19 ♂/15 ♀   | 2 ♂/9 ♀ | 15 ♂/0 ♀ | 36 ♂/24 ♀ |
| R.t. fennicus  | 21 ♂/23 ♀   | 1 ♂/5 ♀ | 0 ♂/0 ♀ | 22 ♂/28 ♀ |
| Hybrids        | 0 ♂/0 ♀     | 6 ♂/4 ♀ | 0 ♂/0 ♀ | 6 ♂/4 ♀ |
| Total          | 40 ♂/38 ♀   | 9 ♂/18 ♀ | 15 ♂/0 ♀ | 64 ♂/56 ♀ |
| Body mass      |              |         |         |       |
| R.t. tarandus  | 19 ♂/19 ♀   | 2 ♂/8 ♀ | 20 ♂/0 ♀ | 41 ♂/27 ♀ |
| R.t. fennicus  | 18 ♂/22 ♀   | 1 ♂/4 ♀ | 0 ♂/0 ♀ | 19 ♂/26 ♀ |
| Hybrids        | 0 ♂/0 ♀     | 6 ♂/4 ♀ | 0 ♂/0 ♀ | 6 ♂/4 ♀ |
| Total          | 37 ♂/41 ♀   | 9 ♂/16 ♀ | 20 ♂/0 ♀ | 66 ♂/57 ♀ |

mass in reindeer, we computed a regression of the body mass against the centroid size for each bone. Shape differences between the different groups were then estimated using a multivariate analysis of variance (MANOVA) of the Procrustes coordinates, with significant interaction (α = 0.05) assumed to reflect group differences. Shape variation was visualised using principal component analysis (PCA) based on the Procrustes coordinates. Finally, the effect of evolutionary allometry (i.e., the effect of centroid size on cross-sectional shape) was assessed using multivariate regressions of shape variables (Procrustes coordinates) on the log-transformed centroid sizes. All morphometric statistics were performed with R studio v.1.1.383 (R Development Core Team, 2011), using “ade4” (Dray & Dufour, 2007) and “geomorph” (Adams & Otaírola-Castillo, 2013) packages.

3 | RESULTS

3.1 | Centroid size variation of bone cross-sections

The Kruskal-Wallis tests found significant overall differences in the size variation of the cross-sections for each long bone in all categories, namely sex, lifestyle, “subspecies + sex,” as well as “subspecies + sex +
lifestyle” (all \( p < .01 \); Table 3). For the “subspecies” category, the size differences were significant only for the humerus, femur and tibia. The pairwise comparisons revealed different patterns of size differentiation distinguishing the bones in the different categories (i.e., subspecies, sex and lifestyle). For stylopodial bones (i.e., humerus and femur), differences were significant between the forest reindeer \((R.t. \ fennicus)\) and the mountain reindeer \((R.t. \ tarandus)\), and between \(R.t. \ fennicus\) and hybrids (all \( p = .01 \)). For zeugopodial bones (i.e., radioulna and tibia), there was a significant difference only between \(R.t. \ fennicus\) and \(R.t. \ tarandus\) (both \( p = .03 \)). However, no significant difference was found between both subspecies and hybrids in the size of the metapodial bones (all \( p > .05 \)). In general, the bony elements of \(R.t. \ fennicus\) were consistently larger than those of \(R.t. \ tarandus\), whilst hybrids were intermediate in size compared to the two-parent subspecies. Regarding sex, males were always significantly larger than females (all \( p << .01 \)). Nevertheless, disparities were observed between the different bone elements for sexes in both subspecies and hybrids (i.e., “subspecies + sex”). For the stylopodium, there were significant differences between all categories (all \( p < .05 \), except between female \(R.t. \ tarandus\) and hybrids (males and females). For the zeugopodium, differences were also significant across groups (all \( p < .05 \), except between female \(R.t. \ tarandus\) and female hybrids, and between male \(R.t. \ tarandus\) and male hybrids. For the metapodial bones, there were no significant differences between female \(R.t. \ fennicus\) and female hybrids, between male \(R.t. \ fennicus\) and male hybrids, between female \(R.t. \ tarandus\) and female hybrids and, finally, between male \(R.t. \ tarandus\) and male hybrids. Regarding lifestyle, there was a significant difference systematically between each category (all \( p < .05 \)), i.e., between free-ranging and captive individuals, between free-ranging and working individuals, and between captive and working individuals, for the zeugopodial and metapodial bones (except for the metatarsal between free-ranging and captive individuals; \( p = .16 \)). For stylopodial bones, there were significant differences between captive and free-ranging individuals and between captives and working individuals (all \( p << .01 \)), but not between free-ranging and working individuals (humerus, \( p = .08 \); femur \( p = .06 \)). As such, captive individuals were consistently smaller than free-ranging and working individuals.

Although there are variations between the different bones, more precise observations could be made when the specimens were analysed whilst also taking into account subspecies, sex and lifestyle (Figure 2, Table 4). Overall, the free-ranging male \(R.t. \ fennicus\) individuals had the largest bone cross-sections. Conversely, the smallest cross-section sizes were found in the free-ranging and captive female \(R.t. \ tarandus\). Although not statistically significant, captive female \(R.t. \ fennicus\) individuals tended to be smaller than their wild counterparts (i.e., free-ranging). In contrast, this size difference was not noticeable between captive and free-ranging females in \(R.t. \ tarandus\). In fact, in females, there were many overlaps in the size range for most bone cross-sections, and few significant differences were found, particularly between captive \(R.t. \ fennicus\), free-ranging and captive \(R.t. \ tarandus\), and captive hybrids. In males, although free-ranging \(R.t. \ fennicus\) individuals remained the largest, working individuals were larger than free-ranging \(R.t. \ tarandus\). As such, the free-ranging \(R.t. \ fennicus\) and working \(R.t. \ tarandus\) did not differ.
significantly, except for the metapodial bones, which were smaller. Male hybrids always appeared to be smaller than their parent subspecies for the stylopodial and zeugopodial bones, but not for the metapodial bones. However, the low number of captive male individuals for both subspecies did not allow us to identify any size differences with other groups, particularly between captives and free-ranging male individuals. Finally, captive hybrids (females and males) appeared to have an intermediate size compared to captive females and males of both subspecies.

### 3.2 Body mass variation amongst reindeer groups

In general, changes in body mass followed changes in the centroid size of bone cross-sections relatively well (Figure 2g). The differences in body mass remained significant between free-ranging and working individuals, between working and captive individuals, as well as between males and females (all \( p < .01 \)). However, no significant difference was observed between both subspecies and hybrids, or between free-ranging and captive individuals (all \( p > .05 \)). Specifically regarding the “subspecies + sex” category, there were significant differences between all groups (all \( p < .05 \)), except between female R.t. fennicus and female hybrids, between male R.t. fennicus and male hybrids, between female R.t. tarandus and female hybrids and, finally, between male R.t. tarandus and male hybrids. In fact, the body mass of the free-ranging female R.t. fennicus did not differ from the body mass of the captive female R.t. fennicus, which differs from the results of centroid size variations, nor between the free-ranging and captive

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**TABLE 2** Definition of landmarks and semilandmarks for each studied bone cross-section shown in Figure 1. LM: Landmarks; CSLM: Equidistant curve semilandmarks

| Bone | Landmark | No. LM | CSLM |
|------|----------|--------|------|
| Humerus (A on Figure 1) | Most cranio-lateral point of maximum curvature of the deltid crest on the periosteum | 3:52 | Outline of the periosteum (n = 50) |
| | Most cranio-lateral point of maximum curvature of the deltid crest on the endosteum | 53:82 | Outline of the endosteum (n = 30) |
| Radioulna (B on Figure 1) | Point of maximum curvature of the caudal edge of the ulna | 4:53 | Outline between LM 1 and LM 2 (n = 50) |
| | Point of maximum curvature of the lateral edge of the radius | 54:83 | Outline of the endosteum (n = 30) |
| | Most caudo-lateral point of maximum curvature of the endosteum |
| Metacarpal (C on Figure 1) | Point of maximum curvature of the central trough on the periosteum | 3:52 | Outline of the periosteum (n = 50) |
| | Point of maximum curvature of the central trough on the endosteum | 53:82 | Outline of the endosteum (n = 30) |
| Femur (D on Figure 1) | Most caudo-lateral point of maximum curvature of the linea aspera on the periosteum | 3:52 | Outline of the periosteum (n = 50) |
| | Most caudo-lateral point of maximum curvature of the linea aspera on the endosteum | 53:82 | Outline of the endosteum (n = 30) |
| Tibia (E on Figure 1) | Most caudo-medial point of maximum curvature of the lateral edge on the periosteum | 3:52 | Outline of the periosteum (n = 50) |
| | Most caudo-medial point of maximum curvature of the lateral edge on the endosteum | 53:82 | Outline of the endosteum (n = 30) |
| Metatarsal (F on Figure 1) | Point of maximum curvature of the central trough on the periosteum | 3:52 | Outline of the periosteum (n = 50) |
| | Point of maximum curvature of the central trough on the endosteum | 53:82 | Outline of the endosteum (n = 30) |
TABLE 3 Results of the Kruskal-Wallis tests on the centroid size variation of the hind long bones and body mass differences amongst the different categories, according to the subspecies (R.t. tarandus, R.t. fennicus and hybrids), sex (male = ♂ and female = ♀) and lifestyle (free-ranging, captive and working). A significant contribution was considered for p-value < .05 (in italics)

|                | Df  | Chi-squared | p-value  |
|----------------|-----|-------------|----------|
| Humerus        |     |             |          |
| Subspecies (ssp.) | 2  | 9.401       | 9.090e-03|
| Sex            | 1  | 60.673      | 6.740e-15|
| Lifestyle      | 2  | 19.249      | 6.609e-05|
| Ssp.*sex       | 5  | 74.161      | 1.392e-14|
| Ssp.*sex*lifestyle | 10 | 76.575      | 2.347e-12|
| Radioulna      |     |             |          |
| Subspecies (ssp.) | 2  | 5.371       | 6.9e-01  |
| Sex            | 1  | 64.840      | 8.121e-16|
| Lifestyle      | 2  | 17.152      | 1.885e-04|
| Ssp.*sex       | 5  | 72.446      | 3.171e-14|
| Ssp.*sex*lifestyle | 9  | 74.435      | 2.043e-12|
| Metacarpal     |     |             |          |
| Subspecies (ssp.) | 2  | 1.388       | .500     |
| Sex            | 1  | 81.943      | 8.241e-16|
| Lifestyle      | 2  | 14.758      | 6.241e-04|
| Ssp.*sex       | 5  | 88.436      | 2.126e-16|
| Ssp.*sex*lifestyle | 9  | 89.539      | 2.014e-15|
| Femur          |     |             |          |
| Subspecies (ssp.) | 2  | 9.272       | 9.696e-03|
| Sex            | 1  | 52.221      | 4.959e-13|
| Lifestyle      | 2  | 22.325      | 1.420e-05|
| Ssp.*sex       | 5  | 66.417      | 5.693e-13|
| Ssp.*sex*lifestyle | 10 | 69.602      | 5.291e-11|
| Tibia          |     |             |          |
| Subspecies (ssp.) | 2  | 6.455       | .040     |
| Sex            | 1  | 56.550      | 5.478e-14|
| Lifestyle      | 2  | 18.191      | 1.122e-04|
| Ssp.*sex       | 5  | 68.465      | 2.138e-13|
| Ssp.*sex*lifestyle | 10 | 70.423      | 3.673e-11|
| Metatarsal     |     |             |          |
| Subspecies (ssp.) | 2  | 4.497       | .106     |
| Sex            | 1  | 69.166      | 2.126e-16|
| Lifestyle      | 2  | 8.238       | .016     |
| Ssp.*sex       | 5  | 81.297      | 4.492e-16|
| Ssp.*sex*lifestyle | 10 | 82.483      | 1.634e-13|
| Body mass      |     |             |          |
| Subspecies (ssp.) | 2  | 2.548       | .280     |
| Sex            | 1  | 88.519      | 2.126e-16|
| Lifestyle      | 2  | 29.648      | 3.647e-07|
| Ssp.*sex       | 5  | 93.135      | 2.126e-16|
| Ssp.*sex*lifestyle | 10 | 95.643      | 4.043e-16|

female R.t. tarandus, or between the free-ranging and working male R.t. tarandus. For the free-ranging male R.t. fennicus, the body mass seemed relatively similar to the body mass of R.t. tarandus lato sensu individuals, in contrast to the variations in centroid size. Despite wide variability, most of these individuals even had a lower body mass than R.t. tarandus individuals. Whilst the free-ranging male R.t. fennicus were almost always significantly bigger than working reindeer, the opposite was observed through the body mass where wild male R.t. fennicus individuals were significantly less heavy than working R.t. tarandus. However, it would appear that body mass varied significantly more than the variations in the centroid size of the skeletal elements, particularly for the wild reindeer R.t. fennicus. Finally, the correlation between centroid size and body mass is good in reindeer (Figure 3; all p << .01; R² = 0.48–0.64) indicating that centroid size could be a relatively good approximation of the body mass for this species in subsequent analyses.

3.3 | Shape variation of skeletal elements

Unlike what we have previously observed concerning size variations of bone cross-sections, the MANOVA analyses revealed no significant difference in shape between subspecies, sex as well as lifestyle (Table 5). Significant differences were only found in groups from the “subspecies + sex” category for the metacarpal, tibia and metatarsal, and in groups from the “subspecies + sex + lifestyle” category for the femur.

- **Stylopodium:** For the humerus, the main divergence in cross-sectional shape was expressed along PC1 (57.37% of the total variance; Figure 4a). Despite considerable overlaps, captive (amongst both sexes and including both subspecies and hybrids) and working (male R.t. tarandus) individuals were more distributed on the negative values of PC1, involving a relatively thick cortical bone. Conversely, the variation in the shape of the cross-section along the positive values of PC1 showed a much thinner cortical bone thickness, where more wild/free-ranging individuals were located. The variation along PC2 (13.41% of the total variance) illustrated quite a sexual distinction. The different groups of females taken individually tended to distribute more towards the positive values of PC2, compared to their male counterparts. Thus, this implied a less rounded circumference but more extended craniocaudally, unlike the humerus of males, which extended slightly more mediocaudally.

A relatively similar distribution of the different reindeer groups could be observed in the morphospace in the femur analysis. The PCA on the femoral cross-sectional shape showed the main divergence between captive and working individuals with wild/free-ranging individuals along PC1 (56.14% of the total variance; Figure 4b). The cross-sectional shape changes associated with domestication (i.e., captivity and selection) on the negative scores involved a thick cortical bone, whilst the associated shape changes towards positive scores showed...
a reduced cortical bone thickness. PC2 also showed a slight sexual distinction in the morphospace (16.60% of the total variance), where females were more distributed towards the negative values. This implied a more elongated cross-sectional shape craniocaudally, whereas on the positive values (showing more male individuals) cross-sections were more extended mediolaterally.
TABLE 4  Multi-test comparisons (p-values) of the log-transformed centroid sizes for each bone analysed and of the log-transformed body mass between the different reindeer groups (pairwise Wilcoxon rank tests after the “Benjamini–Hochberg” correction). A significant contribution was considered for p-value < .05 (in italics)

| Bone       | R.t. fennicus ♀ free ranging | R.t. fennicus ♀ captive | R.t. fennicus ♂ free ranging | R.t. fennicus ♂ captive | R.t. tarandus ♀ free ranging | R.t. tarandus ♀ captive | R.t. tarandus ♂ free ranging | R.t. tarandus ♂ captive | R.t. tarandus ♂ working | Hybrid ♀ captive | Hybrid ♂ captive |
|------------|-------------------------------|------------------------|-----------------------------|------------------------|-----------------------------|------------------------|-----------------------------|------------------------|---------------------|------------------|------------------|
| Humerus    |                               |                        |                             |                        |                             |                        |                             |                        |                    |                  |                  |
| R.t. fennicus ♀ captive | 0.645 | - | - | - | - | - | - | - | - | - | - |
| R.t. fennicus ♀ free ranging | 4.282e-10 | 1.617e-04 | - | - | - | - | - | - | - | - | - |
| R.t. fennicus ♂ captive | 0.291 | 0.436 | 0.165 | - | - | - | - | - | - | - | - |
| R.t. fennicus ♂ free ranging | 7.041e-05 | 0.666 | 2.941e-07 | 0.278 | - | - | - | - | - | - | - |
| R.t. tarandus ♀ captive | 7.023e-04 | 0.171 | 6.265e-06 | 0.313 | 1.000 | - | - | - | - | - | - |
| R.t. tarandus ♀ free ranging | 7.079e-05 | 0.005 | 0.244 | 0.543 | 1.617e-04 | 7.023e-04 | - | - | - | - | - |
| R.t. tarandus ♂ captive | 0.916 | 0.645 | 0.066 | 1.000 | 0.064 | 0.279 | 0.500 | - | - | - | - |
| R.t. tarandus ♂ free ranging | 1.098e-05 | 0.004 | 0.165 | 0.297 | 9.358e-05 | 4.525e-04 | 0.922 | 0.313 | - | - | - |
| Hybrid ♀ captive | 0.026 | 0.197 | 6.690e-04 | 0.500 | 0.585 | 0.645 | 0.012 | 0.367 | 0.009 | - | - |
| Hybrid ♂ captive | 0.396 | 0.279 | 0.005 | 0.916 | 0.003 | 0.022 | 0.165 | 0.916 | 0.079 | 0.081 | - |
| Radioulna   |                               |                        |                             |                        |                             |                        |                             |                        |                    |                  |                  |
| R.t. fennicus ♀ captive | 0.408 | - | - | - | - | - | - | - | - | - | - |
| R.t. fennicus ♀ free ranging | 8.942e-11 | 2.289e-04 | - | - | - | - | - | - | - | - | - |
| R.t. fennicus ♂ captive | - | - | - | - | - | - | - | - | - | - | - |
| R.t. fennicus ♂ free ranging | 0.002 | 0.279 | 1.573e-07 | - | - | - | - | - | - | - | - |
| R.t. tarandus ♀ captive | 0.026 | 0.620 | 2.852e-06 | - | 0.629 | - | - | - | - | - | - |
| R.t. tarandus ♀ free ranging | 1.573e-04 | 0.024 | 0.024 | - | 1.701e-04 | 6.060e-04 | - | - | - | - | - |
| R.t. tarandus ♂ captive | 0.781 | 0.476 | 0.390 | - | 0.165 | 0.387 | 0.930 | - | - | - | - |
| R.t. tarandus ♂ free ranging | 2.097e-06 | 0.006 | 0.557 | - | 1.072e-04 | 4.114e-04 | 0.099 | 0.421 | - | - | - |
| Hybrid ♀ captive | 0.058 | 0.390 | 5.130e-04 | - | 1.000 | 0.955 | 0.011 | 0.387 | 0.008 | - | - |
| Hybrid ♂ captive | 0.017 | 0.090 | 0.024 | - | 6.060e-04 | 0.002 | 0.745 | 0.918 | 0.065 | 0.023 | - |
| Metacarpal   |                               |                        |                             |                        |                             |                        |                             |                        |                    |                  |                  |
| R.t. fennicus ♀ captive | 0.564 | - | - | - | - | - | - | - | - | - | - |
| R.t. fennicus ♀ free ranging | 1.672e-10 | 1.368e-04 | - | - | - | - | - | - | - | - | - |
| R.t. fennicus ♂ captive | - | - | - | - | - | - | - | - | - | - | - |
| R.t. fennicus ♂ free ranging | 0.013 | 0.747 | 3.494e-09 | - | - | - | - | - | - | - | - |
| R.t. tarandus ♀ captive | 0.106 | 0.947 | 8.987e-07 | - | 0.747 | - | - | - | - | - | - |
| R.t. tarandus ♀ free ranging | 7.757e-09 | 0.007 | 1.808e-04 | - | 1.214e-08 | 2.232e-06 | - | - | - | - | - |

(Continues)
### TABLE 4 (Continued)

|                | R. t. fennicus ♀ free ranging | R. t. fennicus ♀ captive | R. t. fennicus ♂ free ranging | R. t. fennicus ♂ captive | R. t. tarandus ♀ free ranging | R. t. tarandus ♀ captive | R. t. tarandus ♂ free ranging | R. t. tarandus ♂ captive | R. t. tarandus ♂ working | Hybrid ♂ captive | Hybrid ♀ captive |
|----------------|--------------------------------|--------------------------|--------------------------------|--------------------------|-------------------------------|--------------------------|-------------------------------|--------------------------|----------------------------|-----------------|-----------------|
| R. t. tarandus ♂ captive | 0.800                         | 0.756                    | 0.947                          | -                        | 0.262                         | 0.351                    | 1.000                         | -                        | -                          | -               | -               |
| R. t. tarandus ♂ working  | 6.143e-08                     | 7.256e-04                | 0.025                          | -                        | 1.997e-07                    | 1.530e-05                | 0.117                         | 0.963                    | -                          | -               | -               |
| Hybrid ♀ captive      | 0.262                         | 0.947                    | 4.743e-04                      | -                        | 0.947                         | 0.947                    | 4.301e-04                    | 0.747                    | 0.001                      | -               | -               |
| Hybrid ♂ captive      | 4.301e-04                     | 0.034                    | 0.564                          | -                        | 4.020e-04                    | 0.002                    | 0.776                         | 0.947                    | 0.947                      | 0.020           | -               |

**Femur**

|                | R. t. fennicus ♀ captive | R. t. fennicus ♂ free ranging | R. t. fennicus ♂ captive | R. t. tarandus ♀ free ranging | R. t. tarandus ♀ captive | R. t. tarandus ♂ free ranging | R. t. tarandus ♂ captive | R. t. tarandus ♂ working | Hybrid ♂ captive | Hybrid ♀ captive |
|----------------|--------------------------|--------------------------------|--------------------------|-------------------------------|--------------------------|-------------------------------|--------------------------|----------------------------|-----------------|-----------------|
| R. t. tarandus ♂ captive | 0.256                     | -                              | -                        | -                             | -                         | -                             | -                        | -                          | -               | -               |
| R. t. tarandus ♂ free ranging | 5.588e-09                | 9.410e-04                      | -                        | -                             | -                         | -                             | -                        | -                          | -               | -               |
| R. t. fennicus ♂ captive | 0.194                     | 0.512                          | 0.512                    | -                             | -                         | -                             | -                        | -                          | -               | -               |
| R. t. tarandus ♀ free ranging | 0.006                     | 0.751                          | 1.180e-05                | 0.359                         | -                         | -                             | -                        | -                          | -               | -               |
| R. t. tarandus ♀ captive | 3.032e-04                 | 0.386                          | 5.492e-06                | 0.333                         | 0.390                       | -                             | -                        | -                          | -               | -               |
| R. t. tarandus ♂ free ranging | 6.964e-04                | 0.018                          | 0.017                    | 0.386                         | 0.001                       | 9.410e-04                    | -                         | -                          | -               | -               |
| R. t. tarandus ♂ captive | 0.882                     | 0.624                          | 0.043                    | 0.748                         | 0.386                       | 0.258                         | 0.611                    | -                          | -               | -               |
| R. t. tarandus ♂ working  | 5.217e-05                | 0.010                          | 0.181                    | 0.512                         | 6.464e-04                   | 3.771e-04                    | 0.299                    | 0.258                      | -               | -               |
| Hybrid ♂ captive      | 0.035                     | 0.607                          | 9.410e-04                | 0.512                         | 0.933                       | 0.766                         | 0.018                    | 0.624                      | 0.010           | -               |
| Hybrid ♀ captive      | 0.787                     | 0.386                          | 0.019                    | 0.655                         | 0.067                       | 0.016                         | 0.162                    | 0.882                      | 0.061           | 0.225           |

**Tibia**

|                | R. t. fennicus ♀ captive | R. t. fennicus ♂ free ranging | R. t. fennicus ♂ captive | R. t. tarandus ♀ free ranging | R. t. tarandus ♀ captive | R. t. tarandus ♂ free ranging | R. t. tarandus ♂ captive | R. t. tarandus ♂ working | Hybrid ♂ captive | Hybrid ♀ captive |
|----------------|--------------------------|--------------------------------|--------------------------|-------------------------------|--------------------------|-------------------------------|--------------------------|----------------------------|-----------------|-----------------|
| R. t. tarandus ♂ captive | 0.424                     | -                              | -                        | -                             | -                         | -                             | -                        | -                          | -               | -               |
| R. t. tarandus ♂ free ranging | 8.173e-10                | 4.140e-04                      | -                        | -                             | -                         | -                             | -                        | -                          | -               | -               |
| R. t. fennicus ♂ captive | 0.183                     | 0.436                          | 0.907                    | -                             | -                         | -                             | -                        | -                          | -               | -               |
| R. t. tarandus ♀ free ranging | 0.006                     | 0.285                          | 8.848e-06                | 0.339                         | -                         | -                             | -                        | -                          | -               | -               |
| R. t. tarandus ♀ captive | 0.003                     | 0.183                          | 8.848e-06                | 0.339                         | 0.912                       | -                             | -                        | -                          | -               | -               |
| R. t. tarandus ♂ free ranging | 0.002                     | 0.028                          | 0.005                    | 0.543                         | 9.497e-04                   | 9.497e-04                    | -                        | -                          | -               | -               |
| R. t. tarandus ♂ captive | 0.655                     | 0.487                          | 0.171                    | 0.748                         | 0.386                       | 0.288                         | 0.782                    | -                          | -               | -               |
| R. t. tarandus ♂ working  | 8.848e-06                | 0.007                          | 0.205                    | 1.000                         | 6.464e-04                   | 6.464e-04                    | 0.205                    | 0.436                      | -               | -               |
| Hybrid ♂ captive      | 0.017                     | 0.205                          | 0.001                    | 0.500                         | 0.951                       | 0.551                         | 0.012                    | 0.386                      | 0.009           | -               |
| Hybrid ♀ captive      | 0.241                     | 0.174                          | 0.033                    | 0.655                         | 0.013                       | 0.009                         | 0.398                    | 0.907                      | 0.152           | 0.046           |

**Metatarsal**

|                | R. t. fennicus ♀ captive | R. t. fennicus ♂ free ranging | R. t. fennicus ♂ captive | R. t. tarandus ♀ free ranging | R. t. tarandus ♀ captive | R. t. tarandus ♂ free ranging | R. t. tarandus ♂ captive | R. t. tarandus ♂ working | Hybrid ♂ captive | Hybrid ♀ captive |
|----------------|--------------------------|--------------------------------|--------------------------|-------------------------------|--------------------------|-------------------------------|--------------------------|----------------------------|-----------------|-----------------|
| R. t. tarandus ♂ captive | 0.816                     | -                              | -                        | -                             | -                         | -                             | -                        | -                          | -               | -               |
| R. t. fennicus ♂ free ranging | 5.465e-11                | 2.090e-04                      | -                        | -                             | -                         | -                             | -                        | -                          | -               | -               |
|                  | R. t. fennicus ♀ free ranging | R. t. fennicus ♀ captive | R. t. fennicus ♂ free ranging | R. t. fennicus ♂ captive | R. t. tarandus ♀ free ranging | R. t. tarandus ♀ captive | R. t. tarandus ♂ free ranging | R. t. tarandus ♂ captive | R. t. tarandus ♂ working | Hybrid ♂ captive |
|------------------|-------------------------------|-------------------------|-------------------------------|-------------------------|-------------------------------|-------------------------|-------------------------------|-------------------------|-------------------------|------------------|
| R. t. fennicus ♀ captive | 0.170                         | 0.447                   | 1.000                         | -                       | -                             | -                       | -                             | -                       | -                       | -                |
| R. t. tarandus ♀ free ranging | 0.024                         | 0.186                   | 9.878e-09                     | 0.229                   | -                             | -                       | -                             | -                       | -                       | -                |
| R. t. tarandus ♀ captive | 0.134                         | 0.420                   | 2.563e-06                     | 0.314                   | 0.589                         | -                       | -                             | -                       | -                       | -                |
| R. t. tarandus ♀ free ranging | 4.000E-04                     | 0.072                   | 1.147e-05                     | 0.314                   | 4.766e-05                     | 7.268e-04               | -                             | -                       | -                       | -                |
| R. t. tarandus ♀ captive | 0.278                         | 0.487                   | 0.447                         | 0.764                   | 0.173                         | 0.250                   | 0.924                         | -                       | -                       | -                |
| R. t. tarandus ♀ working | 1.147e-05                     | 0.024                   | 0.003                         | 0.487                   | 1.147e-05                     | 2.804e-04               | 0.170                         | 0.959                   | -                       | -                |
| Hybrid ♀ captive | 0.728                         | 0.944                   | 6.689e-04                     | 0.500                   | 0.337                         | 0.387                   | 0.031                         | 0.237                   | 0.012                   | -                |
| Hybrid ♂ captive | 4.000e-04                     | 0.072                   | 0.165                         | 0.683                   | 6.689e-04                     | 0.010                   | 0.396                         | 0.924                   | 0.944                   | 0.026            |

Body mass

|                  | R. t. fennicus ♀ captive | R. t. fennicus ♂ free ranging | R. t. fennicus ♂ captive | R. t. tarandus ♀ free ranging | R. t. tarandus ♀ captive | R. t. tarandus ♂ free ranging | R. t. tarandus ♂ captive | R. t. tarandus ♂ working | Hybrid ♂ captive |
|------------------|-------------------------|-------------------------------|-------------------------|-------------------------------|-------------------------|-------------------------------|-------------------------|-------------------------|------------------|
| R. t. fennicus ♂ captive | 0.950                   | -                             | -                       | -                             | -                       | -                             | -                       | -                       | -                |
| R. t. fennicus ♂ free ranging | 5.933e-07               | 0.033                         | -                       | -                             | -                       | -                             | -                       | -                       | -                |
| R. t. fennicus ♂ captive | 0.159                   | 0.489                         | 0.503                   | -                             | -                       | -                             | -                       | -                       | -                |
| R. t. tarandus ♂ free ranging | 0.049                   | 0.376                         | 2.02e-06                | 0.197                         | -                       | -                             | -                       | -                       | -                |
| R. t. tarandus ♂ captive | 0.024                   | 0.235                         | 8.800e-06               | 0.322                         | 0.581                   | -                             | -                       | -                       | -                |
| R. t. tarandus ♂ free ranging | 4.496e-10               | 0.001                         | 0.058                   | 0.177                         | 1.625e-06               | 7.079e-06               | -                       | -                       | -                |
| R. t. tarandus ♂ captive | 0.021                   | 0.209                         | 0.517                   | 1.000                         | 0.056                   | 0.087                         | 1.000                   | -                       | -                |
| R. t. tarandus ♂ working | 5.933e-07               | 0.007                         | 0.024                   | 0.197                         | 1.387e-06               | 2.896e-04               | 0.011                   | 1.000                   | -                |
| Hybrid ♂ captive | 0.355                   | 0.449                         | 1.157e-03               | 0.489                         | 0.974                   | 0.639                         | 0.001                   | 0.209                   | 0.007            |
| Hybrid ♂ captive | 3.244e-05               | 0.024                         | 0.296                   | 0.383                         | 0.001                   | 0.002                         | 0.489                   | 1.000                   | 0.105            | 0.024            |
Zygopodium: For the radioulna, the first two axes of the PCA expressed 55.99% of the total variance (Figure 5a). PC1 (42.43%) roughly distributed between free-ranging male R.t. tarandus on the positive part and free-ranging female R.t. tarandus, captive and working individuals on the negative part. Moreover, the working male R.t. tarandus could be distinguished relatively well from the free-ranging female R.t. tarandus on the negative part. However, wild R.t. fennicus individuals amongst both sexes showed an important intragroup variation along both axes. On the negative values of PC1, the shape of the radioulna revealed a triangular cross-section more extended cranially, whilst the shape was more ellipsoidal and extended mediolaterally on the positive values. The variation along PC2 (13.56% of the total variance) once again showed quite a sexual distinction between groups. Indeed, the females were more distributed towards the negative values of PC2 compared to their male counterparts. The medial

**FIGURE 3** Regression between log-transformed centroid size (CS) and log-transformed body mass (M), amongst subspecies (R.t. tarandus, R.t. fennicus and hybrids), sex (male = ♂ and female = ♀) and lifestyle (free ranging, captive and working). (a) Stylopod: humerus and (b) femur; (c) zeugopod: radioulna and (d) tibia; (e) metapod: metacarpal and (f) metatarsal. A significant contribution was considered for p-value < .05
and lateral edges of the radioulna seemed more extended craniocaudally in females than in males whereas, conversely, the cranial and caudal edges were more extended mediolaterally.

For the tibia, the differences between groups appeared to be more marked (Figure 5b), on both the first axis of the PCA (39.71% of the total variance) and on the second axis (22.68%). Captive individuals in both sexes and both subspecies, as well as working reindeer, tended to be distributed on the negative values of PC1, resulting in a more rounded shape and a thick cortical bone. In contrast, more free-ranging and wild individuals were found on the positive values, which were characterised by a more rectangular cross-sectional shape with a thinner cortical bone. Along PC2, females could be distinguished from males in almost all categories. In general, males distributed more towards the negative values compared to their female counterparts. This resulted in a more ellipsoidal and elongated shape mediolaterally in females, and more lozenge-shaped and craniomedially extended.

- Metapodials: Despite the overlaps, the metacarpal appeared to show sexual distinctions along PC1 (53.36% of the total variance)
in the different groups (Figure 6a). In fact, females were distributed more towards the negative values of PC1 and were more characterised by a thick cortical bone, the presence of a concavity on the medial and lateral edges of the metacarpal and a deep central trough. On the positive values of PC1, there were more males whose cross-section shape was characterised instead by a thinner cortical bone and a shallower central trough. As such, female *R. t. fennicus* individuals were clearly distinguishable from male *R. t. fennicus* in the morphospace. This distinction was, however, slightly less clear in *R. t. tarandus*. On the other hand, working reindeer (male *R. t. tarandus*) seemed quite similar morphologically to the other males, particularly free-ranging and captive *R. t. tarandus* individuals. The variation along PC2 (14.42% of the total variance) showed quite a distinction between subspecies. More specifically, free-ranging *R. t. fennicus* were more distributed towards the positive values of PC2 and had a more triangular shape with a relatively deep central trough, whilst free-ranging *R. t. tarandus* were located towards the negative values with a more rectangular shape and a shallower central trough. Captive individuals in both subspecies seemed to occupy a roughly intermediate location in the morphospace compared to wild *R. t. fennicus* and *R. t. tarandus* individuals. However, captive female *R. t. fennicus* were morphologically closer to their free-ranging counterparts, as were captive female *R. t. tarandus* with the free-ranging female *R. t. tarandus*. Hybrid individuals also appeared to be intermediate in shape with their parent species: hybrid females were intermediate compared

**FIGURE 4** Scatter plots of the two first axes (PC 1 and PC 2) of the principal component analyses performed on the shape data of the stylopodial bones, and the visualisation of shape variation via deformation of the mean shape along the negative and positive PC1 and PC2 values (magnified by a scale factor of 0.1). (a) Humerus and (b) femur. The proportion of the total variance expressed by axes PC1 and PC2, respectively, is indicated in brackets.
to female *R. t. tarandus* and female *R. t. fennicus*, and male hybrids were intermediate compared to male *R. t. tarandus* and male *R. t. fennicus*.

For the metatarsal, these distinctions seemed less evident (Figure 6b). Indeed, the greatest distinctions in the morphospace concerned free-ranging females and males *R. t. fennicus* along PC1 (35.39% of the total variance). This resulted in a more rectangular bone cross-section, a shallower central trough and a thicker cortical bone in the free-ranging female *R. t. fennicus* on the negative values along PC1, whilst the shape is more rounded with a deeper central trough and thinner cortical bone in the free-ranging male *R. t. fennicus* with positive values along PC1. However, all of the other categories overlapped extensively and could show considerable intragroup variations, such as the working reindeer. In addition, the variations along PC2 (18.19% of the total variance) did not allow distinctions between groups.

### 3.4 | Allometry

Allometry was significant for all bone elements (all $p << .01$). However, the allometric pattern varied widely depending on the bone. The percentage of shape variance related to size was relatively lower for the humerus (5.19%) and radioulna (5.37%) compared to the femur (8.94%) and tibia (11.36%), but was quite high for the metapodials (metacarpal: 29.93%; metatarsal: 25.68%). Multivariate regressions of
shape scores (Procrustes coordinates) against the log-transformed centroid size showed that male individuals, with the largest centroid size, relatively easy to distinguish from female reindeer for the stylopodial and zeugopodial bones (Figure 7). Only male hybrids had an intermediate size or shape, which caused overlaps with male and female individuals. Generally, captive and working individuals had either lower shape scores or a lower centroid size than free-ranging individuals. For the stylopodial and zeugopodial bones (Figure 7a–d), the free-ranging female R. t. fennicus showed the highest values in centroid size than the captive female R. t. fennicus and the female R. t. tarandus for similar shape score. Although similar in size to their free-ranging counterparts, the captive female R. t. tarandus tended to have lower shape scores. Despite the overlaps, this observation could also be made in males. For similar shape scores, the free-ranging male R. t. tarandus had lower values in size than wild R. t. fennicus. However, working reindeer tended to have lower shape scores compared to free-ranging individuals. The distinction between these groups was similar and consistent with previous analyses (i.e., size and shape), although when controlling for allometry, morphological variations showed that this was less evident for the metapodial bones (Figure 7e,f). Indeed, clusters of the different groups overlapped more for the metacarpal and the metatarsal compared to the stylopodial and zeugopodial bones. The overlaps mainly concerned the free-ranging and working male R. t. tarandus and male hybrids, free-ranging and captive female R. t. fennicus and female hybrids, and free-ranging and captive female R. t. tarandus. For a given size, the female R. t. fennicus had lower shape scores than the female R. t. tarandus, whilst in males, the free-ranging R. t. fennicus had higher shape scores than free-ranging and working R. t. tarandus for similar shape scores.

**FIGURE 6** Scatter plots of the two first axes (PC 1 and PC 2) of the principal component analyses performed on the shape data of the metapodial bones, and the visualisation of shape variation via deformation of the mean shape along the negative and positive PC1 and PC2 values (magnified by a scale factor of 0.1). (a) Metacarpal and (b) metatarsal. The proportion of the total variance expressed by axes PC1 and PC2, respectively, is indicated in brackets.
Our study confirmed that taxonomy, ecology and sex had a relatively large impact on size variation in Finnish modern reindeer populations. Firstly, we showed that *R.t. fennicus*, the wild forest reindeer, had significantly larger bones than *R.t. tarandus*. As previously hypothesised, this could be partially explained by marked etho-ecological differences between the two subspecies and an adaptation to their respective biotopes (Pelletier et al. 2020, 2021; Puputti & Niskanen, 2009). Indeed, *R.t. fennicus* is a reindeer subspecies better adapted to the closed environments of the taiga, with a deep and soft snow cover, which explains its overall longer legs and greater withers height of 10–15 cm, whilst *R.t. tarandus* prefers more open areas and lives on hard-packed tundra snow (Nieminen & Helle, 1980).

In addition to these ecological discrepancies, bone sizes also varied quite widely between sexes in both subspecies. Male reindeer had...
significantly larger cross-sectional bone elements than female reindeer, which is explained by a strong sexual dimorphism (Melnycky et al., 2013; Pelletier et al., 2020, 2021; Pupputi & Niskanen, 2009; Reimers et al., 1983; Weinstock, 2000). Beyond these intrinsic and extrinsic factors that characterise the natural variability of modern Finnish reindeer populations, our results indicate that the long bones are also strongly affected by selection imposed by humans, particularly during a lifetime of growth in captivity or when used to perform domestic tasks.

Although we only had a small sample of captive male individuals for our study, we found that individuals bred in captivity generally had smaller bone cross-sections than free-ranging reindeer. This apparent reduction in size of the bony elements, and by extension, body size, of captive versus wild individuals is a well-known feature of the domestication syndrome and has been long observed in many other domestic species (e.g., Davis, 1981; Dayan, 1994; Morey, 1992; Rowley-Conwy et al., 2012; Zeder et al., 2006; Zohary et al., 1998). The fact that domesticated individuals are smaller in size than wild individuals is a characteristic that has already been identified in reindeer (Pupputi & Niskanen, 2009). However, most captive individuals in our study were born in the wild and did not have a long ancestry in zoos (Pelletier et al., 2020, 2021), implying that the effects of a reduction in mobility had immediately noticeable consequences on the body size of the wild individuals. The body size reduction in captivity seemed significantly more evident in wild forest reindeer (R. t. fennicus) than in mountain reindeer (R. t. tarandus). This could partially be explained by the fact that there are no longer any wild modern R. t. tarandus in Finland. Indeed, free-ranging R. t. tarandus are left in free-range for much of the year, but are also kept in corrals by herders during the winter in order to avoid substantial losses in the herds (e.g., due to food shortages, periods of intense cold, predation, as well as train and car accidents). Thus, the impact of captivity on these R. t. tarandus individuals was barely perceptible in our sample but could probably occur amongst completely wild R. t. tarandus populations.

Finally, although size differences were not systematically significant between free-ranging and working individuals, we noted that amongst male R. t. tarandus, working reindeer tended to be larger. This is because working reindeer are selected for their physical properties and ability to perform domestic work (Korhonen, 2008). Thus, in such cases there would be no increase in the body size of individuals subjected to the pressure of domestication, but a prior selection of the most robust individuals in order to subsequently use them for transport, pulling, riding or racing.

4.2 | Pattern of body mass variations

Our results showed that body mass variations in modern Finnish reindeer roughly followed the size variations of bone cross-sections. The good correlation between mass and centroid size measurements suggests that centroid size would be a reasonable measure of body mass for this species, which is consistent with previous studies in other taxa (Berner, 2011; Cassini et al., 2012; Ercoli & Prevosti, 2011; Iskjaer et al., 1989; MacLaren et al., 2018). Although we found roughly the same pattern of differentiation for the centroid size between the majority of groups (i.e., significant differences between free-ranging and working individuals, between working and captive individuals, as well as between males and females), no significant differences were observed between both subspecies, or between free-ranging and captive individuals. In particular, body mass values in wild male R. t. fennicus are highly variable, and even most these individuals had a lower body mass than male R. t. tarandus. This observation is contrary to what has been noted regarding centroid size in which free-ranging male R. t. fennicus were almost always larger than R. t. tarandus individuals (Figure 2). In addition, the body mass observed in captive female individuals is similar to their free-ranging counterparts, unlike what we previously observed regarding centroid size, where the captive individuals were smaller.

These observations are consistent with the finding that captivity increases body weight (e.g., Harbers et al., 2020; O’Regan & Kitchener, 2005; Zhou et al., 2015). In reindeer, captivity causes profound changes in the pace of activity compared to wild individuals, which are generally gregarious and migratory, as well as in feeding and reproductive behaviours. In the wild, reindeer undergo great variations in body mass depending on the season (Couturier, 2007; Reimers, 1983; Weladji et al., 2002). Before winter, reindeer achieve their maximum weight in order to be capable of dealing with the harsh winter climate and generally become relatively thin by the end of winter (Crête et al., 1993; Soppela & Nieminen, 2001). During the rutting season, adult males are also thin as a result of fights related to reproduction and lack of feeding (Jacobi, 1931). In contrast, competition between males is reduced or non-existent in captivity. This could explain why there is greater variation in body mass in wild male R. t. fennicus in our sample compared to other reindeer groups.

In addition, reindeer kept in captivity, ranched or bred according to the free-ranging system are fed by their owners throughout the year or part of the year (Helle & Jaakkola, 2008). Thus, they do not face winter food shortages or difficulty in finding food. Nowadays in Finland, R. t. fennicus are only present in the wild, unlike semi-domestic R. t. tarandus, which are kept in corrals and fed by herders during the winter. Thus, this could also explain why R. t. tarandus are proportionately heavier than R. t. fennicus and exhibit less variation in body mass, although they have a smaller body size.

4.3 | Pattern of shape variations

Regarding the overall morphology of the femur and humerus, we noted that the females tended to have a rather extended bone cross-section craniocaudally, whilst in males, the cross-sections tended to be more circular or even extended mediolaterally. Although slightly less visible, this pattern of morphological variation between the sexes also appeared to be reflected in the radioulna and tibia. This tendency for the stylopodial and zeugopodial bones would indicate a morpho-functional adaptation in the heaviest individuals (i.e., males) in order to resist mediolateral flexion. Although these results are generally
Captive and working individuals showed more circular cross-sections of the shaft associated with an increase in cortical bone thickness compared to their wild counterparts, particularly for the humerus, femur and tibia. These results are consistent with a recent study by Niinimäki et al. (in press), which indicated greater bone strength in the stylopodial and zeugopodial bones in captive and working reindeer. This confirms the interrelated effects of changes in locomotor and feeding behaviours and increasing body mass on the bone shape and bone volume of the shaft. Our observations also appear to be consistent with a recent experiment conducted to appre-hend the impact of reduced mobility in modern suids, in which captivity has been shown to jointly increase the body mass and bone volume of the shaft of the humerus (Harbers et al., 2020). In that study, it was suggested that developmental disruptions due to body mass increase in captivity have changed the biomechanical loads during growth. The authors also pointed out that growth in captivity has a significant impact on increasing muscle mass, beyond what is possible under natural conditions. This could be due to the cumulative and interdependent consequences of an increased body mass, a protein rich diet, as well as stereotypical behaviour increasing the frequency of muscle use.

It has previously been shown that free-ranging reindeer have greater stability in the elbow joint and larger insertion areas for the different flexor and extensor muscles for the digits, particularly due to repetitive flexing of the elbow articulation when digging for food under the snow (Niinimäki & Salmi, 2016; Pelletier et al., 2020). Indeed, Fennoscandian reindeer can spend over 8 h per day, 7 months per year, foraging for lichen buried beneath the snow using their fore-limbs (Korhonen, 2008). However, this activity is reduced or even absent in captivity because reindeer are fed by their owners. As mentioned above, this change in the foraging pattern of domestic reindeer involves significantly less seasonal variations in body mass than in wild individuals and, in some cases, leads to an increase in body mass. In addition, captive reindeer are morphologically adapted to prolonged periods of static loading, notably through greater stability of the shoulder, better resistance to adduction of the humerus, and a widening of articular surfaces, trochanters or condyles of more caudal limb elements (Niinimäki & Salmi, 2016; Pelletier et al., 2020, 2021). Beyond these effects of increased body mass and changes in feeding behaviours, the increase in the amount of cortical bone in captive individuals could also be associated with a prolonged standing lifestyle and increased axial loading and/or muscle loading (Niinimäki & Salmi, 2016; Niinimäki et al., in press).

In the case of working reindeer, individuals are specially selected for their physical abilities and traits and are trained for several months of the year for running and pulling. This could partially explain the increase in muscle volume compared to free-ranging individuals. However, it should be noted that apart from their training, which only takes place during the winter, working individuals were left in free-range for the rest of the year, just like free-ranging individuals. Thus, activity levels could be similar for most of the year, leading to similar shape and robustness requirements. This is probably why the morpho-logical differences between working and free-ranging R. t. tarandus are tenuous or even absent from the articular surfaces and the ligament/muscular insertions of the long bone epiphyses of the forelimb (Pelletier et al., 2020). In contrast, working reindeer are morphologi-cally better suited to the need for a large range of motion in the hip and knee joint (Pelletier et al., 2021; Salmi, Niinimäki, & Pudas, 2020). Although they are critical to changes in direction during locomotion, the forelimb long bones are actually mainly adapted to support body mass (Rollinson & Martin, 1981). The hind limb bones are more suit-able for propulsion and are impacted by external pressures (e.g., Hanot et al., 2017; Mallet et al., 2019; McGuigan & Wilson, 2003). Whilst work-related stresses seemed to affect the external morphology of the various parts of the fore- and hind limb long bones differently, our study of bone cross-sections demonstrates that these selective pressures are significantly affected by the increase in the cortical bone thickness, particularly for both the stylopodium and zeugopodium.

Finally, we observed a significant effect of centroid size on bone shape (i.e., the effect of allometry) for all bony elements. However, the percentage of the total variance in shape related to size varied greatly according to the cross-section studied. It has already been observed that allometry was more pronounced in the epiphyses of the forelimb than in the hind limb (Pelletier et al., 2020, 2021), which would appear to indicate that these elements are more affected by body mass. This must therefore be attributable to a mopho-functional adaptation of these bones because the reindeer must support a greater part of their body mass on their forelimbs than on their hind limbs, particularly because of the weight of their antlers. In contrast, for cross-sections the allometry is more pronounced in the hind limb than in the forelimb, reflecting the possibility of greater external pressures on the diaphy-ses. Lastly, we noted that the allometry was relatively strong for the metacarpal and metatarsal cross-sections (i.e., 29.93 and 25.68% of the total variance, respectively). This would reflect greater involvement of the metapodial diaphyses in supporting the limbs and therefore the body mass, but could also suggest lower safety factors for these bones compared to the stylopodial and zeugopodial bones. As such, morpho-logical differences in the metapodials were particularly marked between sexes, especially on the metacarpals (Figure 6a), which would be an additional argument regarding the impact of the weight-bearing functions of the skeletal elements (e.g., sexual dimorphism, muscle vol-ume, antlers larger and heavier in males). In their recent work, Niinimäki et al. (in press) already assumed that the metapodials did not respond similarly to the frequency and magnitude of loading compared to more proximal limb elements. This could also be due to the metapodials probably reflecting the locomotor behaviour more than the long bones (Christiansen, 2002). Indeed, individuals living in closed habitats, as in the case of wild Finnish forest reindeer (R. t. fennicus), tend to have long limb elements relative to their body weight, unlike individuals that have adapted to the mountainous regions—such as domesticated mountain reindeer (R. t. tarandus), which have propor-tionately shorter limb elements (Scott, 1985).
Nowadays, reindeer herding is widely practised in most of the tundra and taiga areas by around 30 indigenous reindeer herder groups, from Eastern Siberia and Northern Mongolia to Northern Fennoscandia (Reindeer Herding, 2021). It is historically recognised that the domestication of the reindeer, from at least the Iron Age (ca. 800–900 AD), had a far-reaching impact on the subsistence, ways of life, economy and cosmology of many of these peoples in Northern Eurasia. Despite the importance of this reindeer husbandry in the history of the Arctic people, the origin of reindeer herding is still highly debated, due to the fact that it appears to have been gradual and not synchronous either in the different regions or with the same amplitude (Bjørklund, 2013; Lundmark, 2007; Tegengren, 1952). Thus, reindeer bones collected from archaeological sites could provide direct evidence of this important transition in the socio-economic structure and history of the reindeer herding people of Eurasia and provide a unique opportunity to study the reindeer domestication process. Our methodology would appear to be highly suited to the application to fossil reindeer materials as the shafts of the long limb bones are often numerous due to marrow extraction (Harlin et al., 2019). Through environmental, (i.e., populations mainly from central Finland), genotype (i.e., R.t. fennicus and R.t. tarandus) and phenotype (i.e., free-ranging, captive and working) control, our study allowed us to highlight the interdependent variations of the body weight and morphology of the internal structure of the bone shafts, mainly due to anthropogenic selection. These variation patterns associated with behavioural changes in domestic versus wild individuals provide valuable information on the early effects of the selection on bone morphology and could be beneficial to the archaeological record.

However, the reindeer domestication process is even more difficult to define as there is great variability in the types and practices of herding throughout Eurasia, as well as complex human-reindeer relationships. Reindeer may be left to range free in a restricted geographical area and under fairly close supervision by herders (e.g., amongst the Komi herders of northwestern Siberia [Dwyer & Istomin, 2008] or the Tozhu Tuwan herders of southern Siberia [Stépanoff, 2017]), left to range free for part of the year but corralled during the winter in order to be protected and fed (e.g., amongst the Sámi herders of Northern Fennoscandia [Helle & Jaakkola, 2008; Ingold, 1980]) or even hitched or kept inside enclosures or houses (e.g., amongst the Evenk herders of central Siberia [Anderson et al., 2017]; the Tsaatan herders of central Siberia [Haas et al., 2019; Inamura, 2005]; the Selkup herders of northern Siberia [Plezonka et al., 2020]). In some cases, locomotor activity is further altered by human control as reindeer can also be used for other purposes such as transport, pulling, riding or racing [Anderson et al., 2017; Inamura, 2005; Korhonen, 2008; Mirov, 1945; Salmi, Niihimäki, & Pudas, 2020; Stépanoff, 2017]. Hence, the impact of selection on skeletons could be expressed in very different degrees (i.e., more or less pronounced) in time and space.

In addition, since domesticated reindeer are mostly left in free-range by herders, it is not uncommon for hybridisation resulting from crossbreeding between wild (R.t. fennicus) and domestic (R.t. tarandus) herds to occur in areas in which their distribution ranges overlap (Nieminen & Helle, 1980; Nieminen & Ojutkangas, 1986; Reed et al., 2008, 2011). Wild individuals could even be captured to incorporate them into domestic herds to avoid consanguinity (Sommerseth, 2011). The main problem of the potential presence of hybrids in archaeological contexts could be the large morphometric overlaps with their parents, since it has been shown that they could exhibit either morphological traits more similar to a particular parent, or an intermediate morphology and size (Evín et al., 2015; Hanot et al., 2017, 2019; Sävriama et al., 2018). In our study, female hybrids have a size intermediate between female R.t. fennicus and R.t. tarandus and male hybrids have a size intermediate between male R.t. fennicus and R.t. tarandus, making them even closer to female R.t. fennicus. Regarding morphology, the hybrids (both sexes included) were generally closer to R.t. tarandus than to R.t. fennicus. However, as the hybrids in our sample were captive individuals, the morphological variation associated with at sedentary lifestyle, expressed by a greater bone cortical thickness, took precedence over that of the subspecific variation. In any event, the presence of hybrids in an archaeological site could lead to more confusion in interpreting fossil material.

It is still challenging to identify the origin of reindeer domestication and it is difficult to consider the reindeer as a purely domestic animal, in the same way as most European bovines, caprines, equids or suids. This is why many scholars consider reindeer to be still in the early stages of the domestication process (Baskin, 2000; Reimers & Colman, 2006), and that it could potentially serve as an excellent model species for understanding how morphological changes take place during the initial stages of selection and domestication. Thus, our results could ultimately be extrapolated beyond this species. The fact that most zoo individuals were born in the wild, and not in captivity, further indicates that the effects of reduced mobility can be seen immediately, without prior selection. It would therefore be interesting to compare this observation of early changes in other domestic ungulate species born in the wild and then bred in captivity. The characteristics observed in racing and pulling reindeer might also be similar to other draft or racing animals, such as bovines or equids (e.g., Bartosiewicz & Gál, 2013; Shackelford et al., 2013).

However, certain nuances should be considered before a methodological transfer is made to other taxa. For example, it is often assumed that centroid size/body size can provide a good estimate of the body weight of an animal, which makes it possible to study the effects of allometry (e.g., Campione & Evans, 2012; Dick & Clemente, 2017; Mallet et al., 2019). Although we have generally observed such a correlation in reindeer, it is important to note that we have also observed (1) a large variation in the weight of wild individuals compared to domestic individuals, particularly in different reproductive and feeding behaviours and (2) the significant impact of captivity and selection (i.e., anthropogenic stimuli) on bone size and body mass. As the shape variation of limb long bones is related to body mass, and may be more pronounced for heavier species (Schmidt & Fischer, 2009), anthropogenic impact is a parameter which could bias this model even more. Thus, the plastic responses of the bone cross-
sections observed in this work constitute a good initial stage in the identification of the impact of human control on the behaviour of wild animals, transferable to other species, but also to the archaeological record. In any case, a careful analysis of the size, shape and allometry of animal bones, as well as the archaeological context (i.e., geographic, chronological and cultural), are all essential parameters to be taken into consideration in order to better understand the early process of domestication and herding management.

5 | CONCLUSION

Beyond the effects of taxonomy, etho-ecology and sex, we have demonstrated that patterns of variation in size, shape and cortical bone thickness of long limb bone cross-sections in modern reindeer populations were strongly impacted by human influence. Growth in captivity or the selection of individuals to perform domestic tasks induce significant changes in feeding and locomotor behaviours, which can affect body size, body mass and the shape and strength of long bone diaphyses. An increase in body mass, associated with a decrease in body size, has been recorded in individuals kept in total captivity (i.e., in a zoo) and, to a lesser extent, in free-ranging R.t. tarandus individuals (i.e., captive during winter and in free-range during summer). This would partially be due to the potential changes in feeding behaviours (i.e., fed by their owners) compared to wild individuals (i.e., foraging for food buried beneath the snow). Captive reindeer showed increased cortical bone thickness, possibly related to better body mass support and prolonged periods in a static position. In contrast, the larger size and body mass of working reindeer is a selective choice by owners seeking the best physical traits and abilities in these individuals. An increase in cortical bone thickness was also noted in these particular individuals but may be more attributable to a bone response to the stresses imposed during running and pulling. Despite relatively different functions and lifestyles amongst domestic reindeer (i.e., captivity versus traction), in both cases we recorded an increase in cortical bone thickness of the long bones in response to behavioural changes, particularly for the stylopodium and zeugopodium. The metapodial shafts appear to be more involved in supporting body mass. These plastic changes associated with selection and captivity could prove to be powerful proxies to better understand the functional changes induced by domestication on limb bone morphology, and could ultimately be adapted for other domesticated ungulate species that are corralled, fed or used for domestic tasks (e.g., bovines, camelids, caprines, equids and suids). Further studies allowing increased understanding of the impact of mobility reduction on the morphometric diversity of reindeer should be conducted in the future in order to complement our study. It could also significantly contribute to identifying early reindeer management through the archaeological record, thereby comprehending the evolution of past reindeer herding practises amongst the different indigenous peoples of Eurasia.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

Maxime Pelletier: Conceptualization; formal analysis; investigation; methodology; visualization; writing - original draft; writing-review & editing. Sirpa Niinimäki: Resources. Anna-Kaisa Salmi: Conceptualization; funding acquisition; supervision; writing-review & editing.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Adams, D. C., & Otárola-Castillo, E. (2013). Geomorph: An R package for the collection and analysis of geometric morphometric shape data. Methods in Ecology and Evolution, 4, 393–399. https://doi.org/10.1111/2041-210X.12035
Adams, D. C., Rohlf, F. J., & Slice, D. E. (2004). Geometric morphometrics: Ten years of progress following the “revolution”. Italian Journal of Zoology, 71, 5–16. https://doi.org/10.1080/1125000409356545
Albarella, U. (2002). “Size matters”: How and why biometry is still important in zooarchaeology. In K. Dobney & T. O’Connor (Eds.), Bones and the man: Studies in honour of Don Brothwell (pp. 51–62). Oxbow Books.
Anderson, D. G., Harrault, L., Milek, K. B., Forbes, B. C., Kuoppamaa, M., & Plekanov, A. V. (2019). Animal domestication in the high Arctic: Hunting and holding reindeer on the l’Amlal peninsula, Northwest Siberia. Journal of Anthropological Archaeology, 55, 101079. https://doi.org/10.1016/j.jaara.2019.101079
Anderson, D. G., Kvie, K. S., Davydov, V. N., & Raed, K. H. (2017). Maintaining genetic integrity of coexisting wild and domestic populations: Genetic differentiation between wild and domestic Rangifer with long traditions of intentional interbreeding. Ecology and Evolution, 7, 6790–6802. https://doi.org/10.1002/ece3.3230
Arbuckle, B. (2005). Experimental animal domestication and its application to the study of animal exploitation in prehistory. In J.-D. Vigne, J.
Inamura, T. (2005). The transformation of the Community of Tsataan Reindeer Herders in Mongolia and their relationships with the outside world. Senri Ethnological Studies, 69, 123–152. http://doi.org/10.15021/00002643

Ingold, T. (1980). Hunters pastoralists and ranchers: Reindeer economies and their transformation. Cambridge University Press. https://doi.org/10.1017/CBO9780511558047

Iskajer, C., Slade, N. A., Childs, J. E., Glass, G. E., & Korch, G. W. (1989). Body mass as a measure of body size in small mammals. Journal of Mammalogy, 70, 662–667. https://doi.org/10.2307/1381447

Jacobi, A. (1931). Das Rentier – eine zoologische Monographie der Gattung Rangifer. Akademische Verlagsgesellschaft.

Kilbourne, B. M., & Hutchinson, J. R. (2019). Morphological diversification of biomechanical traits: Mustelid locomotor specializations and the macroevolution of long bone cross-sectional morphology. BMC Ecology and Evolution, 19, 37. https://doi.org/10.1186/s12862-019-1349-8

Korhonen, T. (2008). Poroerotus. Historia, toiminta ja tekniset ratkaisut. Suomalaisen Kirjallisuuden Seura.

Lieberman, D. E., Polk, J. D., & Demes, B. (2004). Predicting long bone size through time and across geographical space. Quaternary International, 125, 156–171. https://doi.org/10.1016/j.quaint.2003.12.001

Lundmark, L. (2007). Reindeer pastoralism in Sweden 1550–1950. Rangifer, 3, 12–9. https://doi.org/10.7557/2.27.3.264

MacLaren, J. A., Hulbert, R. C., Jr., Wallace, S. C., & Nauwelaerts, S. (2018). A morphometric analysis of the forelimb in the genus Tapirus (Perissodactyla: Tapiridae) reveals influences of habitat, phylogeny and size through time and across geographical space. Zoological Journal of the Linnean Society, 184, 499–515. https://doi.org/10.1093/zoolinnean/zly019

Mallet, C., Cornette, R., Billet, G., & Houssaye, A. (2019). Interspecific variation in the limb long bones among modern rhinoceroses-extent and drivers. PeerJ, 7, e7647. https://doi.org/10.7717/peerj.7647

McGuigan, M. P., & Wilson, A. M. (2003). The effect of gait and digital flexor muscle activation on limb compliance in the forelimb of the horse Equus caballus. Journal of Experimental Biology, 206, 1352–1366. https://doi.org/10.1242/jeb.00254

Melnycy, N. A., Weladji, R. B., Holand, Ø., & Nieminen, M. (2013). Scaling of antler size in reindeer (Rangifer tarandus); Sexual dimorphism and variability in resource allocation. Journal of Mammalogy, 94, 1371–1379. https://doi.org/10.1644/12-MAMM-A-282.1

Mirov, N. T. (1945). Notes on the domestication of reindeer. American Anthropologist, 47, 393–408. https://doi.org/10.1525/aa.1945.47.3.02a00030

Morey, D. F. (1992). Size, shape and development in the evolution of the domestic dog. Journal of Archaeological Science, 19, 181–204. https://doi.org/10.1016/0305-4403(92)90049-9

Murashkin, A. I., Kolpakov, E. M., Shumkin, V. Y., Khartanovich, V. I., & Moiseyev, V. G. (2016). Kola Oleneostrovsky grave field: A unique burial site in the European Arctic. In P. Ulin & K. Nordqvist (Eds.), New sites, new methods (pp. 186–199). The Finnish Antiquarian Society, ISKOS 21.

Nieminen, M., & Helle, T. (1980). Variations in body measurements of wild and semi-domestic reindeer (Rangifer tarandus) in Fennoscandia. Annales Zoologici Fennici, 17, 275–283.

Nieminen, M., & Ojutkangas, V. (1986). Genetic variation in Finnish wild and semidomestic reindeer (Rangifer tarandus). Rangifer, 6(1-App), 115. https://doi.org/10.7557/2.6.1-App.630

Niinimäki, S., Härkönen, L., Puolakka, H.-L., van den Berg, M., & Salmi, A.-K. (in press). Cross-sectional properties of reindeer long bones and metapodials allow identification of activity patterns. Archaeological and Anthropological Sciences.

Niinimäki, S., & Salmi, A.-K. (2016). Enthesal changes in free-ranging versus zoo reindeer – Observing activity status of reindeer. International Journal of Osteoarchaeology, 26, 314–323. https://doi.org/10.1002/oa.2423

O'Regan, H. J., & Kitchener, A. C. (2005). The effects of captivity on the morphology of captive, domesticated and feral mammals. Mammal Review, 35, 215–230. https://doi.org/10.1111/j.1365-2907.2005.00070.x

Parsi-Pour, P., & Kilbourne, B. M. (2020). Functional morphology and morphological diversification of hind limb cross-sectional traits in mustelid mammals. Integrative Organismal Biology, 2, 02302. https://doi.org/10.1093/obi/obz032

Pearson, O. M., & Lieberman, D. E. (2004). The aging of Wolff’s “law”: Ontogeny and responses to mechanical loading in cortical bone. American Journal of Physical Anthropology, 125, 63–99. https://doi.org/10.1002/aja.20155

Pelletier, M., Kotiaho, A., Niinimäki, S., & Salmi, A.-K. (2020). Identifying early stages of reindeer domestication in the archaeological record: A 3D morphological investigation on forelimb bones of modern populations from Fennoscandia. Archaeological and Anthropological Sciences, 12, 169. https://doi.org/10.1007/s12520-020-01123-0

Pelletier, M., Kotiaho, A., Niinimäki, S., & Salmi, A.-K. (2021). Impact of selection and domestication on hind limb bones of modern reindeer populations: Archaeological implications for early reindeer management by Sámi in Fennoscandia. Historical Biology. https://doi.org/10.1080/09196954.2021.1947268

Piezonka, H., Poshek honova, O., Adaev, V., & Rud', A. (2020). Migration and its effects on life ways and subsistence strategies of boreal hunter-fishers: Ethnoarchaeological research among the Selkup, Sib eria. Quaternary International, 541, 189–203. https://doi.org/10.1016/j.quaint.2019.07.005

Price, E. O. (2002). Animal domestication and behavior. CABI Publishing.

Profico, A., Bondioli, L., Raia, P., O’Higgins, P., & Marchi, D. (2021). Morphomap: An R package for long bone landmarking, cortical thickness, and cross-sectional geometry mapping. American Journal of Physical Anthropology, 174, 129–139. https://doi.org/10.1002/aja.24140

Pupputi, A.-K., & Niskanen, M. (2008). The estimation of body weight of the reindeer (Rangifer tarandus L) from skeletal measurements: Preliminary analysis and application to archaeological material from 17th- and 18th-century northern Finland. Environmental Archaeology, 13, 153–164. https://doi.org/10.1179/119463108X342372

Pupputi, A.-K., & Niskanen, M. (2009). Identification of semi-domesticated reindeer (Rangifer tarandus tarandus, Linnaeus 1758) and wild forest reindeer (r.t. fennicus, Lönnberg 1909) from postcranial skeletal measurements. Mammalian Biology, 74, 49–58. https://doi.org/10.1016/j.mambio.2008.03.002

Reimers, E. (1983). Growth rate and body size differences in Rangifer, a study of causes and effect. Rangifer, 3, 3–15. https://doi.org/10.7557/2.3.1.463

Reimers, E., & Colman, J. E. (2006). Reindeer and caribou (Rangifer tarandus) response towards human activities. Rangifer, 26, 55–71. https://doi.org/10.7557/2.26.2.188

Reimers, E., Klein, D. R., & Sorumgard, R. (1983). Calving time, growth rate and body size of Norwegian reindeer on different ranges. Alpine Research, 13, 256–268. https://doi.org/10.1002/alr.3260130304

Reed, K. H., Flagstad, Ø., Bjørnstad, G., & Hufthammer, A. K. (2011). Eluci dating the ancestry of domestic reindeer from ancient DNA approaches. Quaternary International, 238, 83–88. https://doi.org/10.1016/j.quaint.2010.07.031

Reed, K. H., Flagstad, Ø., Nieminen, M., Holand, Ø., Dwyer, M. J., Rav, N., & Vila, C. (2008). Genetic analyses reveal independent domestication origins of Eurasian reindeer. Proceedings of the Royal Society B: Biological Sciences, 275, 1849–1855. https://doi.org/10.1098/rspb.2008.0332
