REVIEW ARTICLE

Paleopathology, Entheseal Changes, and Cross-Sectional Geometry: The Zooarchaeology of Working Animals

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ABSTRACT

Morphological changes in the skeletons of working animals such as reindeer, horse, and cattle have long been observed and documented in the archaeological record. Activities such as riding, carrying cargo on their backs, and pulling vehicles like sleds and ploughs throughout an animal's life history cause alterations and variations to skeletal tissue. Such alterations include paleopathological lesions, entheseal changes (EC)—alterations in muscle, tendon, and ligament attachment sites on bone—and variations in cross-sectional bone geometry (CSBG). These clues are helpful for reconstructing human-animal relationships in faunal remains of our archaeological past. However, other factors influence the morphological appearance of skeletal tissue besides working activities, such as age, sex, body size, nutrition, genetics, environmental factors, and management by human caretakers. This article explores how paleopathological lesions, EC, and CSBG in faunal skeletal remains are examined to reconstruct working activity and changes to human-animal relationships in the archaeological record. In particular, we discuss two primary topics of inquiry: (1) a review of paleopathological identifiers in working animals such as cattle, horse, camel, and reindeer; and (2) how EC and CSBG are understood in terms of bone functional adaptation, and their application in working and non-working animals such as reindeer and horse. Next, we analyze each topic highlighting their benefits and limitations, including how they contribute to archeological understandings of human-animal relationships in the past, as well as their implications for future research.

Keywords: entheseal changes, bone functional adaptation, paleopathology, human-animal relationships, draught animals, domestication

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INTRODUCTION

Changes to animal skeletons are one of the most valuable zooarchaeological approaches to recognize the presence of domestic animals used for their labour in the past. The advent of animal labour had a significant impact on human societies allowing people to travel, produce more food, and transport larger/heavier loads more effectively (Sherratt 1983; Anthony and Brown 2011). Previous research on animal labour has focused on husbandry practices (Losey et al. 2018; Zeder 2006; Russell 2012), as well as the presence of equipment such as ploughs (Bartosiewicz, Van Neer, and Lentacker 1997; Greenfield 2010; Marković and Bulatović 2013; Sherratt 1983), wheeled vehicles (Anthony 2007; Burmeister 2017), sleds (Losey et al. 2018; Pitul'ko and Kasparov 1996; 2017), and harnessing (Anthony and Brown 2011; Fribus et al. 2019; Legrand 2006; Losey et al. 2021). Although extensive, these studies fall short in that they do not directly examine the physiological demand of animal labour largely because material culture related to traction, riding, and carrying is generally rare or absent in the archaeological record (Thomas et al. 2021, 85). Osteological evidence, however, fills this gap providing a valuable way to infer the presence of and to reconstruct such activity directly observed on animal remains. Not only does examining skeletal morphology help scholars better understand the overall process of animal domestication through human history, but it can also reframe how archaeologists examine the impact of daily human-animal relations, physical activities, and their contribution to large-scale changes over time.

Skeletal changes occurring from biomechanical loading include the development of paleopathological lesions, entheseal changes (EC), and differences in cross-sectional bone geometry (CSBG). Except for acute, traumatic events during work, these changes are a result of long-term habitual activity resulting from the nature of specific relationships between people and animals. These include activities such as pulling, carrying cargo on their backs, and being ridden. Additionally, as we elaborate further in this paper, there are a multitude of biological, environmental, and behavioural factors that also contribute to skeletal change that must be fully considered in any study.

This paper reviews the contributions of paleopathological lesions, EC, and CSBG to zooarchaeological research on working animals, while highlighting the limitations inherent in using these lines of evidence. First, we demonstrate the ways that numerous types of paleopathological lesions have been tied to certain forms of activity and exertion, which must be considered specific to certain species. To do so, we highlight three species of domestic animals that are the most well studied: cattle (*Bos taurus*) and horses (*Equus caballus*) and reindeer (*Rangifer tarandus*). Second, we analyze EC, which allows researchers to reconstruct animal movement and mechanical stress through observations of animal entheses, that is where tendons, ligaments, and muscles connect to bone. Comparison between animals known to have been worked versus those that did not work indicates the effects of labour on the skeleton. Such initiatives have been well demonstrated in humans, (e.g., Hawkey and Merbs 1995; Henderson et al. 2017) but only recently employed in reindeer and horse populations (Niinimäki and Salmi 2016; Bindé et al. 2019). Finally, we investigate CSBG to understand changes in the cross section of long bone diaphyses caused by mechanical loading and make use of similar comparison between worked and non-worked individuals to infer activity. Taken together, each of these methods provide valuable insights into the relationships and mutual activities enacted by people and domestic animals.

PALEOPATHOLOGY OF WORKING ANIMALS

Investigating the ways that animals have been used for activities such as draught work, riding, and carrying cargo demonstrate how people have made use of animal labour in the past. One such avenue is through examining pathological lesions on animal remains from archaeological sites. Both transportation and subsistence practices changed drastically with the introduction of animal labour (Bendrey 2014, 260). Long-term and habitual work, for instance, can manifest as lesions on various parts of the skeleton, such as the distal limbs, vertebrae, scapulae, hip joints, skulls, and teeth. The following section reviews paleopathological lesions that have been used to identify working animals from archaeological sites.

Determining whether an animal was consistently and habitually used for traction, riding, or cargo, and the intensity of that use is not straightforward since many of the activity-related lesions discussed below have multifactorial etiologies that complicate confidence in causality. Animals are not biomechanically adapted for such work; they evolved carrying out natural locomotion and behaviour without the physical stress of pulling or carrying excess weight that humans have employed them to do (Levine, Whitwell, and Jeffcott 2005, 94; Bartosiewicz 2008, 154; Thomas et al. 2018; Salmi, Niinimäki, and Poulakka 2020, 50). Even domesticated species have not adequately changed enough through artificial selection to be optimized for human-managed work. Further, many lesions associated with working animals also have other factors such as age, sexual dimorphism, environment, and genetic predisposition that influence their expression and can be misinterpreted as signs of labour exploitation (Upex and Dobney 2012). The frequency and severity of lesions present on non-working animal populations acts as a control sample to compare with animals known to have been worked. The patterns of lesions on non-working animals illustrates what can be expected from normal activity during life. The different lesion frequency and severity shown in known-working animal skeletons, therefore, reflects potential indicators of labour exploitation and those indicators can be looked for on archaeological faunal remains (Flensborg and Kaufmann 2012; Taylor, Bayarsaikhan, and Tuvshinjargal 2015; Thomas et al. 2018).

Some species have been more thoroughly studied for draught, riding, and cargo related lesions than others. Many domesticated species are either not well studied, or lesions have not proven to be effective indicators of working activity. While horses, cattle, and reindeer have received significant attention in paleopathological research, other domestic species such as llamas (*Lama glama*) and dogs (*Canis familiaris*) have been explored to a lesser extent (Defrance 2010; Izeta and Cortés 2006; Latham and Losey 2019; Labarca and Gallardo 2015). Patterns of lesions on the skeleton used to identify one species of draught animal may not work for others and those patterns may be specific to a species, equipment, and the nature of the work done.

Horse skeletons are known to show several pathological lesions related to riding and draught use. Much of the literature has focused on lesions on the cranium, mandible, teeth, and spine (Bendrey 2007; Onar et al. 2012; Taylor, Bayarsaikhan, and Tuvshinjargal 2015; Levine, Whitwell, and Jeffcott 2005). Crania and mandibles may show pathological indicators of working activity associated with the use of bits and with strenuous activity such as running or pulling loads. A bit sits within the diastema of the horse's mouth in the space between the incisors or canines and the premolars. Its presence and movement cause irritation in locations dependant on the type of bit used. A strait-shaped bit sitting on the mandibular diastema has been shown to stimulate new bone formation and bone loss on the dorsal surface of the mandibular diastema in horses from Iron Age Britain (800 BC – CE 100) (Bendrey 2007). Robin Bendrey developed a grading system for quantifying these lesions on the diastema in which "palpable small plaques of new bone formation (discontinuous changes) or continuous slight changes" (value of 2) or any degree of bone loss differentiate between a horse that was bitted and one that was not (2007, 1043–44). These changes may reflect how much rein pressure was used. Similarly, a curb bit has been suggested to cause lesions on the bony palate, sometimes severe enough to cause perforations of the bone as seen in Byzantine horses recovered in Istanbul (Onar et al. 2012).

Bit use also wears and damages the dentition, particularly the mandibular second premolar. A rectangular area of wear of the mesial edge of this tooth (greater than 5mm in height) has been used as an indicator of bit wear as opposed to normal wear from chewing food (Bendrey 2007). A bevel on the mesial-occlusal corner (forward facing margin of tooth towards the plane where the maxillary and mandibular cheek-teeth contact) of this molar may also indicate bit chewing behaviour or intentional rasping (to prevent serious chipping and cracking) but can also result from malocclusion. More pronounced tooth wear could occur if the horse habitually held the bit firmly between its upper and lower teeth causing a worn depression on the occlusal surface of the second premolars (Bartosiewicz and Gál 2013, 134).

Cranial morphological changes have been linked with riding behaviour and exersion as seen in horses in Mongolia (Taylor, Bayarsaikhan, and Tuvshinjargal 2015) and China (Li et al. 2020). Medial and lateral grooves present on the dorsal border of the premaxilla are thought to develop through activity from the muscles and cartilage when flaring their nostrils (Taylor, Bayarsaikhan, and Tuvshinjargal 2015, 859). Similarly, a more pronounced nuchal ligament attachment may develop with increased neck and head movement associated with riding; however, the etiology is complex, with advancing age and increased behavioral stress causing similar developments (Taylor, Bayarsaikhan, and Tuvshinjargal 2015, 857–58).

Horse vertebrae are especially susceptible to lesions caused by pressure from the weight of the rider which can cause osteophytes to develop on the thoracic vertebrae on the lateral and ventral margins of the vertebral body as well as on and adjacent to the articular processes (periarticular osteophytes) (Levine, Whitwell, and Jeffcott 2005). Since the spinous processes carry much of the rider's weight, they develop impinging or overriding distal ends that start to touch and overlap with neighboring spinous processes (Levine, Whitwell, and Jeffcott 2005, 104). The above lesions are also associated with congenital conditions or the natural ageing process; however, riding activity does seem to accelerate these processes (Levine, Whitwell, and Jeffcott 2005). In contrast, horizontal fissures (oriented mediolaterally) on the epiphyses of the vertebral body do not seem to develop naturally in non-working horses (Levine, Whitwell, and Jeffcott 2005, 98). Horizontal fissures are speculated to occur from poorly fitting saddles and jumping the horse while riding (Levine, Whitwell, and Jeffcott 2005, 98).

More extreme occurrences of osteophytes can develop into ankylosis, or fusion, of two or more vertebrae with some severe conditions observed in archaeological equid remains (Onar et al. 2012; Janeczek et al. 2014; Fribus et al. 2019). Nemanja Marković and colleagues (2019) caution against confusing these lesions for Diffuse Idiopathic Skeletal Hyperostosis (DISH), a disease that similarly causes vertebral fusion but does not seem to have an etiology associated with draught use. The way horses were used has a major effect on how pathological conditions may manifest on the vertebrae. As expected, horses used to pull chariots or similar vehicles show lower frequencies of lesions and very few occurrences of horizontal fissures on the epiphyses and impinging spinous processes (Li et al. 2020, 29572). Riding horses can be differentiated from those used to pull chariots through this difference in lesion frequency.

Cattle have an extensive history of draught use by humans. As such, a significant amount of research has focused on identifying osteological evidence of working cattle (Bartosiewicz 2008; Bartosiewicz Van Neer, and Lentacker 1993; 1997; De Cupere et al. 2000; Groot 2005; Holmes, Thomas, and Hamerow 2021; Milisauskas & Kruk 1991; Rassadnikov 2019; Telldahl 2012; Thomas 2008; Thomas et al. 2018, 2021; Thomas & Johannsen, 2011). Indications of draught work include skeletal lesions on the distal limbs, hip joint, horn cores, and first thoracic vertebra. Alternative or complicating factors in developing pathological conditions need to be considered including age, body weight, genetic predisposition, nutrition, environment, shelter, long distance travel, and veterinary care (Telldahl 2012; Holmes, Thomas, and Hamerow 2021; Rassadnikov 2021).

Ring-shaped depressions near the base of horn cores have been interpreted as evidence of yokes being fixed to, exerting pressure, and stimulating adaptive remodelling on the horns (Milisauskas and Kruk 1991; Bartosiewicz, Van Neer, and Lentacker 1997, 12, 72; Bartosiewicz and Gál 2013, 131–32; Thomas et al. 2018). However, similar depressions have been known to develop on the horn cores of non-working cattle. Richard Thomas and colleagues (2018) provide an example of a feral bull at least ten years old at death showing a similar ring-shaped depression. This animal was never worked. The etiology of this lesion may be like "thumbprint" depressions representing localized resorption of bone minerals found on several domesticated and wild bovids (Thomas et al. 2018, 142). A similar impression on the first thoracic vertebra has been suggested to be caused by pressure from yokes that rest over the neck and shoulder (Bartosiewicz, Van Neer, and Lentacker 1997, 12; De Cupere et al. 2000, 255). Unlike horses, vertebral pathological defects are not prevalent in working cattle (Bartosiewicz 2008, 156–57), though twisting deformation of the spine may indicate that animals were part of a team, consistently on either the right or left side of a plough (Upex and Dobney 2012, 199–200).

Cattle naturally have high tendencies towards pathological defects in the distal limbs, especially in the forelimb where approximately two-thirds of their body weight rests (Bartosiewicz, Van Neer, and Lentacker 1993; Bartosiewicz 2008, 160–61). As a result, the metacarpals tend to develop asymmetry more easily (Bartosiewicz, Van Neer, and Lentacker 1993; Groot 2005; Rassadnikov 2019). The skeletal element becomes wider and more robust with a greater mineral density and thicker cortical bone on the medial portion of the diaphysis. This condition develops with advanced age and is intensified by larger body weight and increased physical activity (Bartosiewicz, Van Neer, and Lentacker 1993). Other elements of the distal limbs in cattle are also prone towards pathological defects and lesions, especially the phalanges and metapodials. (Bartosiewicz, Van Neer, and Lentacker 1993; Bartosiewicz 2008, 160–61). These lesions include exostosis, ankylosis, periarticular lipping, and eburnation, and have been observed in draught oxen, feral cattle, and aurochs (Thomas et al. 2021, 88). In cattle that have been used for draught work however, more biomechanical power is needed to propel forward coming from the hindlimbs (Bartosiewicz, Van Neer, and Lentacker 1997, 157; Holmes, Thomas, and Hamerow 2021, 265), especially when gaining initial momentum when pulling a heavy load (Bartosiewicz and Gál 2013, 152). As such, an increased frequency of lesions in hindlimb elements are suggestive of draft cattle (Bartosiewicz 2008, 156, 162; Bartosiewicz and Gál 2013, 152). The Pathological Index method developed by László Bartosiewicz, Wim Van Neer, and An Lentacker (1997) demonstrate this pattern which quantifies the presence and severity of lesions on phalanges and metapodials on an individual, facilitating comparison both within and between populations (see also Holmes, Thomas, and Hamerow 2021). When applied to entire assemblages of faunal remains from archaeological sites, this method reveals larger trends of lesion frequency, severity, and skeletal distribution. However, herd management practices of non-working cattle should be considered. The availability of shelter, travel for pasturing, veterinary care, and diets that encourage fast weight gain also promote development of pathological lesions that overlap with what is seen in draught cattle (Rassadnikov 2021).

The increased severity of work done by the hindlimb is also explored in hip joint disease, developing lesions on the femoral head and acetabulum (Groot 2005; Bartosiewicz, Van Neer, and Lentacker 1997, 12). However, Richard Thomas and colleagues (2021, 85) outline problems with relating hip joint disease to draught work: factors other than draught use contribute to hip joint disease (for example age, sex, body weight, and management practices), such lesions occur infrequently, the elements are often fractured antemortem or postmortem which hinders identification, and only extreme cases are often reported.

Reindeer also work in a variety of activities including pulling sleds, carrying cargo on their backs, riding, and racing (Salmi, Niinimäki, and Pudas 2020; Nomokonova et al. 2020). Vertebral pathological lesions have been found in higher frequencies in working reindeer. In a study involving twenty-six working (pulling, carrying, and racing) reindeer and one hundred and eight non-working reindeer skeletons from Scandinavia and Siberia, the working reindeer scored higher pathological indices for joint disease on the cervical, thoracic, and lumber vertebrae (Salmi, Niinimäki, and Pudas 2020). In these cases, degenerative joint disease was indicated by osteophyte growth on vertebral bodies, articular surface erosion, new bone growth on vertebral processes, and ankylosis between vertebral bodies; warped spinous processes were also observed in this study. Lower cervical and thoracic vertebra showed degenerative joint disease in two Finnish racing reindeer (non-ridden individuals), suggesting that force from the harnesses contributed to the onset of disease on the animals' spines. Reindeer from Siberia that were worked and have known histories had some deformed spinous processes on their vertebrae, possibly caused by asymmetrical harnessing, and osteophytes had developed on the margins of the vertebral bodies (Salmi, Niinimäki, and Poulakka 2020, 51). Riding may have caused these lesions. An individual reindeer ridden by a heavy person is similar example; this animal had ankylosis of four thoracic (T9–12) vertebrae (Salmi, Niinimäki, and Pudas 2020, 63).

Pathological lesions on the distal limb bones, including phalanges, metapodials, and calcanei have been identified as indicators of working reindeer. The Pathological Index has been applied to the analysis of lesions on reindeer phalanges and metapodials and was expanded to record vertebral, coxal, and long bone lesions as well (Salmi, Niinimäki, and Pudas 2020, 60). For individuals from Northern Scandinavia and Siberia that were known to have pulled sleds, the authors found that the forelimb phalanges showed greater pathological changes such as exostoses and lipping compared with the hindlimb (Salmi, Niinimäki, and Pudas 2020; Salmi et al. 2021, 6; Nomokonova et al. 2020).

Additionally, an irregular new bone growth on the caudal side of a reindeer calcaneus from Iarte VI, located in the Iamal Peninsula of Arctic Siberia, may have been caused by a work-related injury (Nomokonova et al. 2020). Although the cause in this case is not certain, the calcaneus can be injured by a sled running accidentally into the back of the leg. Anna-Kaisa Salmi, Sirpa Niinimäki, and Tuula Pudas (2020, 61) also saw a high occurrence of calcaneus and talus lesions, but only a relatively small sample (4 individuals) of those elements were available.

Other domesticated animals used for draught work in Siberia have either not received as much attention or have been found not to have strong pathological indicators of work. For dogs for instance, no such connections between labour and pathological lesions have been found that adequately differentiate working and non-working individuals. Katherine Latham and Robert Losey (2019) investigated whether a greater frequency of spondylosis deformans is experienced by sled dogs; however, this disease was found to be multifactorial and happened at similar frequencies in sled dogs and wolves, with a slightly greater occurrence in non-transportation dogs.

Although no studies identify working camels using osteological lesions, llamas used for carrying cargo in the Andes have been found to have increased frequencies of lesions on phalanges (forelimb and hindlimb) and vertebrae compared to non-working camelids

(Izeta and Cortés 2006; Defrance 2010; Labarca and Gallardo 2015).

As demonstrated, paleopathology of draught animals provides promising value for identifying working animals and investigating the nature and intensity of animal labour exploitation. In all cases, it is crucial to remember that many of the lesions associated with work have complex etiologies related to age, sex, nutrition, trauma, genetic susceptibility, and other factors (Thomas et al. 2018). This is often addressed using comparison between lesions frequencies on working and non-working animals, as labour exploitation can exaggerate conditions occurring with age (Levine, Whitwell, and Jeffcott 2005). Although the number of domesticated species investigated in the literature is limited, existing methods and general trends can be adapted to other species to provide insight into the occurrence and intensity of draught, riding, and cargo animals from archaeological contexts.

RESEARCH ON ENTHESEAL CHANGES IN WORKING ANIMALS

Researchers seek to reconstruct physical activity in zooarchaeological remains to identify changes in human-animal relations throughout history. As demonstrated above, examining paleopathological markers on faunal remains has been helpful to locate domestication-related activities in the archaeological record (e.g., Bartosiewicz, Neer, and Lentacker 1997; De Cupere et al. 2000; Telldahl 2012). However, identification of more specific physical activities would require further study of muscle use and its various effects on skeletal remains. Instead, researchers use variations to entheses–attachment sites for muscles, tendons, and ligaments on bone–called entheseal changes (EC) to identify more specific physical activity patterns in human and faunal remains (Jurmain et al. 2012; Salmi and Niinimäki 2016). EC have a multifactorial etiology, meaning that there are other factors such as age, sex, body size, and population genetics that influence entheseal morphology and complicate our interpretations (Benjamin et al. 2002; Henderson et al. 2017; Jurmain et al. 2012).

Examining the effect of physical activity on EC and other non-pathological skeletal morphologies requires researchers to utilize methodologies under the concept of bone functional adaptation, formerly known as Wolff's Law (Ruff, Holt, and Trinkaus 2006; Wolff 1986). This concept is understood as "form follows function," meaning that trabecular and cortical skeletal tissue remodels over time to disperse mechanical loading forces (Benjamin et al. 2006; Ruff, Holt, and Trinkaus 2006). Essentially, mechanical overloading causes microdamage to musculoskeletal tissue and stimulates bone cells into osteoblastic (bone-forming) and osteolytic (bone-reducing) activity, continuing this process through stages of growth, destruction, and maintenance over time (Benjamin et al. 2006; Ruff, Holt, and Trinkaus 2006).

In this case, entheses act to dissipate mechanical stress across the hard-soft tissue boundary when muscles contract to create movement, which distributes force more efficiently (Benjamin et al. 2002; 2006). The transfer of strain is essential for minimizing the risk of damage such as tearing and avulsion fractures in which the soft tissue is pulled away from the bone (Benjamin et al. 2002; Ruff, Holt, and Trinkaus 2006). The structures surrounding the enthesis, such as bursae and fat pads, are also part of an "organ complex," as they assist in dissipating mechanical stress and thus are also affected by the same factors that influence entheseal morphology (Benjamin and McGonagle 2009). Entheses are split into two histological types, fibrous (FE) and fibrocartilaginous (FCE), varying in shape and size depending on their attachment sites (Benjamin et al. 2002; 2006). It is essential to acknowledge the two types of entheses because their histology and attachment angle affect their morphological appearance differently, therefore impacting their interpretation through EC analysis (Villotte et al. 2010; Henderson et al. 2017).

EC, formerly known as musculoskeletal stress markers (Hawkey and Merbs 1995), are non-pathological reflections of bone formation and destruction that can vary from osteophytic activity producing roughness, bony crests, ridges, and enthesophytes or osteolytic formations like erosions, cavitations and macro- and microporosity (Foster, Buckley, and Tayles 2014; Hawkey and Merbs 1995; Henderson et al. 2017). EC methods work under the concept of bone functional adaptation, which defines how skeletal architecture remodels over time to disperse mechanical loading more efficiently (Wolff 1986; Ruff, Holt, and Trinkaus 2006). In other words, microdamage at the hard-soft tissue boundary on entheses encourages blood flow and bone cell activity that alters its shape, size, and appearance (Jurmain et al. 2012). Under this assumption, EC that have more morphological changes are attributed to higher physical activity levels. However, this does not imply that individuals showing little to no EC did not participate in activities, as the etiology of EC is multifactorial (for a more detailed summary of human EC research, see Sick 2021).

The first methods developed to study EC in the 1980s and 1990s were observational. In 1995, Dianne Hawkey and Charles Merbs created the first method intended for widespread use, visually scoring three EC features using a three-point ordinal scale. This protocol and others in the early 2000s (e.g., Mariotti, Facchini, and Belcastro 2004; 2007) have since been criticized for failing to integrate clinical literature, having poor intra and interobserver error, and their simplistic interpretations regarding physical activity given new knowledge on the multifactorial etiology of EC (Jurmain et al. 2012; Villotte et al. 2010). The most up-to-date scoring protocol, called the Coimbra method (Henderson et al. 2013; 2017), was adapted from previous works (Mariotti, Facchini, and Giovanna Belcastro 2004; 2007; Villotte et al. 2010) and intended for fibrocartilaginous entheses only, split into two Zones. Zone 1 is the thin margin of the enthesis reflecting the most oblique angle of soft tissue, and Zone 2 is essentially the rest of the entheseal surface (Henderson et al. 2013; 2017). Additionally, this method considers the impact of age, sex, and body size on EC by using multivariate statistics, allowing for higher observer reliability (Henderson et al. 2013; 2017).

Observational methods have some drawbacks, namely the influence of human subjectivity on observer bias and the low statistical power of ranked scoring systems, which reduces observer error and negatively impacts the detection of statistical patterns (Nolte and Wilczak 2013). A recent workaround is to apply quantification protocols that use 2D and 3D technology to examine the shape and size of entheses to identify EC patterns, due to having high precision and low observer error (Sick 2021). However, these methods are expensive (e.g., Nolte and Wilczak 2013; Nikita et al. 2019). Quantification studies have proven helpful in examining the direct link between EC and activity in experimental animal models (e.g., Zumwalt 2006; Rabey et al. 2015; Wallace et al. 2017; Turcotte et al. 2022), and more recent applications in archaeological remains (e.g., Karakostis et al. 2021). However, the first visual methods explicitly created for non-human animals weren't considered until recently (e.g., Bindé, Cochard, and Knüsel 2019; Salmi and Niinimäki 2016; Niinimäki and Salmi 2016; Salmi, Niinimäki, and Pudas 2020; Niinimäki and Salmi 2021. See Table 1 for summary).

Niinimäki and Salmi (2016) and, later, Salmi and Niinimäki (2016) explore the effect of a visual EC method modified from Villotte (2010) and the Coimbra method (Henderson et al. 2013; 2016). The first study examined pathological lesions and EC on four male reindeer with known life histories of racing, riding, and pulling sleds (Niinimäki and Salmi 2016). Though the sample size was too small to draw links between activity in this case, the authors' later publication expanded their study to twenty five male and female zoo reindeer and twenty-eight free-ranging males and females using the same modified scoring protocol (Salmi and Niinimäki 2016). They found that the elbow flexors in larger male free-ranging reindeer showed higher EC scores than the zoo reindeer, which they attributed to differences in feeding behaviour (Salmi and Niinimäki 2016). For example, free-ranging animals repeatedly dug through the snow to eat lichen throughout the winter, whereas humans fed zoo reindeer through the cold months, effectively negating this behavior (Niinimäki and Salmi 2016). The authors also found zoo reindeer with more EC in the subscapularis, where such an attachment is associated with engaging their shoulder bracing apparatus for standing still over long periods (Hull, Niinimäki, and Salmi 2020).

Salmi, Niinimäki, and Tuula Pudas (2020) applied the same scoring method to twenty six working reindeer used for pulling, riding, and racing and fifty non-working reindeer in a more extensive study. Working reindeer found higher scores for the triceps brachii attachment (proximal humerus), which works to pull body weight over the shoulder joint, affecting this muscle when bearing additional weight (Salmi, Niinimäki, and Pudas 2020). In the hindlimb, EC scores of the proximal femur (especially the vastus lateralis and quadriceps femoris, responsible for hip and knee flexion) were significantly higher in working reindeer, attributed to the range of motion required for greater speed in racing. Overall, they found higher EC scores in working reindeer on muscle attachments used to extend and flex the shoulder, hip, and knee joints, possibly inferring to various activities involving pulling, carrying, and racing (Salmi, Niinimäki, and Pudas 2020).

Though reindeer are the primary species examined in non-human EC research, Marion Bindé, David Cochard, and Christopher Knüsel (2019) expanded these studies to equids by analyzing the remains of thirty nine captive but non-working horses, donkeys, and zebras using protocols modified from Villotte (2010), the Coimbra method (Henderson et al. 2013; 2017), and the method by Salmi and Niinimäki (2016; Bindé, Cochard, and Knüsel 2019). These animals were unworked, as this study aimed to establish a baseline for entheseal variation and the influence of age and sex on EC in the appendicular skeleton by ranking EC into categories of A, B, and C (Bindé, Cochard, and Knüsel 2019). Like reindeer, the results showed both age and sex to be significant confounding biological variables. Older individuals (16 or older) typically increase in B and C scores in some entheses, with one exception being a ligament on the second phalanx (Bindé, Cochard, and Knüsel 2019). In contrast, other muscle insertion sites on bone showed no changes among all age sites. These include the biceps brachii, flexor digitorum superficialis, triceps brachii, and the medial collateral ligament of the posterior proximal phalanx (Bindé, Cochard, and Knüsel, 2019). As for sex differences, males showed higher EC frequencies except for flexor digitorum superficialis on the femur and the medial collateral ligament on the posterior proximal phalanx (Bindé, Cochard, and Knüsel, 2019). Interestingly, neither age or sex affected two entheses on the humerus and showed only slight variation, indicating that these attachments may be a valuable indicator of activity in zooarchaeological remains (Bindé, Cochard, and Knüsel, 2019).

In terms of confounding factors affecting EC morphology, age, sex, and body size were found to have significant effects in non-human studies on reindeer and equids, albeit in different ways considering anatomical differences between species. Age was a significant contributor to EC morphology in all these studies, though this variable had to be metrically estimated in three of them (Bindé, Cochard, and Knüsel 2019; Niinimäki and Salmi 2021; Salmi, Niinimäki, and Pudas 2020). Human EC studies note that entheseal degeneration in older individuals tend to be greater, which may be caused by overall reduction in physical activity and osteoblast reduction due to the natural aging process (Henderson et al., 2017). In addition, the accumulation of muscle use, mechanical overloading, and acute events of physical trauma through the years may also explain these findings (Villotte et al., 2010). Since age seems to have a similar impact on equids and reindeer, Bindé, Cochard, and Knüsel (2019) caution the inclusion of older estimated individuals where age is unknown since this can bias EC analysis. Additionally, body size was a significant contributor, where all studies had EC score distributions favouring larger males (Bindé, Cochard, and Knüsel 2019; Niinimäki and Salmi 2016; Salmi and Niinimäki 2016; Salmi et al. 2021). Although multivariate analysis is helpful in separating the influence of these factors on entheseal morphology, there are other limitations when considering their impact on reindeer and equids. For instance, the intertwined nature of sexual dimorphism and body size in non-human studies is still debatable in terms of entheseal morphology (Bindé, Cochard, and Knüsel, 2019; Niinimäki, 2012). Niinimäki and Salmi (2021) note that measurements to estimate sex in reindeer are biased with weight estimation because of sexual dimorphism, suggesting that assessment of sex reflects body size rather than hormonal differences. Additionally, males in two reindeer studies (Niinimäki and Salmi 2021; 2016) were castrated, whereas others were not. Despite the observation that all larger-bodied individuals were exclusively male, hormonal differences in this sample may have unknown effects on EC variation (Niinimäki 2012).

Some other potential influences when adapting EC methods to non-humans could include differences in average lifespans between species or effects of bipedal versus quadrupedal locomotion on EC (Ruff, Holt, and Trinkaus 2006). Moreover, anatomical differences from humans seem to reflect EC

Article	**Species**	**Sex**	**Age**	**Life Histories/known activities**	**Total # of ind. used**
Salmi and Niinimäki (2016)	*Rangifer tarandus*	Male	5.5 to 11-13 years	Pulling sleds, carrying loads, riding	**4**
Niinimäki and Salmi (2016)	*R. tarandus*, *R. fennicus*, and hybrids (*R. tarandus x R. fennicus*)	Male (18), Female (36)	2-10 years, average age 3.5-4.5 years	2 working (pulling, carrying and racing) and 51 nonworking	**53**
Salmi, Niinimäki, and Pudas (2020)	*R. tarandus*, *R. fennicus*, hybrids	Male	3-10 years	26 Working (pulling, carrying, and racing) and 50 nonworking	**81**
Niinimäki and Salmi (2021)	*R. tarandus*, *R. fennicus*, hybrids	Male, Female	2-10 years, average age 3.5-4.5 years	Nonworking	**53**
Bindé et al. 2019	*Equus caballus*, Prezwalski's horses (*E. caballus prezwalski*) donkey (*E. Asinus*), mule (*E. asinus x E. caballus*), zebra (*E. greyvi, E. burchelli*)	Male (20), Female (19)	50 days to >20 years	Nonworking	**39**

Table 1–*Summary of EC research in non-human animals (Source: Created by Jessica Sick 2022)*

variation differently, supported by observations of some fibrocartilaginous entheses on horses and reindeer reflecting greater normal variability than expected in humans (Benjamin, Evans, and Copp 1986; Bindé, Cochard, and Knüsel 2019). For instance, the amount of expected EC reflecting bone resorption was observed less in non-humans compared to human studies, again indicating that EC differ between species (Bindé, Cochard, and Knüsel 2019; Niinimäki and Salmi 2021)

Despite these contradictory factors, the application of EC methods to reindeer and equids reveals some benefits in terms of reconstructing patterns of activity compared to humans. For one, EC research tends to reflect the overall intensity and duration of mechanical loading on entheses, which is then attributed to more specific physical activities (Lieverse et al. 2013). These activities are easier to analyze in working animals because said work is better described, more specific, and typically lifelong (Salmi et al. 2021). For example, reindeer used for pulling sleds usually begin working before adulthood and typically perform such work throughout life, whereas human occupations are more difficult to track due to their high variability in EC literature (Alves Cardoso and Henderson 2013; Salmi et al. 2021). Overall, EC studies in non-humans have shown merit in reconstructing past activity in working animals. Future research will allow studies to compare wild and domesticated animals of the same species to pinpoint milestones in human change, such as human migration and cultural transitions from hunting and gathering to agriculture or pastoralism (Salmi et al., 2021). In addition, these studies may also reveal transitions in human-animal interactions regarding how they train, work, and breed livestock, indicating broader social or economic changes

CROSS-SECTIONAL BONE GEOMETRY AND BONE BIOMECHANICS IN WORKING ANIMALS

Although EC can indicate more specific activities, CSBG analysis in long bones has an extensive history and better understood methodology and association with activity. (Jurmain et al. 2012; Ruff, Holt, and Trinkaus 2006). In animals, a cross-sectional study has also shown direct associations between bone plasticity and its response to human-controlled activities in donkeys (Shackelford, Marshall, and Peters 2013). In addition, new research on types of human-raised and wild reindeer populations in the North has extended the use of CSBG methods to not only evaluate the efficacy of EC scoring methods (Niinimäki and Salmi 2021) but to demonstrate its potential as a valuable indicator of changes in human-animal relations over time (Pelletier Niinimäki, and Salmi 2021).

Pelletier, Niinimäki, and Salmi (2021) argue that quantification analysis such as 2D-geometric and morphometrics can compare CSBG properties between species to identify differing impacts of locomotion on bone structure, including parameters such as body size, sex, and habitual activity. Their study examined the cross-sections of eighty nine free-range, twenty eight non-working, and twenty working male and female reindeer, noticing some interesting trends. They found non-working reindeer and free-ranging reindeer (captive during the winter) had increased body mass, decreased body size, and thicker cortical cross-sections than wild reindeer. The authors attributed this to differences in feeding and locomotion behaviour, such as wild reindeer foraging through the snow for lichen or captive reindeer requiring more body support for standing still for long periods (Pelletier, Niinimäki, and Salmi 2021; Niinimäki and Salmi 2016; Hull, Niinimäki, and Salmi 2020). This behaviour typically begins in adolescence, when bone growth is the most susceptible to activity (Jurmain et al., 2012; Niinimäki and

Salmi, 2021). The authors argue that future studies using CSBG in juveniles could prove a helpful tool for reconstructing activity (Pelletier, Niinimäki, and Salmi 2021).

Given the intertwined nature with CSBG and EC in bone functional adaptation and our better understanding of CSBG properties, authors have used CSBG in human EC studies to understand better their covariation with activity, as well as to test the efficacy of EC methods (Niinimäki 2012; Michopoulou, Nikita, and Henderson 2017; Michopoulou, Nikita, and Valakos 2015). Niinimäki and Salmi (2021) explored the covariation in reindeer by analyzing the cross-sections and EC of 50 wild forest, domesticated free-range, and zoo reindeer. They found that bone formation on almost every examined enthesis was positively associated with CSBG values, further establishing their relationship from previous studies on humans (Niinimäki and Salmi 2021; Pelletier, Niinimäki, and Salmi 2021). Additionally, they found that entheses on the humerus effectively separated different groups of reindeer based on activity levels that size nor age could entirely account for, implying activity as a possible underlying factor causing these observations (Niinimäki and Salmi 2021; Salmi, Niinimäki, and Pudas 2020). They also noticed translation on entheseal variability from humans to reindeer might also cause false rejections or acceptances of an enthesis in its link to activity based on visual observation, reflecting the same concerns as Bindé, Cochard, and Knüsel (2019) (Niinimäki and Salmi 2021). To counter this, they suggest using methods specific to each enthesis and always considering potential cross-species differences. The authors also stress that these results are tentative due to their indirect interpretive nature, considering the multifactorial etiology of EC and its association with CSBG values. However, they are optimistic in using these methods and encourage future research of this type to consider CSBG as a supporting or alternative method to reconstruct activity among non-humans.

CONCLUSION

There are multiple different pathways to explore observable morphological changes in faunal skeletal remains to reconstruct human-animal relations. Paleopathological markers such as vertebral fusion or exostoses in the limbs and hip joints can indicate pulling and riding activities in reindeer, horse, and cattle. Some markers are more specific to the working lives of certain species, such as cranial shape and tooth wear in horses from bridles and bits, or indentations in the horn cores of cattle. Non-pathological indicators based upon bone functional adaptation such as EC and CSBG have been well-demonstrated in human skeletal remains, but only recently applied to horse and reindeer. Observational studies applying a new EC method in free ranging and zoo reindeer showed different EC patterns in the forelimb and shoulder, attributed to differences in wild feeding behaviour and low mobility in captivity. Additionally, the new observational scoring protocol by Bindé, Cochard, and Knüsel in 2019 using EC on unworked equids serves as a useful baseline for future studies identifying working activity in equid skeletal remains.

However, researchers must also consider other influences of faunal skeletal morphology besides activity, as their etiology is multifactorial. EC expression in both working and non-working reindeer and equids tend to be highest in older, larger males due to the confounding effects of age, sex and body size on EC morphology. Additionally, these factors seem to affect skeletal morphology differently between species. Pathological lesions are naturally more prevalent in draught cattle and appear more frequent in working horse and reindeer, whereas a study examining the same connection in dogs failed to find similar patterns (Latham and Losey 2019; Levine, Whitwell, and Jeffcott 2005; Salmi, Niinimäki, and Pudas 2020; Telldahl 2012). This type of research can help to reveal new insights into the integrated nature of daily human-animal interactions and its impact on long-term changes in skeletal morphology. The presence of domesticated animals such as horse and reindeer in archaeological sites do not directly imply that these animals were worked unless accompanied by supplementary material or ethnographic data, only that they lived their lives alongside—or adjacent to—humans. Examination of EC and CSBG values may further reveal information regarding their roles in daily life, such as whether they were exclusively used for certain tasks such as carrying and pulling loads or had a more flexible and varied life histories. By integrating statistical protocols, experimental animal models, and additional biomechanical data such as CSBG, researchers have been able to demonstrate more clear links between physical activity and skeletal morphology in working animals. Future research of this type is encouraged to further benefit studies examining human-animal relationships using faunal skeletal remains..

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