



Covariation between enthesal changes and cross-sectional properties of reindeer long bones – Considering bone functional adaptation as partial contributing factor

Sirpa Niinimäki^{*,1}, Anna-Kaisa Salmi²

History, Culture and Communication Studies, University of Oulu, Finland

ARTICLE INFO

Keywords:

Reindeer
Rangifer tarandus tarandus
Rangifer tarandus fennicus
Physical activity
Bone biomechanical properties

ABSTRACT

Enthesal changes and bone cross-sectional properties are used as skeletal activity markers for different animal species, although most studies are targeted on humans. While there is compelling evidence on the association between activity and bone cross-sectional properties, studies on association of enthesal changes to activity have presented more contradictory results. In previous research, covariation between enthesal changes and bone cross-sectional properties is considered a possible result of common underlying factor. However, these studies are performed predominantly on human material. We provide beyond-species scope by studying this covariation in reindeer skeleton. The results will provide platform for discussing bone functional adaptation pathway in which activity modifies enthesal appearance. The material are wild forest reindeer, domesticated free-ranging reindeer and zoo reindeer of Northern and North-East Finland. We found that bone formation in most studied entheses (25 out of 27) were associated with increased values in bone cross-sectional properties and proxies of bone/body size. Features of bone resorption, when significant, were also associated with increased values in bone cross-sectional properties and bone/body size. We conclude that as enthesal changes were associated with bone cross-sectional properties and bone/body size, the observed variation at reindeer entheses likely reflects skeletal robusticity. While causal factors resulting in association between skeletal robusticity and enthesal appearance cannot be evidenced, bone functional adaptation can be hypothesized as at least a partial contributing mechanism to enthesal appearance.

1. Introduction

Physical activity reconstruction through skeletal changes such as changes in muscle attachment sites (entheses) and bone cross-section properties hold great potential for the analysis of past everyday life, subsistence activities and identities in human osteology (e.g., Hawkey and Merbs, 1995; Churchill and Morris, 1998; Molnar, 2006, 2010; Jurmain et al., 2012). In animals, physical activity reconstruction can contribute to the analysis of draught animal use as well as animal feeding and mobility patterns (Shackelford et al., 2013; Niinimäki and Salmi, 2016). However, the use of these methodologies has been hindered by methodological and etiological uncertainties (Jurmain et al., 2012). For instance, what contributing factors do these different skeletal changes reflect and how do they relate to each other?

Enthesal changes – then called musculoskeletal stress markers – were originally considered to reflect stress directed to bones via muscle use in intensive physical activity (Hawkey and Merbs, 1995) by means of changes in bone robusticity and stress lesions at an enthesis. This was based on the observation that there were substantial differences in the manifestation of entheses and ligament attachment of the upper limb between human populations of different subsistence strategies (Hawkey and Merbs, 1995). The method published by Hawkey and Merbs (1995) was originally intended for observing those muscle and ligament attachments presented in the paper, but the method was soon applied on other entheses as well (e.g. Churchill and Morris, 1998; Weiss, 2003, 2007; Molnar, 2006, 2010). There was further confusion with application of the method when stress lesions were not considered separately but as a continuum to bone robusticity (stress beyond robusticity), or

* Corresponding author at: History, Culture and Communication Studies, P.O. Box 1000, 90014, University of Oulu, Finland.

E-mail address: sirpa.niinimaki@oulu.fi (S. Niinimäki).

¹ 0000-0001-9510-5259.

² 0000-0002-0745-385X.

summed, but not investigated separately appreciating potentially different underlying promoting factors. This in addition to several bias factors – potentially partially resulting from combining robusticity and stress lesions (Foster et al., 2014) – and unproven relationship of the changes to physical activity resulted in severe critique against the method. The method was found to be affected by age (Weiss, 2003; Niinimäki, 2011; Alves-Cardoso and Henderson, 2010; Michopoulou et al., 2015; Godde et al., 2018) and body size (Churchill and Morris, 1998; Niinimäki, 2011; Weiss et al., 2010; Michopoulou et al., 2015; Godde et al., 2018). Several other methods were created for observing changes at entheses attempting to circumvent some of the problems (Robb, 1998; Mariotti et al., 2004; Zumwalt, 2005; Galtés et al., 2006). A new aspect on enthesal studies was presented by Villotte (2006), where he stressed that, drawing from clinical literature, the type of muscle-bone attachment – fibrous or fibrocartilaginous – should be considered in the method. In 2009 a workshop was established by researchers focused on enthesal studies in a meeting in Coimbra, Portugal to create a new standardized method appreciating the state-of-the-art understanding of entheses (Henderson et al., 2010, 2013). Variability captured by the different entheses scoring by these methods as well have been associated with age (Villotte, 2006 method in Villotte et al., 2010; Mariotti et al., 2004 method in Milella et al., 2012; Coimbra method in Acosta et al., 2017), which indicates that age is a considerable contributing factor for entheses appearance, regardless of observation method. In addition to difference in muscle-bone attachment, there is also a distinction in the features that are scored at the entheses.

Features scored at the entheses – bone formation or bone resorption – have received varying attention in methodological studies. First studies used either a continuum from bone formation to bone resorption (emphasizing thus bone resorption) or a summed score of bone formation and bone resorption scores. After the work of Coimbra workgroup focus has shifted to bone resorption over bone formation, and fibrocartilaginous entheses over fibrous entheses as the most promising trait for observing activity. However, Foster et al. (2014) contributed to balance this discussion by focusing on bone formation (as bone robusticity) reviewing literature on anatomy and functional anatomy of entheses. Foster et al. (2014) formulated that features observed at entheses are bone robusticity, which is considered normal adaptation, and enthesopathies as abnormal modification, including cortical defects in form of erosion, porosity, and cavitation (Foster et al., 2014, cf. Drapeau, 2008, Mariotti et al., 2004, and Milella et al., 2012). These two modifications may have different etiologies and should therefore be studied separately, a point emphasized in both Villotte and Knüsel (2013) in addition to Foster et al. (2014). In this paper we consider indirect evidence of bone functional adaptation as potential causal factor for both of these changes at entheses, but we use terms “bone formation” and “bone resorption” as term “enthesopathy” already indicates pathological origin and bone functional adaptation would therefore not be expected to contribute to entheses appearance.

Bone cross-sectional properties – robusticity and shape – are used as skeletal activity markers, where the association between physical activity and bone diaphyseal strength and shape has been evidenced more conclusively on empirical data (i.e., Stock and Shaw, 2007; Nikander et al., 2009; Niinimäki et al., 2017, 2019). Activity reconstructions from bone cross-sectional properties are based on beam theory (Lieberman et al., 2004; Ruff et al., 2006; Stock and Shaw, 2007) and mechanostat theory (Frost, 1987; Turner, 1998; later refined into concept of functional muscle-bone unit by Schoenau and Frost, 2002, and bone functional adaptation by Ruff et al., 2006). The former explains changes in cross-sectional shape as modifications of external dimensions of bone shaft towards the principal or usual direction of stress, as the bone is strongest in the direction where the bone surface is furthest away from the cross-section centroid (Forwood and Burr, 1993; Ruff et al., 2006; Shaw and Stock, 2009). Bone is adapted to “normal/usual” level of mechanical loading with removal or accrual of bone mass with changing levels of mechanical loading. This allows bone build-up to usual

direction of stress while bone mass is reduced in those directions not under osteogenic loading. Furthermore, muscle loading can arguably provide localized osteogenic signals (Niinimäki et al., 2013b, see also Judex and Carlson, 2009). While loading from atypical direction is more osteogenic (Lanyon, 1987), this would be evident in bone robusticity rather than shape indicators (Niinimäki et al., 2017, 2019). The latter, bone functional adaptation, explain changes in bone robusticity with activity, as mechanical loading comes in terms of gravitational and muscle loading (Lanyon and Rubin, 1984; Frost, 1987; Lanyon, 1987, 1996; Heinonen et al., 2002; Judex and Carlson, 2009; Robling, 2009), where gravitational loading seems to be more important than muscle loading for adding bone mass (Niinimäki et al., 2019). In addition, loading frequency and magnitude of loading contribute to bone robusticity (Lanyon and Rubin, 1984; Lanyon, 1987, 1996; Umemura et al., 2002; Ruff et al., 2006; Nikander et al., 2009; Niinimäki et al., 2017, 2019). Body weight provides intrinsic loading on bones (Seeman et al., 1996; Schiessl et al., 1998; Ruff, 2000; Schoenau and Frost, 2002; Brianza et al., 2007), where bone tissue is distributed proportionally further from the cross-sectional centroid with increased body mass (Brianza et al., 2007). Thus, controlling for body size effects on bone robusticity is crucial before inferring activity.

In lack of direct evidence on promoting factors for enthesal appearance, such as longitudinal studies on modification of entheses to different types of activity (loading), several studies have investigated the association between enthesal changes and bone cross-sectional properties, hypothesizing that should there be an association, it may be because of common underlying promoting factor. The relationship between these two skeletal activity markers has been studied with mixed results. Using Hawkey and Merbs (1995) method a relationship has been found between aggregated muscle marker scores and bone cross-sectional properties (Weiss, 2003; Niinimäki, 2012), while single muscle entheses were associated rarely and exhibiting no clear overall patterns (Bridges, 1997; Weiss, 2003; Michopoulou et al., 2015). In addition, Ibáñez-Gimeno et al. (2013) found an association between enthesal changes and bone strength in humerus. Enthesal scores observed using methods by Mariotti et al. (2004), Villotte et al. (2010) and “Coimbra” method as published in Henderson et al. (2010) and Henderson et al. (2013) have not been associated with increased bone cross-sectional properties (Michopoulou et al., 2017). Foster et al. (2014) criticized that studies combining (continuum or summed) robusticity and stress lesion/enthesopathy scores may be misleading as similar etiology should not be assumed. In this paper we study this association between bone formation in reindeer skeleton based on methodology presented in Niinimäki and Salmi (2016) and bone resorption (erosion, porosity and cavitation), observations based on methodology presented in Henderson et al. (2010) and Henderson et al. (2013) for human entheses. Reindeer entheses have been associated with feeding behavior (i.e. intensity of digging for lichen from under the snow; Niinimäki and Salmi, 2016) and draught or cargo use (especially when combined with palaeopathological analysis; Salmi and Niinimäki, 2016; Salmi et al., 2020). Furthermore, long bone cross-sectional properties are indicative of different activity patterns in the reindeer (Niinimäki et al., submitted). Our aim is to study the variation (bone formation and resorption) in reindeer entheses in relation with bone cross-sectional properties and in relation with bone/body size. The results of this study provide valuable information in the relationship between enthesal changes and bone cross-sectional properties beyond human species and allow hypothesizing on potential common underlying contributing factors. This study will also contribute to the understanding the relationship of reindeer skeletal changes and physical activity, allowing methodology to be used to enhance our understanding of reindeer domestication and past reindeer herding practices.

2. Material and methods

The material are Finnish reindeer (including wild forest reindeer

Rangifer tarandus fennicus, free-ranging reindeer *Rangifer tarandus tarandus*, and zoo reindeer of both subspecies and their hybrids; Table 1) housed at the Zoological Museum, Biodiversity unit, in the University of Oulu. The sample does not come with complete context information regarding age, sex and weight. Unfortunately, features available for age estimation, such as epiphyseal fusion, provided only “at least” -ages denoting skeletal maturity whereas skeletal element allowing estimating age after reaching skeletal maturity, such as dental attrition, were not available for this sample. As for sex, splitting the sample based on sex would have reduced significantly to allow for robust statistical analyses to be performed. Furthermore, as metric estimations of sex have been noted to bias with weight estimation due to sexual dimorphism in reindeer (Puputti and Niskanen, 2008) estimated sex would have been rather an estimate of size and not, for example, representative hormonal effects on the relationship between EC and bone cross-sectional properties between the sexes. No other sex estimation methods were

applicable to this sample. Body size has been found to associate with bone cross-sectional properties as well as entheses, therefore the association of EC with body weight was investigated. Body weight was used, when known. When necessary, weight was estimated based on the correlation between long bone lengths and weight (Puputti and Niskanen, 2008). These equations used have been derived from this material using those individuals with existing weight information (Puputti and Niskanen, 2008).

It should be noted, however, that some of the individuals on which the weight estimation equations are based had died of starvation, the material may not be representative of true weights of the individuals. Furthermore, the weight of a reindeer depends on what part in the yearly life cycle the individual had died, body weight being greatest in the Autumn and lowest in the Spring. Therefore, we also calculated bone element sizes to circumvent these problems. Bone cross-sectional properties scale to body size, and often used proxy is weight (Ruff et al.,

Table 1
Bone elements per individual.

Individual	Humerus	Radioulna	Metacarpal	Femur	Tibia	Metatarsal	Subspecies
5371	x	x	x	x	x	x	Tarandus
12099			x			x	Tarandus
12758	x	x	x				Tarandus
17987				x	x	x	Tarandus
17988	x	x	x				Tarandus
17989	x	x	x				Tarandus
17990		x	x			x	Tarandus
17991				x	x	x	Tarandus
17992	x	x		x	x	x	Tarandus
17994	x	x	x	x	x	x	Tarandus
18603	x	x	x	x	x	x	Tarandus
21258		x					Fennicus
21263	x	x	x	x	x	x	Tarandus
21275				x	x	x	Fennicus
22069	x	x	x	x	x	x	Fennicus
22070	x	x	x	x	x	x	Fennicus
22071	x	x	x	x	x	x	Fennicus
22073	x	x	x	x	x	x	Fennicus
22078			x			x	Fennicus
23942	x	x	x	x	x	x	Fennicus
23944				x	x	x	Fennicus
23945		x	x	x	x	x	Fennicus
24047	x	x	x		x	x	Fennicus
24048	x	x		x	x	x	Fennicus
24050	x	x	x	x	x	x	Fennicus
25006	x	x	x	x	x	x	Fennicus
25410	x	x		x	x	x	Hybrid*
25853	x	x		x	x	x	Tarandus*
26382	x	x	x	x	x	x	Tarandus*
26383	x	x	x	x	x	x	Hybrid*
26384	x	x	x	x	x	x	Hybrid*
26385	x	x	x	x	x	x	Tarandus*
26386	x	x		x	x	x	Tarandus*
26525	x	x	x	x	x	x	Tarandus*
26678	x	x		x	x	x	Fennicus
27029	x	x	x	x		x	Fennicus
27597	x	x	x	x	x	x	Fennicus
27794	x	x	x	x	x	x	Hybrid*
27819	x	x		x	x	x	Unknown
27824	x	x		x	x	x	Hybrid*
27825		x	x		x	x	Fennicus*
27829	x	x	x	x	x	x	Tarandus*
27840	x	x		x	x	x	Fennicus*
27850		x	x	x	x	x	Hybrid*
27854	x	x		x		x	Tarandus*
27963	x	x	x	x	x	x	Fennicus
28012	x	x		x	x		Hybrid*
28058	x	x	x	x	x	x	Fennicus*
28061	x	x	x	x	x	x	Hybrid*
28452	x	x	x	x	x	x	Tarandus*
28453	x	x	x	x	x	x	Tarandus*
28467	x	x		x	x	x	Hybrid*
32327	x	x	x	x	x	x	Fennicus*

* Zoo individual.

1994; Seeman et al., 1996; Schiessl et al., 1998; Schoenau et al., 2000; Schoenau and Frost, 2002; Parfitt, 2004), sometimes height (Feik et al., 1996) or a product of (reconstructed) body weight, and muscle moment arm length (Ruff, 2000, Ruff, 2003). However, body size is a multidimensional concept, and thus we created a size variable that would capture the multi-dimensional nature of body size (after Niinimäki et al., 2017, 2019). We performed a principal component analysis (PCA) for the following measurements: for humerus interarticular length (Niinimäki et al., submitted), trochlear height (Puputti and Niskanen, 2008) and width (von den Driech, 1976); for radioulna interarticular length (Niinimäki et al., submitted), proximal and distal physiological (articular) breadth (von den Driech, 1976); for metacarpal interarticular length (Niinimäki et al., submitted) proximal physiological (articular) depth and breadth (von den Driech, 1976); for femur interarticular length (Niinimäki et al., submitted), caput diameter and distal physiological (articular) breadth (von den Driech, 1976); for tibia interarticular length (Niinimäki et al., submitted), proximal and distal physiological (articular) breadth (von den Driech, 1976); for metatarsal interarticular length (Niinimäki et al., submitted) proximal physiological (articular) depth and breadth (von den Driech, 1976). From single measurement component loading, distal physiological breadth in radioulna and interarticular length in metacarpal loaded less heavily (0,7 relative to 0,9) with the first and only principal component (PC), and final PC's extracted for these bones are based on interarticular breadth and proximal physiological breadth for radioulna and proximal physiological (articular) depth and breadth for metacarpal. All remaining components per bone element loaded highly (0,9) with the only component extracted, and this single components for each bone element explained well total variation in body size. All long bone elements and metapodials were studied, but all bone elements were not present for all individuals. Bone elements present per individual are presented in Table 1.

The method for observing changes at reindeer entheses (Niinimäki and Salmi, 2016) was based on prior knowledge of the enthesal studies on humans, such as considering fibrous and fibrocartilaginous entheses separately, and creating separate scoring protocols for area and margin for fibrocartilaginous entheses (Villotte, 2006, 2013). Most importantly, all scored long bone entheses were examined individually with site-specific scoring systems created appreciating the existing variation in a specific attachment site (Niinimäki and Salmi, 2016). Three-stage categories were then created and described for scoring (Niinimäki and Salmi, 2016). For this study, we included those entheses omitted from the original publication based on visually determined limited (but three-scaled) variation at an enthesis. These were origin for *Extensor radius carpi* and insertion for *Brachiocephalicus* in humerus, third trochanter (housing insertion for *Gluteal* muscles and origin for *Tensor fascia lata*) in femur, *Teres minor* origin in scapula, and *Psoas minor* origin, and origins for *Biceps femoris* and *Gluteus* in innominate. In addition, bone resorption traits (erosion in both fibrous and fibrocartilaginous entheses, and for area of fibrocartilaginous entheses only: fine and macro porosity and cavitation) were observed according to Coimbra method criteria (Henderson et al., 2010, 2013), modified further into presence/absence scores. Number of observations per categories and traits are presented in Tables 2a and 2b.

The method for obtaining bone cross-sectional properties from reindeer long bones (Niinimäki et al., submitted) was created based on prior extensive research and methodology (e.g., Ruff and Hayes, 1983; Ruff, 1992, 2003; Ruff et al., 1994, 2015). Cross-sectional location is usually defined to a percentage of bone length, although a recent study indicates that anatomically selected cross-sections may possibly provide meaningful definition, although the association between activity and cross-sectional properties are less clear (Niinimäki et al., 2017). Bone length measurement used to define a percentage of bone length is usually interarticular length as it is considered to better represent functional muscle levers and thus be more relevant for studying activity than maximum bone length (Ruff and Hayes, 1983; Sládek et al., 2010;

Table 2a
Number of observations per bone formation category and per trait per category of bone resorption in humerus and scapula.

Bone	Humerus										Scapula		
	Deltoid	Teres minor	Triceps brach	Teres major	Infraspinatus	Subscapularis	Supraspinatus	Extensor radius carpi	Brachiocephalicus	Lat extensor	Ulnaris lateral	Superficial and deep flexor	Teres minor
Bone formation	13/10/19	11/10/20	15/13/14	10/13/19	20/14/6	8/16/18	17/20/2	22/12/9	20/18/5	20/16/7	16/19/2	23/15/5	13/14/12
Erosion				40/2		41/1	37/1	29/7			1/40	1/42	28/11
Fine por	37/5	35/6					35/14					1/42	
Macro por												1/42	
Cavitation													

Table 2b
Number of observations per bone formation category and per trait per category of bone resorption in radioulna, femur, tibia and innominate.

Bone	Radioulna			Femur			Tibia			Innominate				
	Anconeus	Flexor profundus ulnaris	Biceps brachialis, Z2	Flexor profundus digiti, Z2	Vastus lateralis	Iliacus and Psoas major	Vastus medialis	Gluteal and Tensor fascia lata	Semimembranosus	Gastrocnemius	Sartorius and Gracilis	Rudimentary fibula	Psoas minor	Gluteus and biceps femoris
Bone formation	15/9/11	10/16/10	11/20/5	10/16/9	18/15/5	18/17/3	17/16/5	19/11/8	14/12/12	19/13/6	11/13/14	8/11/19	17/12/7	8/15/13
Erosion		35/1	33/3	34/1	36/2		35/3		24/14	18/18	24/14	36/2	32/3	27/9
Fine por	28/8	31/5		33/2	33/5	37/1						37/1		
Macro por	29/7	26/10		33/2	29/9	37/1						29/9		
Cavitation	3/33	28/8			36/2									

Erosion is observed for Zone 1 for fibrocartilaginous entheses unless otherwise specified.

Davies and Stock, 2014; Mongle et al., 2015). Interarticular length for reindeer long bones and metapodials are described in Niinimäki et al. (manuscript), and cross-sectional properties were observed at 50% of this measurement (Niinimäki et al., submitted). Bones were scanned using a peripheral quantity computed tomography (pQCT) scanner (Stratec XCT Research SA+). Bone cross-sectional properties provided by this equipment include several bone robusticity and strength variables (total area TA, cortical area CA, moment of inertia planes I_x and I_y , and polar second moment of area J).

For statistical analysis bone cross-sectional properties, bone element size and known/estimated body weight was divided into categories according to bone formation scores per each observed enthesis (1–3). For bone resorption (erosion, fine and macro porosity and cavitation) presence/absence categories were created for statistical comparison. Association of a single enthesis score was studied within bone element, within limb element and across all studied bone elements (humerus, radioulna, metacarpal, femur, tibia, and metatarsal). Comparisons between groups (bone formation 1–3 and bone resorption 0–1) were made using one-way analysis of variance (ANOVA). Directions of differences were checked from group means (data not shown). Statistical analysis was performed using SPSS.

3. Results

Bone formation in the entheses at proximal humerus were associated mainly with increased bone cross-sectional properties and size of upper limb bone elements, with two exceptions. First, bone formation at *Supraspinatus* attachment was not significantly associated with bone cross-sectional properties or size of any limb element (Tables 3a and 3b). Second, bone formation at *Infraspinatus*, which was associated with increased values in bone cross-sectional properties of all other limb elements, i.e. not restricted within bone or limb element (Table 3a). Bone formation at distal humeral entheses were associated with increased values in bone cross-sectional properties and size of all studied bone elements (Table 3a). While erosion was observed in several of the humeral entheses, significant association with increased values in bone cross-sectional properties was observed only in the entheses for *Deltoid* and *Extensor radius carpi* (Table 3a). The only other bone resorption trait associated with increased values in bone cross-sectional properties was fine porosity at the entheses for *Supraspinatus* and *Lateral extensor* (Table 3a). Of these, erosion score for *Extensor radius carpi* was associated with several cross-sectional properties and size of all studied bone elements.

In radioulna, bone formation at all the observed entheses were associated with increased values in bone cross-sectional properties of all studied bone elements, i.e. not restricted within radioulna or even within the forelimb (Table 3b). Of bone resorption traits, fine and macro porosity at the entheses for *Anconeus* and *Flexor profundus ulnaris* were associated with increased values in multiple bone cross-sectional properties and size, not restricted within radioulna (Table 3b). In addition, cavitation in *Flexor profundus ulnaris* was found to be associated with increased values in CA and I_x of tibia (Table 3b).

In proximal femur, bone formation scores at the *Vastus lateralis* and *Vastus medialis* entheses were associated with increased values in bone cross-sectional properties and size mainly within hind limb (Table 3b). The other two entheses studied in the proximal femur were lesser trochanter (attachments for *Iliacus* and *Psoas major*) and third trochanter (attachments for *Gluteal* muscles and *Tensor fascia lata*) where association of increased values in bone cross-sectional properties and bone size were not restricted within femur or even hind limb (Table 3b). Bone resorption in these entheses, while present in low frequency, was not associated with bone cross-sectional properties or size (Table 3b). In the distal femur only one enthesis was exhibiting variation allowing its scoring, that of origin for *Gastrocnemius*. Variation in this enthesis was associated with increased values in bone cross-sectional properties and size of all the studied bone elements (Table 3b). While erosion was

Table 3a

Significant differences between bone robusticity and resorption scores with N per element of observed bone resorption features in humerus and scapula.

Bone	Humerus, proximal								Humerus, distal						Scapula	
	Deltoid F		Teres minor F	Triceps brachialis F (o)	Teres major F	Infraspinatus FC	Subscapularis FC	Supraspinatus FC	Extensor carpi FC	Brachiocephalicus F		Lateral extensor FC (o)	Ulnaris lateral FC	Superficial and deep flexor FC	Teres minor FC (o)	
Trait	BF	E	BF	BF	BF	BF	BF	FP	BF	E	BF	BF	FP	BF	BF	BF
Weight	0,027	0,211	0,095	0,114	0,381	0,002	0,221	0,105	0,000	0,000	0,023	0,001	0,124	0,038	0,007	0,000
<i>Humerus cross-sectional properties and size</i>																
TA	0,007	0,265	0,050	0,015	0,276	0,007	0,032	0,051	0,000	0,000	0,000	0,000	0,169	0,002	0,000	0,000
CA	0,018	0,195	0,019	0,125	0,399	0,002	0,031	0,157	0,000	0,000	0,007	0,002	0,103	0,003	0,001	0,000
IX	0,018	0,166	0,051	0,038	0,331	0,011	0,046	0,050	0,000	0,000	0,000	0,001	0,102	0,002	0,000	0,000
IY	0,015	0,181	0,047	0,038	0,424	0,004	0,034	0,063	0,000	0,000	0,001	0,001	0,130	0,002	0,000	0,000
J	0,016	0,171	0,048	0,037	0,368	0,007	0,039	0,055	0,000	0,000	0,000	0,001	0,113	0,002	0,000	0,000
Size	0,008	0,181	0,027	0,079	0,113	0,014	0,332	0,055	0,001	0,001	0,000	0,011	0,349	0,025	0,004	0,000
<i>Radioulna cross-sectional properties and size</i>																
TA	0,027	0,133	0,071	0,105	0,484	0,002	0,025	0,060	0,000	0,000	0,000	0,001	0,114	0,001	0,000	0,000
CA	0,008	0,147	0,008	0,088	0,307	0,001	0,011	0,141	0,000	0,001	0,002	0,000	0,103	0,000	0,000	0,000
IX	0,030	0,091	0,056	0,091	0,452	0,004	0,046	0,051	0,000	0,000	0,000	0,001	0,143	0,002	0,000	0,000
IY	0,015	0,174	0,039	0,061	0,439	0,002	0,008	0,073	0,000	0,001	0,001	0,000	0,066	0,000	0,000	0,000
J	0,018	0,139	0,042	0,068	0,438	0,002	0,015	0,063	0,000	0,000	0,000	0,000	0,085	0,001	0,000	0,000
Size	0,029	0,053	0,050	0,111	0,096	0,038	0,266	0,038	0,006	0,001	0,000	0,005	0,379	0,024	0,012	0,000
<i>Metacarpal cross-sectional properties and size</i>																
TA	0,176	0,054	0,419	0,205	0,622	0,007	0,057	0,015	0,000	0,000	0,008	0,003	0,041	0,008	0,001	0,000
CA	0,053	0,011	0,048	0,225	0,381	0,006	0,068	0,026	0,000	0,000	0,005	0,001	0,024	0,001	0,000	0,000
IX	0,107	0,044	0,195	0,113	0,552	0,010	0,064	0,009	0,000	0,000	0,001	0,002	0,047	0,005	0,000	0,000
IY	0,127	0,036	0,300	0,173	0,636	0,007	0,044	0,018	0,000	0,000	0,004	0,002	0,031	0,003	0,000	0,000
J	0,117	0,038	0,250	0,143	0,622	0,008	0,051	0,013	0,000	0,000	0,002	0,002	0,036	0,003	0,000	0,000
Size	0,116	0,156	0,108	0,072	0,053	0,069	0,251	0,045	0,005	0,024	0,001	0,013	0,973	0,164	0,044	0,000
<i>Femur cross-sectional properties and size</i>																
TA	0,074	0,055	0,231	0,013	0,229	0,037	0,232	0,038	0,000	0,000	0,002	0,002	0,248	0,011	0,001	0,000
CA	0,208	0,030	0,267	0,233	0,382	0,006	0,271	0,451	0,000	0,009	0,169	0,022	0,293	0,004	0,010	0,006
IX	0,130	0,027	0,245	0,032	0,274	0,022	0,186	0,069	0,000	0,000	0,005	0,004	0,229	0,005	0,001	0,000
IY	0,057	0,032	0,152	0,029	0,289	0,014	0,198	0,088	0,000	0,001	0,006	0,003	0,192	0,005	0,001	0,000
J	0,093	0,028	0,201	0,030	0,281	0,018	0,190	0,075	0,000	0,000	0,005	0,003	0,211	0,004	0,001	0,000
Size	0,076	0,049	0,122	0,055	0,019	0,061	0,410	0,014	0,048	0,026	0,001	0,038	0,577	0,145	0,153	0,000
<i>Tibia cross-sectional properties and size</i>																
TA	0,059	0,808	0,170	0,028	0,169	0,030	0,225	0,189	0,002	0,001	0,001	0,002	0,507	0,005	0,001	0,000
CA	0,031	0,688	0,028	0,066	0,055	0,048	0,248	0,921	0,001	0,055	0,008	0,007	0,857	0,002	0,005	0,000
IX	0,055	0,838	0,113	0,023	0,112	0,032	0,292	0,211	0,004	0,011	0,000	0,002	0,530	0,001	0,000	0,000
IY	0,066	0,608	0,144	0,045	0,228	0,038	0,147	0,245	0,001	0,001	0,003	0,002	0,483	0,003	0,001	0,000
J	0,060	0,691	0,130	0,033	0,178	0,035	0,192	0,226	0,001	0,003	0,001	0,002	0,496	0,002	0,001	0,000
Size	0,076	0,630	0,098	0,036	0,004	0,223	0,380	0,229	0,047	0,133	0,000	0,011	0,547	0,035	0,030	0,000
<i>Metatarsal cross-sectional properties and size</i>																
TA	0,102	0,305	0,268	0,062	0,204	0,006	0,046	0,179	0,000	0,000	0,007	0,006	0,156	0,010	0,001	0,000
CA	0,048	0,054	0,093	0,037	0,057	0,020	0,121	0,203	0,000	0,001	0,006	0,001	0,105	0,003	0,001	0,000
IX	0,057	0,228	0,157	0,037	0,157	0,012	0,065	0,120	0,000	0,001	0,002	0,003	0,118	0,005	0,000	0,000
IY	0,142	0,139	0,319	0,041	0,172	0,016	0,063	0,113	0,000	0,000	0,006	0,004	0,115	0,009	0,001	0,000
J	0,086	0,183	0,217	0,038	0,170	0,013	0,061	0,114	0,000	0,000	0,003	0,013	0,114	0,006	0,000	0,000
Size	0,130	0,059	0,185	0,059	0,019	0,118	0,429	0,068	0,005	0,024	0,006	0,003	0,819	0,041	0,073	0,000

BF – bone formation, E – erosion, FP – fine porosity. Significant differences between observed groups (per bone formation and presence/absence scores of bone resorption) are bold-faced.

frequently observed (18 cases out of 36; Table 2b) at *Gastrognemius* origin, it was not associated with significantly increased values in bone cross-sectional properties or size (Table 3b).

Of the entheses in tibia, the observed bone formation was associated with increased values in bone cross-sectional properties and size of all studied bone elements (Table 3b). Of the studied bone resorption traits for these entheses, only macro porosity in rudimentary fibula was associated with an increase in some of the bone robusticity and strength variables of femur and tibia, while it was associated with the size of all studied bone elements (Table 3b).

Finally, bone formation at *Teres minor* origin at scapula was associated with increased values in bone cross-sectional properties and size of all bone elements while bone resorption, namely erosion, was not (Table 3a). For the innominate, bone formation at the origin for *Psoas minor* was associated with increased values in bone cross-sectional properties and size of all bone elements while bone resorption as erosion was not (Table 3b). The situation was reversed for origin for *Gluteus* and *Biceps femoris*, where erosion was associated with increased values in bone cross-sectional properties and size of all bone elements while the observed bone formation was not (Table 3b).

4. Discussion

The purpose of this study was to examine the relationship between enthesal changes and bone cross-sectional properties in the reindeer skeleton to provide framework for discussing bone functional adaptation as possible partial promoting factor for enthesal changes, and to allow observation of this relationship beyond humans. We found that, for some entheses when association was significant, bone formation and some of the features of bone resorption were associated with increased values in bone cross-sectional properties and increased body size. Furthermore, we discovered that selecting features for scoring as well as relying on visual impression or similar magnitude on the variability of an enthesis may result in false acceptance/rejection of an enthesis to study activity. These results work in part to validate the method as observing activity related changes in bone cross-sectional properties, where association with activity has been more compellingly evidenced. As far as an existing relationship between bone cross-sectional properties supports the use of enthesal changes as activity markers (as suggested in Michopoulou et al., 2015), the scoring system created to observe robusticity at reindeer entheses by Niinimäki and Salmi (2016) should be able to capture bone robusticity.

According to our results, regardless of muscle attachment type -fibrous or fibrocartilaginous- and whether origin or insertion, bone formation was associated with increased values of bone robusticity and strength as observed from bone cross-sectional properties and size, as observed from body weight and bone dimensions. The only entheses where bone formation was not associated with studied bone properties was *Subscapularis* in humerus and *Gluteus* and *Biceps femoris* in innominate. In addition, some associations were limited within bone or limb element, whereas some entheses were associated with cross-sectional robusticity, strength, and size of all limb elements. As 15 of the total 26 observed entheses were fibrocartilaginous (not counting third trochanter), our results provide minimal support for the anatomically based hypothesis of Foster et al. (2014) where fibrous entheses may be less responsive to mechanical stress due to their attachment site migrating along growing bone. Furthermore, our result support second anatomically based hypothesis of Foster et al. (2014) where changes in robusticity are restricted to margins of fibrocartilaginous entheses, as apart from two of the studied fibrocartilaginous entheses (*Biceps brachii* and *Flexor profundus digiti*) mainly margins of muscle attachments exhibited variation associated with bone cross-sectional robusticity and strength. This is similar to humans, where *Biceps brachii* attachment area has, indeed, been found to modify with activity (Hawkey and Merbs, 1995). Finally, majority of observation of changes at entheses were on muscle insertions (16 insertions versus 10 origins). While insertions can

be intuitively considered the main location where mechanical loading from muscle action results in enthesal changes, it is evident from our data that origins are modified to muscle activity, as well. This is supported by a study on variation of cortical thickness at muscle attachments (Niinimäki et al., 2013b).

One major concern of Foster et al. (2014) in studies comparing enthesal changes and bone cross-sectional properties was observing robusticity and stress lesion scores in a continuum or as summed traits. Also, Villotte and Knüsel (2013) have stressed that different traits of enthesal change should be studied separately as there may be different etiologies involved. Our study provides information for bone resorption and bone formation separately. According to our data, bone resorption features (erosion, fine and macro porosity, and cavitation) were not a very common find in the observed reindeer entheses, although there was variation in presence/absence and co-occurrences in traits per enthesis. These changes, when relevant, were associated with increased values of bone cross-sectional robusticity and strength, and bone element size.

Our results point towards a positive relationship between enthesal changes and bone cross-sectional properties. Variation in bone cross-sectional properties in relation to activity are explained with bone functional adaptation, and we will now discuss whether this observed covariation between enthesal changes and bone cross-sectional properties could be considered indirect evidence of bone functional adaptation as potential partial promoting factor for enthesal appearance.

Bone functional adaptation as potential contributing factor for enthesal changes is not a new proposal. Churchill and Morris (1998) have suggested that certain aspects of activity, specifically loading intensity is shown at entheses. Lieverse et al. (2009) suggested that rather than type of activity, the intensity and/or duration of activity is evidenced in the entheses. This idea of labor intensity being the contributing factor was considered in the study of Niinimäki (2011) where activity was categorized according to intensity of labor (heavy lifting and getting short of breadth) into heavy and light labor. More recently, Foster et al. (2014) discussed the potential of bone functional adaptation as factor promoting for bone enthesal robusticity.

Indirect evidence of bone functional adaptation promoting enthesal appearance is provided by following observations. First, presented relationship between enthesal changes and bone cross-sectional properties. A relationship, although weak, exists between human entheses and bone cross-sectional properties, regardless of scoring method used for observation (Bridges, 1997; Weiss, 2003; Niinimäki, 2012; Michopoulou et al., 2015, 2017). Our material on reindeer skeleton provided more compelling, beyond species evidence. According to our results, variation present at entheses were associated with increased bone cross-sectional robusticity and size, in some cases even beyond limb element. While an association between two variables may not be indicative of common causal factor (Foster et al., 2014), the results of association between-species can still be considered a positive indication of common underlying mechanism.

Second, feeding behavior (digging for lichen) would have commenced in early life of the reindeer, and it is indeed evidenced in the significantly greater robusticity of entheses among free-ranging reindeer compared to zoo reindeer at the attachment sites of elbow flexors and extensors (Niinimäki and Salmi, 2016). This suggest that increased activity, commenced already in childhood, will result in increased complexity at enthesis, evidenced also for human material (Mariotti et al., 2004; Foster et al., 2014). This opposes the hypothesis with underlying pathological implication for enthesal changes observed considering childhood mobility (Acosta et al., 2017). Acosta et al. (2017) proposed that enthesal changes modify during growth to a specific level of stress, where overload beyond those physiological limits an individual is accustomed to during childhood would result in greater variation in the entheses. In case of reindeer, this is not evident.

Third piece of indirect evidence is the correlation of both enthesal changes and bone cross-sectional properties with size and age. In studies of bone cross-sectional properties, body size is considered to provide a

baseline of loading (Seeman et al., 1996; Schiessl et al., 1998; Ruff, 2000; Schoenau and Frost, 2002; Brianza et al., 2007), which thus needs to be considered before reconstructing activity. Enteseal changes have also been found to covary with body size (Hawkey and Merbs, 1995 scored entheses in Churchill and Morris, 1998; Niinimäki, 2011; Weiss et al., 2010; Godde et al., 2018). Muscle size is also a relevant factor on both enteseal changes and bone cross-sectional properties, where muscle mass/area of an individual is proportioned to one's size as well as activity (Niinimäki et al., 2016; although for enteseal changes hypothesized due to lack of direct evidence, see Foster et al., 2014). Thus, it is likely that body size provides similar the intrinsic baseline of bone functional adaptation for both skeletal activity markers. This result proposes the possibility of size as partial contributing factor resulting in covariation between EC and bone cross-sectional properties where size was also significant (Tables 3a and 3b).

Age provides another intrinsic factor to be considered for both entheses and bone cross-sections. In short, for bone cross-sectional properties, bone is deposited at the periosteal envelope prior to mid-adolescence and at the endosteal envelope after that (Daly, 2007; Ruff et al., 1994; Seeman, 2001). Peak bone mass is achieved during the first thirty years of life based on several factors that include the individual's loading history (Johnston and Slemenda, 1993; Parfitt, 2004). Other age-related changes include expanded medullary cavities and thinner cortices (Martin, 2007; Ruff et al., 1994; Russo et al., 2006; Schiessl et al., 1998; Schoenau et al., 2000). Regarding enteseal changes, intense physical activity in early adulthood results in higher scores in young adults (Niinimäki, 2011), but with advancing age these differences decrease after around 40–50 years (Niinimäki, 2011). This has been found for both fibrous (Hawkey and Merbs, 1995 method for fibrous entheses in Niinimäki et al., 2013b, 2013a) and fibrocartilaginous entheses (Villette et al., 2010 method and results). Age effects at entheses have been related to cumulative long-term activity patterns and/or reduced osteoblast activity resulting in thinner cortical bone with greater diameter and rougher external bone (Nagy, 1998; Weiss, 2007; Foster et al., 2014). Age-related changes in both entheses and cross-sectional properties can be considered coming from same source of changes in bone functional adaptation with age. Another suggestion by Foster et al. (2014) associates leveling effects of age after around 40–50 years to decline in muscle mass after that age. We suggest that it rather reflects decrease in bone mass that would have commence prior a decade or two (see Johnston and Slemenda, 1993; Parfitt, 2004).

Bone resorption traits as studied from humans are mainly considered an enthesopathy, i.e. resulting from loading an enthesis beyond its capacity (Hawkey and Merbs, 1995; Henderson et al., 2010, 2013; Villette et al., 2010; Foster et al., 2014). Therefore, the association between bone resorption and bone cross-sectional properties, where increasing manifestations of bone resorption are associated with increased bone cross-sectional robusticity indicator requires further discussion of enteseal changes also from non-pathological point of view. Firstly, to view bone resorption from point of view of biomechanical loading, Hirschberg (2005) has hypothetically explained the biomechanical principles behind the formation of a tubercle or a pit at a muscle attachment site. Flat bone surfaces model to stress according to whether deposition or resorption thresholds are reached and a tubercle or a pit would form accordingly. This hypothesized etiology would also promote bone functional adaptation, in the micro-scale of an enthesis, where removal or accrual of bone occurs depending on strain thresholds. On the other hand, bone resorption observed following Coimbra method (Henderson et al., 2010, 2013) intended for observing human entheses may not translate between-species, and we were not trained by the developers of the method. Therefore, our results should be considered tentative. We encourage for separate studies for separate traits at entheses, following the suggestions by Villette and Knüsel (2013) and Foster et al. (2014).

Should an association with increased values in bone cross-sectional properties be indicative of entheses appropriate for physical activity reconstructions, the most promising entheses for observing bone

formation would be *Infraspinatus* (proximal humerus), *Extensor radius carpi*, *Brachiocephalicus*, *Lateral extensor*, *Ulnaris lateral*, *superficial and deep flexor* (distal humerus), *Anconeus*, *Flexor profundus ulnaris*, *Biceps brachialis*, *Flexor profundus digiti* (proximal radioulna), lesser trochanter (*Psoas major* and *Iliacus*), third trochanter (*Gluteal* muscles and *Tensor fascia lata*) (proximal femur), *Gastrocnemius* (distal femur), *Semi-membranosus*, *Sartorius* and *Gracilis*, and *rudimentary fibula* (proximal tibia). Most promising bone resorption traits for activity assessment – as far as their association with bone cross-sectional properties would indicate – would be erosion at *Extensor radius carpi* (distal humerus), fine and macroporosity at *Anconeus* and *Flexor profundus ulnaris* (proximal radioulna), and erosion at *Psoas major* (innominate). However, of these studied muscles, only *Subscapularis*, *Flexor profundus ulnaris*, *Biceps brachii*, and *Flexor profundus digiti* were found to be significantly different between zoo and free-ranging reindeer (Niinimäki and Salmi, 2016). Furthermore, distal humeral entheses were most effective separating working reindeer, and when considering proximal humeral entheses in addition, more effective still (Salmi et al., 2020). *Extensor radius carpi*, *Brachiocephalicus*, third trochanter (*Gluteal* muscles and *Tensor fascia lata*) and entheses at scapula (*Teres minor*) and innominate (*Gluteus* and *Biceps femoris* origin, and *Psoas major* origin) were omitted from the original study. Their effectiveness to separate between different activity status of reindeer is yet to be evidenced.

Some thoughts brought about by considering further implications of our results are following. Our results indicate that entheses scoring methods should be created entheses (and species) specifically, as there seem to be unique variability at each entheses in their appearance. Those entheses omitted from original study by Niinimäki and Salmi (2016) due to seemingly small-scale variation were, in fact, closely associated with overall bone robusticity and strength. Our results indicate that not all muscle attachments vary in a similar scale, and thus entheses-specific scoring systems should be created. While general guidelines for scoring bone formation exist for the Coimbra method (Henderson et al., 2010, 2013), it still lacks entheses-specific scoring, which was also critiqued for the Hawkey and Merbs (1995) method. On the other hand, our original method (Niinimäki and Salmi, 2016) apparently failed to find the appropriate feature of bone formation to score at *Supraspinatus* and for *Gluteus* and *Biceps femoris* where the observed variation was not related with bone cross-sectional properties or size. Varying association in single enthesis with bone robusticity and strength cautions rejecting or accepting a method when tested only on a few entheses. More importantly, our results highlight the importance of appreciating the assumed underlying promoting factors for enteseal appearance in method creation but especially when testing the validation of method. The relevance of scoring method for observing activity should be tested against a relevant feature which the method is considered scoring, i.e. if bone functional adaptation is not considered a contributing factor, it is not relevant to compare the enteseal scores with bone cross-sectional properties.

5. Conclusions

In this paper, we examined changes at reindeer entheses in relation with bone cross-sectional properties, and in relation with body size. According to our results, increased values of most bone formation scores, and some bone resorption scores were associated with increased values in bone cross-sectional properties. While an association between enteseal changes and bone cross-sectional properties is not definitive evidence of common underlying factor, this relationship is now indicated to exist beyond species level. Potentially the common underlying factor explaining covariation of enteseal changes with bone robusticity (as cross-sectional properties and size) could be bone functional adaptation. Understanding reindeer enteseal changes as manifestations of skeletal robusticity, arguably related to physical activity reflected through bone functional adaptation, further allows using these specific studied enteseal change scores for physical activity reconstruction of

the reindeer. Their usage will, for instance, promote understanding the role of draught and cargo reindeer and reindeer feeding in reindeer domestication and past reindeer herding practice.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank our anonymous reviewer for the diligent comments and notes on this paper. This research was funded by the European Research Council (ERC Advanced Grant 295458; ERC Starting Grant 756431 for Anna-Kaisa Salmi as principal investigator) and the Academy of Finland (Grant 285774; Project 308322 for Anna-Kaisa Salmi as principal investigator).

References

- Acosta, M.A., Henderson, C.Y., Cunha, E., 2017. The effect of terrain on enthesal changes in the lower limbs. *Int. J. Osteoarchaeol.* 27 (5), 828–838.
- Alves-Cardo, F., Henderson, C.Y., 2010. Enthesopathy formation in the humerus: data from known age-at-death and known occupation skeletal collections. *Am. J. Phys. Anthropol.* 141 (4), 550–560.
- Brianza, S.Z.M., D'Amelio, P., Pugno, N., Delise, M., Bignardi, C., Isaia, G., 2007. Allometric scaling and biomechanical behaviour of the bone tissue: an experimental intraspecific investigation. *Bone* 40, 1635–1642.
- Bridges, P.S., 1997. The relationship between muscle markings and diaphyseal strength in prehistoric remains from West-Central Illinois. *Am. J. Phys. Anthropol.* 24, 82 [abstract].
- Churchill, S.E., Morris, A.G., 1998. Muscle marking morphology and labor intensity in prehistoric Khoisan foragers. *Int. J. Osteoarchaeol.* 8, 390–411.
- Daly, R., 2007. The effect of exercise on bone mass and structural geometry during growth. In: Daly, R., Petit, M. (Eds.), *Optimizing Bone Mass and Strength. The Role of Physical Activity and Nutrition during Growth*. Medical Sport Science Basel, Karger, pp. 33–49.
- Davies, T.G., Stock, J.T., 2014. The influence of relative body breadth on the diaphyseal morphology of the human lower limb. *Am. J. Hum. Biol.* 26 (6), 822–835.
- Drapeau, M., 2008. Enthesis bilateral asymmetry in humans and African apes. *HOMO—J. Compar. Human Biol.* 59, 93–109.
- Feik, S.A., Thomas, C.D.L., Clement, J.G., 1996. Age trends in remodeling of the femoral midshaft differ between the sexes. *Journal of Orthopaedic Research* 14 (4), 590–597.
- Forwood, M.R., Burr, D.B., 1993. Physical activity and bone mass: exercises in futility? *Bone Min.* 21 (2), 89–112.
- Foster, A., Buckley, H., Tayles, N., 2014. Using entheses robusticity to infer activity in the past: a review. *J. Archaeol. Method Theory* 21 (3), 511–533.
- Frost, H.M., 1987. Bone “mass” and the “mechanostat”. A proposal. *Anat. Rec.* 219 (1), 1–9.
- Galtés, I., Rodríguez-Baeza, A., Malgosa, A., 2006. Mechanical morphogenesis: a concept applied to the surface of the radius. *The Anatomical Record Part A* 288A, 794–805.
- Godde, K., Wilson Taylor, R.J., Gutierrez, C., 2018. Enthesal changes and demographic/health indicators in the upper extremity of modern Americans: associations with age and physical activity. *Int. J. Osteoarchaeol.* 28 (3), 285–293.
- Hawkey, D.E., Merbs, C.F., 1995. Activity-induced musculoskeletal stress markers (MSM) and subsistence strategy changes among ancient Hudson Bay Eskimos. *Int. J. Osteoarchaeol.* 5 (4), 324–338.
- Hirschberg, J., 2005. Simulations of mechanical adaptation and their relationship to stress bearing in skeletal tissue. Ph.D. Thesis. University of Western Australia.
- Heinonen, A., Sievänen, H., Kannus, P., Oja, P., Vuori, I., 2002. Site-specific skeletal response to long-term weight training seems to be attributable to principal loading modality: A pQCT study of female weightlifters. *Calcif. Tissue Int.* 70 (6), 469–474.
- Henderson, C., Mariotti, V., Pany-Kucera, D., Perréard-Lopreno, G., Villotte, S., Wilczak, C., 2010. Scoring enthesal changes: proposal of a new standardised method for fibrocartilaginous entheses. 18th European Meeting of the Paleopathology Association.
- Henderson, C., Mariotti, V., Pany-Kucera, D., Villotte, S., Wilczak, C., 2013. Recording specific enthesal changes of fibrocartilaginous entheses: Initial tests using the Coimbra method. *Int. J. Osteoarchaeol.* 23, 152–162.
- Ibáñez-Gimeno, P., De Esteban-Trivigno, S., Jordana, X., Manyosa, J., Malgosa, A., Galtés, I., 2013. Functional plasticity of the human humerus: shape, rigidity, and muscular entheses. *Am. J. Phys. Anthropol.* 150 (4), 609–617.
- Johnston, C.C., Slemenda, C.W., 1993. Determinants of peak bone mass. *Osteoporosis Int. Suppl.* 3 (S1), S54–S55.
- Judex, S., Carlson, K.J., 2009. Is bone's response to mechanical signals dominated by gravitational loading. *Med. Sci. Sports Exerc.* 41 (11), 2037–2043.
- Jurmain, R., Alves Cardoso, F., Henderson, C., Villotte, S., 2012. Bioarchaeology's Holy Grail: The reconstruction of activity. In: Grauer, A.L. (Ed.), *Companion to Paleopathology*. Wiley/Blackwell, New York, pp. 531–552.
- Lanyon, L.E., 1987. Functional strain in bone tissue as an objective and controlling stimuli for adaptive bone remodeling. *J. Biomech.* 20, 1083–1093.
- Lanyon, L.E., 1996. Using functional loading to influence bone mass and architecture: objectives, mechanisms, and relationship with estrogen of the mechanically adaptive process in bone. *Bone* 18 (Supp 11), S37–S43.
- Lanyon, L.E., Rubin, C.T., 1984. Static vs dynamic loads as an influence on bone remodeling. *J. Biomech.* 17, 897–905.
- Lieberman, D.E., Polk, J.D., Demes, B., 2004. Predicting long bone loading from cross-sectional geometry. *Am. J. Phys. Anthropol.* 123 (2), 156–171.
- Lieverse, A.R., Bazaliiskii, V.I., Goriunova, O.I., Weber, A.W., 2009. Upper limb musculoskeletal stress markers among middle Holocene foragers of Siberia's Cis-Baikal region. *Am. J. Phys. Anthropol.* 138 (4), 458–472.
- Mariotti, V., Facchini, F., Belcastro, M.G., 2004. Enthesopathies – proposal of a standardised scoring method and applications. *Collegium Anthropologicum* 1, 145–159.
- Martin, R.B., 2007. The importance of mechanical loading in bone biology and medicine. *J. Musculoskelet. Neuronal Interact.* 7, 48–53.
- Michopoulou, E., Nikita, E., Valakos, E.D., 2015. Evaluating the efficiency of different recording protocols for enthesal changes in regards to expressing activity patterns using archival data and cross-sectional geometric properties. *Am. J. Phys. Anthropol.* 158 (4), 557–568.
- Michopoulou, E., Nikita, E., Henderson, C.Y., 2017. A test of the effectiveness of the Coimbra method in capturing activity-induced enthesal changes. *Int. J. Osteoarchaeol.* 27 (3), 409–417.
- Milella, M., Belcastro, M.G., Zollikofer, C.P.E., Mariotti, V., 2012. The effects of age, sex, and physical activity on enthesal morphology in contemporary Italian skeletal collection. *Am. J. Phys. Anthropol.* 148, 379–388.
- Mongle, C.S., Wallace, I.J., Grine, F.E., 2015. Cross-sectional structural variation relative to midshaft along hominid diaphyses. II. The hind limb. *Am. J. Phys. Anthropol.* 158 (3), 398–407.
- Molnar, P., 2006. Tracing prehistoric activities: musculoskeletal stress marker analysis of a Stone-Age population on the island of Gotland in the Baltic sea. *Am. J. Phys. Anthropol.* 129 (1), 12–23.
- Molnar, P., 2010. Patterns of physical activity and material culture on Gotland, Sweden, during the Middle Neolithic. *Int. J. Osteoarchaeol.* 20, 1–14.
- Nagy, B.L.B., 1998. Age, activity, and musculoskeletal stress markers. *Am. J. Phys. Anthropol.* 26, 168–169 [abstract].
- Nikander, R., Kannus, P., Dastidar, P., Hannula, M., Harrison, L., Cervinka, T., Narra, N. G., Aktour, R., Arola, T., Eskola, H., Soimakallio, S., Heinonen, A., Hyttinen, J., Sievänen, H., 2009. Targeted exercises against hip fragility. *Osteoporos. Int.* 20 (8), 1321–1328.
- Niinimäki, S., 2011. What do muscle marker ruggedness scores actually tell us? *Int. J. Osteoarchaeol.* 21 (3), 292–299.
- Niinimäki, S., 2012. The relationship between musculoskeletal stress markers and biomechanical properties of the humeral diaphysis. *Am. J. Phys. Anthropol.* 147 (4), 618–628.
- Niinimäki, S., Niskanen, M., Niinimäki, J., Nieminen, M., Tuukkanen, J., Junno, J.-A., 2013a. Modeling skeletal traits and functions of the upper body: comparing archaeological and anthropological material. *J. Anthropol. Archaeol.* 32 (3), 347–351.
- Niinimäki, S., Söderling, S., Junno, J.-A., Finnilä, M., Niskanen, M., 2013b. Cortical bone thickness can adapt locally to muscular loading while changing with age. *HOMO – J. Comp. Hum. Biol.* 64 (6), 474–490.
- Niinimäki, S., Salmi, A.-K., 2016. Enthesal changes in free-ranging versus zoo reindeer – observing activity status of reindeer. *Int. J. Osteoarchaeol.* 26 (2), 314–323.
- Niinimäki, S., Narra, N., Härkönen, L., Abe, S., Nikander, R., Hyttinen, J., Knüsel, C., Sievänen, H., 2017. The relationship between loading history and proximal femoral diaphysis cross-sectional geometry. *Am. J. Hum. Biol.* e22965. <https://doi.org/10.1002/ajhb.22965>.
- Niinimäki, S., Narra, N., Härkönen, L., Abe, S., Nikander, R., Hyttinen, J., Knüsel, C., Sievänen, H., 2019. Do bone geometric properties of the proximal femoral diaphysis reflect loading history, muscle properties, or body dimensions? *Am. J. Hum. Biol.* 31, e23246.
- Niinimäki, S., Härkönen, L., Puolakka, H.-L., Berg, M., Salmi, A.-K., submitted. Cross-sectional properties of reindeer long bones and metapodials allow identification of activity patterns. *Archaeol. Anthropol. Sci.*
- Parfitt, A.M., 2004. The attainment of peak bone mass: what is the relationship between muscle growth and bone growth? *Bone* 34 (5), 767–770.
- Puputti, A.-K., Niskanen, M., 2008. The estimation of body weight of the reindeer (*Rangifer tarandus* L.) from skeletal Measurements: preliminary analyses and application to archaeological material from 17th and 18th century Northern Finland. *Environ. Archaeol.* 13 (2), 153–164.
- Robb, J.E., 1998. The interpretation of skeletal muscle sites: a statistical approach. *Int. J. Osteoarchaeol.* 8 (5), 363–377.
- Robling, A.G., 2009. Is bone's response to mechanical signals dominated by muscle forces. *Med. Sci. Sports Exerc.* 41 (11), 2044–2049.
- Ruff, C., 1992. Biomechanical analyses of archaeological human skeletal samples. In: Saunders, S.R., Katzenberg, M.A. (Eds.), *Skeletal Biology of Past Peoples: Research Methods*. New York, Wiley-Liss, pp. 37–58.
- Ruff, C.B., 2000. Body size, body shape, and long bone strength in modern humans. *J. Hum. Evol.* 38 (2), 269–290.
- Ruff, C., 2003. Growth in bone strength, body size, and muscle size in a juvenile longitudinal sample. *Bone* 33 (3), 317–329.

- Ruff, C.B., Hayes, W., 1983. Cross-sectional geometry of Pecos Pueblo femora and tibiae – a biomechanical investigation. I. Method and general patterns of variation. *Am. J. Phys. Anthropol.* 60, 359–381.
- Ruff, C.B., Walker, A., Trinkaus, E., 1994. Postcranial robusticity in Homo. III: ontogeny. *Am. J. Phys. Anthropol.* 93, 35–54.
- Ruff, C., Holt, B., Trinkaus, E., 2006. Who's afraid of the Big Bad Wolff? "Wolff's law" and bone functional adaptation. *Am. J. Phys. Anthropol.* 129 (4), 484–498.
- Ruff, C., Holt, B., Niskanen, M., Sládek, V., Berner, M., Garofalo, M., Garvin, H.M., Hora, M., Junno, J.-A., Schuplerova, E., Vilkkama, R., Whitley, E., 2015. Gradual decline in mobility with adoption of food production in Europe. *Proc. Nat. Acad. Sci.* 112, 7147–7152.
- Russo, C.R., Lauretani, F., Seeman, E., Bartali, B., Bandinelli, S., Di Iorio, A., Guralnik, J., Ferrucci, L., 2006. Structural adaptations to bone loss in aging men and women. *Bone* 38 (1), 112–118.
- Salmi, A.-K., Niinimäki, S., 2016. Enthesal changes and pathological lesions in draught reindeer skeletons – four case studies from present-day Siberia. *Int. J. Paleopathol.* 14, 91–99.
- Salmi, A.-K., Niinimäki, S., Pudas, T., 2020. Identification of working reindeer using palaeopathology and enthesal changes. *Int. J. Paleopathol.* 30, 57–67.
- Schiessl, H., Frost, H.M., Jee, W.S.S., 1998. Estrogen and bone-muscle strength and mass relationships. *Bone* 22 (1), 1–6.
- Schoenau, E., Neu, C.M., Mokov, E., Wassmer, G., Manz, F., 2000. Influence of puberty on muscle area and cortical area of the forearm in boys and girls. *J. Clin. Endocrinol. Metabol.* 85, 1095–1098.
- Schoenau, E., Frost, H.M., 2002. The "muscle-bone unit" in children and adolescents. *Calcif. Tissue Int.* 70 (5), 405–407.
- Seeman, E., 2001. Clinical review 137: Sexual dimorphism in skeletal size, density, and strength. *J. Clin. Endocrinol. Metabol.* 86 (10), 4576–4584.
- Seeman, E., Hopper, J.L., Young, N.R., Formica, C., Goss, P., Tsalamandris, C., 1996. Do genetic factors explain associations between muscle strength, lean mass, and bone density? A twin study. *Am. J. Physiol.-Endocrinol. Metabol.* 270 (2), E320–E327.
- Shackelford, L., Marshall, F., Peters, J., 2013. Identifying donkey domestication through changes in cross-sectional geometry of long bones. *J. Archaeol. Sci.* 40, 4170–4179.
- Shaw, C.N., Stock, J.T., 2009. Intensity, repetitiveness, and directionality of habitual adolescent mobility patterns influence the tibial diaphysis morphology of athletes. *Am. J. Phys. Anthropol.* 140 (1), 149–159.
- Sládek, V., Berner, M., Galeta, P., Friedl, L., Kudrnová, Š., 2010. Technical note: the effect of midshaft location on the error ranges on femoral and tibial cross-sectional parameters. *Am. J. Phys. Anthropol.* 141, 325–332.
- Stock, J.T., Shaw, C.N., 2007. Which measures of diaphyseal robusticity are robust? A comparison of external methods of quantifying the strength of long bone diaphyses to cross-sectional geometric properties. *Am. J. Phys. Anthropol.* 134 (3), 412–423.
- Turner, C.H., 1998. Three rules for bone adaptation to mechanical stimuli. *Bone* 23 (5), 399–407.
- Umemura, Y., Sogo, N., Honda, A., 2002. Effects of intervals between jumps or bouts on osteogenic response to loading. *J. Appl. Physiol.* 93 (4), 1345–1348.
- Villotte, S., 2006. Connaissances médicales actuelles, cotation des enthesopathies: nouvelle méthode. *Bulletins et mémoires de la Société d'Anthropologie de Paris* 18, 65–85.
- Villotte, S., 2013. Practical protocol for scoring the appearance of some fibrocartilaginous entheses on the human skeleton. <https://www.academia.edu/1427191/Practical_protocol_for_scoring_the_appearance_of_some_fibrocartilaginous_entheses_on_the_human_skeleton>.
- Villotte, S., Castex, D., Couallier, V., Dutour, O., Knüsel, C., Henry-Gambier, D., 2010. Enthesopathies as occupational stress markers: evidence from the upper limb. *Am. J. Phys. Anthropol.* 142, 224–234.
- Villotte, S., Knüsel, K., 2013. Understanding enthesal changes: definition and life course changes. *Int. J. Osteoarchaeol.* 23, 135–146.
- von den Driech, A., 1976. Das Vermessen von Tierknochen aus Vor- und Frühgeschichtlichen Siedlungen. Universität München, München.
- Weiss, E., 2003. Understanding muscle markers: aggregation and construct validity. *Am. J. Phys. Anthropol.* 121 (3), 230–240.
- Weiss, E., 2007. Muscle markers revisited: activity pattern reconstruction with controls in a Central California Amerind population. *Am. J. Phys. Anthropol.* 133 (3), 931–940.
- Weiss, E., Corona, L., Schultz, B., 2010. Sex differences in musculoskeletal stress markers: problems with activity pattern reconstructions. *Int. J. Osteoarchaeol.* 22, 70–80.
- Zumwalt, A., 2005. A new method for quantifying the complexity of muscle attachment sites. *Anat. Rec.* 286B (1), 21–28.