International Journal of Osteoarchaeology
Int. J. Osteoarchaeol. **21**: 292–299 (2011)
Published online 15 December 2009 in Wiley Online Library
(wileyonlinelibrary.com) DOI: 10.1002/oa.1134

What do Muscle Marker Ruggedness Scores Actually Tell us?

SIRPA NIINIMÄKI*
Department of Biology, University of Oulu, P.O.Box 3000, 90014, Finland

ABSTRACT Musculoskeletal stress markers (MSM) have been used to reconstruct activity patterns and labour intensity of past populations. Age and size have been found to correlate with MSM, and these aspects should be considered in activity reconstructions. The aim of this study was to find out the nature and the effects of labour intensity, age and size on MSM. Study material were skeletons ($N = 108$) of individuals of known age, sex and occupation housed at the Natural History Museum, Finland. MSM were scored for Pectoralis major, Deltoid, Teres major and Biceps brachii. These scores were combined to reflect total activity of an individual. Geometric mean of humeral measurements was used as a size indicator and radial tuberosity size was used as a muscle size indicator. Factors explaining MSM were studied using ANCOVA. This included age, size, muscle size, sex, labour intensity, and their interactions. Age and muscle size were the most significant factors explaining MSM, where muscle attachment areas and MSM grow with advancing age. Muscle attachment areas and skeletal frame size were also found to correlate. Least squares regression parameter estimates were used to study the effects of labour intensity, sex and side on MSM. It was found that in early life scores are higher in heavy labour group, but there is less age-related increase in these scores. This could mean that bone is unable to respond to heavy and continuous loading with surface structure. Therefore labour intensity cannot be reliably recorded in old individuals. Also age and size (as reflected in muscle attachment area) affect MSM and these aspects should be considered before making assumptions on labour intensity.

Key words: musculoskeletal stress markers; age; physical activity; labour intensity

Introduction

Bones react to their mechanical environment during life primarily by modelling and Haversian remodelling, which affect bone shape, size and morphology (Lieberman *et al.*, 2003; Ruff *et al.*, 2006). Diaphyseal cross-sectional properties and muscle marker morphology are both affected by this remodelling and thus reflect mechanical environment.

Musculoskeletal stress markers (MSM) occur on entheses, which are sites where a muscle, a tendon or a ligament inserts onto the periosteum and into the underlying bony cortex. Daily repetitive exercise directs minor strain to these insertion sites, which stimulates osteon remodelling by increased blood flow. This results in a hypertrophy of the bone forming excess bone growth such as a crest, or lesion of bone like pitting (Hawkey & Merbs, 1995; Ruff *et al.*, 2006). Therefore MSM have been used by anthropologists to examine habitual activity patterns of past populations (e.g. Kennedy, 1989 and references therein; Hawkey & Merbs, 1995; Nagy & Hawkey, 1995; Chapman, 1997; Nagy, 1999; Cook & Dougherty, 2001; Eshed *et al.*, 2004; Molnar, 2006). Data on modern female tennis players show that bone is affected by activity also started after menarche where average duration of activity was 10 years (Kannus *et al.*, 1995). MSM are little influenced by childhood exercise, because entheses migrate along the growing bone (Enlow, 1990). MSM do not start to form before longitudinal growth has stopped. Childhood exercise should be more evident in diaphyseal strength, which reflects more overall intensity of physical activity.

Determining MSM has been deemed subjective (e.g. Kennedy, 1998; Zumwalt, 2006; Weiss, 2007), but Hawkey and Merbs' (1995) scoring system has been used consecutively in several studies (e.g. Eshed *et al.*, 2004; Molnar, 2006; Weiss, 2003, 2004, 2007). This scoring system is explicit and the depiction of scores for robusticity, stress lesions and ossification are supported by photographs. Entheses are evaluated with these scores, each score having a scale from 0 to 3

* Correspondence to: Department of Biology, University of Oulu, P.O. Box 3000, 90014, Finland.
e-mail: sirpa.niinimaki@oulu.fi

Received 19 May 2009
Revised 6 October 2009
Accepted 20 October 2009

according to development of the given feature. Robusticity category indicates ruggedness of muscle attachment, which is presented by sharp edges or ridges of bone; stress lesions are depicted by pitting of bone; ossification is shown as exostosis of bone.

There are also more recently developed methods for scoring MSM. Villotte (2006) and Havelková and Villotte (2007) suggest different scoring categories for fibrous and fibrocartilaginous muscle insertion sites, where there are three groups for fibrocartilaginous muscle insertion sites and fourth for fibrous insertion site. Mariotti *et al*. (2004) suggests scoring enthesis as osteopythic or osteolythic development using a scale from 0 to 3. In this study I have used the Hawkey and Merbs (1995) method for scoring for two reasons: this method is more established and my results are therefore comparable to other studies, and because the methodology of these three scoring systems is based on visual scale scoring of bone surface remodelling morphology.

Hawkey and Merbs (1995) scoring system has been modified by Molnar (2006) and Weiss (2007) where both combined stress lesion scores and robusticity scores to form a scale from 0 to 6 to indicate total muscle use. The ossification score was not included in the combined scale, because it is not considered to be activity related but rather an indication of trauma to the insertion site, such as impact injury on muscle-bone attachment site (Hawkey & Merbs, 1995; Eshed *et al*., 2004; Molnar, 2006; Weiss, 2007). Molnar (2006) and Weiss (2007) further suggest that the scores of individual muscles should be combined to create aggregated MSM scores (hereafter referred to as combined MSM score) because this combined score would be less sensitive to anomalies. The use of combined MSM score, however, gives an indication of total level of activity rather than indicating which individual muscles were preferred in relation to other muscles.

Not only physical activity but also age affects MSM. Older individuals tend to have higher scores than young individuals (Kennedy, 1989; Churchill & Morris, 1998; Nagy, 1998; Robb, 1998; Mariotti *et al*., 2004; Molnar, 2006; Weiss, 2003, 2004, 2007). Age effects on MSM are likely to be due to the cumulative effects of more repetitions in long-term activity patterns (Nagy, 1998). Age differences could also be related to changes in bone structure due to the reduction in osteoblast activity resulting in a thinner cortical bone with a greater external diameter (Mays, 2000). Robb (1998) found that muscle markings increase progressively with age from biological maturity to 40–50 years. After this age the process of surface marking may level off. Robb (1998) suggested several reasons for this, such that it may be a self-limiting process, activity regime may change, or activity may decrease with advancing age. Also peak bone mass is attained before 30 years after which it begins to decrease (Forbes, 1987; Anderson, 2001).

MSM have been found to correlate with body size (Weiss, 2003, 2004, 2007) and muscle insertion size (Churchill & Morris, 1998) whereas body size has been found to correlate with muscle insertion size in non-human primates (Zumwalt *et al*., 2000) and sheep (Zumwalt, 2006). Also muscle size (as reflected in soft-tissue girth in upper arm) has been found to correlate ($r = 0.917$; $N = 50$) with muscle insertion size of Biceps brachii in apes (Niskanen & Junno, 2009). These studies show that the aspects of body size, muscle size and muscle marker ruggedness scores have been found to correlate, but the correlation between all of these aspects has not been considered before.

MSM have been found to be sexually dimorphic in some studies (Churchill & Morris, 1998; Wilzcak, 1998; Weiss, 2003, 2004, 2007). This was argued to be a result of a larger weight and musculo-skeletal robusticity in males, or sexual division of labour (Robb, 1998; Wilzcak, 1998; Weiss, 2003, 2004; 2007; Wescott and Cunningham, 2006).

The aim of this study is to find out how the intensity of physical activity reflects in combined MSM score and its relationship between age, labour intensity as reported occupation, body size as estimated from geometric mean of humeral measurements and muscle size as reflected in radial tuberosity. In addition I will investigate how sex and side dominance affect MSM. I expect to find that age and size increase the ruggedness of MSM and that heavy physical activity compared to light physical activity increases MSM scores more intensely with advancing age.

Materials and methods

Natural History Museum skeletal material was used in this study. This collection is housed in University of Helsinki and it comprises of early 20th century Finns collected by the Anatomy Department of Helsinki University in the 1920s and 1930s. This material includes 108 individuals of known sex, age and occupation (Telkkä, 1950; Hopsu & Hämäläinen, 1957). This material was divided into two groups according to the occupation: heavy and light labour (appendix 1). Labour intensity could be assessed for 48 individuals, which are the number cases in analysis concerning labour intensity effects. Labour was considered heavy if it included a lot of lifting, moving heavy loads or getting short of breath (Chaffin, 1981).

MSM were scored for the insertion sites of Pectoralis major, Teres major, Deltoid and Biceps brachii muscles using the scoring system of Hawkey and Merbs (1995). This system was adapted to indicate total muscle use by combining stress lesion scores and robusticity scores to form a scale from 0 to 6 as suggested by Molnar (2006) and Weiss (2007). Muscle scores were then combined to represent total activity of an individual as suggested by Weiss (2003, 2004, 2007). Radial tuberosity area was used as a muscle size indicator based on information on apes (Niskanen & Junno, 2009). Even though locomotion differences between humans and apes may contribute to different relationship between muscle size and radial tuberosity area, this is the only available approximation for muscle size. Radial tuberosity area was calculated using the following formula for an ellipse:

Radial tuberosity area $= \pi \cdot a \cdot b$, where a and b are semi axis

Size was adjusted using ratios (Albrecht *et al.*, 1993). For this study I chose geometric mean of humeral measurements to represent size because it represents the volume of humerus. Geometric mean was calculated from humeral maximum length, humeral head antero-posterior breadth and distal humeral epicondylar breadth measurements. Geometric mean rather than estimation of weight (as in Zumwalt *et al.*, 2000; Zumwalt, 2006) was used as a size indicator because humeral dimensions are connected with muscle forces, load and lever arms rather than weight (Ruff, 2003; Weiss, 2004), but humeral measurements also correlate with the overall size.

Only those individuals where all the selected measurements could be taken and all the muscle insertions could be scored were included in this study. Variables age, size, muscle size and combined MSM score were normally distributed and linearly dependent (Table 1), therefore Pearson correlation was used to find the dependencies between these variables (Tables 2 and 3). Least squares regression (LSQ) equations were used to study the difference in the development of combined MSM score with age in three groups: heavy and light labour, left and right side, and males and females (Table 4). Differences between groups in their relationship with age and MSM score were studied also controlling for size. Combined MSM score was divided by muscle attachment size. Group specific size adjusted LSQ-equations are presented in Table 5.

Table 2. Pearson correlations for variables

	MSM	Muscle size	Size
Age	**0,536** ($N = 108$)	0,179 ($N = 111$)	0,005 ($N = 114$)
MSM		**0,364** ($N = 115$)	0,244 ($N = 115$)
Muscle size			**0,661** ($N = 118$)

Numbers in bold denotes a significant correlation at $p > 0.001$. N is the number of cases.

Analysis of covariance (ANCOVA) was used to find out the effects of sex and labour intensity as categorical factors and age, muscle size and size as covariates, and the interactions of these variables on combined MSM score (Tables 6 and 7). The best model predicting combined MSM score was chosen with custom model from the covariates, fixed factors and their interactions based on their significance and observed power.

Results

The difference in the development of combined MSM score with age in different groups of labour intensity, sex and side were studied using LSQ-equations estimates' slopes and intercepts. These parameter estimates were compared between the following groups: heavy-light labour, male-female and left-right side. Number of individuals per group and average ages in groups are in Table 1. Note that there are only 19

Table 1. Group specific means and standard deviations for variables

Group	N	Age	MSM	Muscle size	Size
All	108	47.26 ± 16.99	9.7 ± 4.42	266.19 ± 56.91	91.9 ± 4.95
Male	89	46.42 ± 16.21	10 ± 4.33	282.39 ± 44.34	93.53 ± 3.56
Female	19	51.21 ± 20.27	8.08 ± 4.6	205.63 ± 33.03	84.26 ± 2.97
Heavy	89	46.89 ± 15.44	10.25 ± 4.3	284.46 ± 43.00	93.45 ± 3.74
Light	13	45.08 ± 17.37	8.54 ± 5.51	233.70 ± 48.21	90.19 ± 6.12
Right	91	47.26 ± 16.84	10.46 ± 4.66	270.20 ± 56.91	92.23 ± 5.33
Left	100	47.19 ± 17.12	9.2 ± 4.8	262.53 ± 54.56	91.49 ± 4.87

Results are expressed as mean $\pm$ SD.

Table 3. Sex specific Pearson correlations for variables

	MSM	Muscle size	Size
Age	**0,545/0,648** (N = 89/19)	0,218/**0,723** (N = 89/21)	0,099/0,282 (N = 90/23)
MSM		0,262/**0,570** (N = 93/21)	0,123/0,226 (N = 93/21)
Muscle size			**0,430**/0,269 (N = 94/22)

Numbers in bold denotes a significant correlation at $p > 0.001$. N is the number of cases for males and females (N = males/females).

Table 4. Regression equations for groups in relation with age

Variable	R^2	Slope	95% Interval	Intercept	95% Interval	N
Heavy labour	0.535	0.149	0.066/0.232	3.255	−0.854/7.363	35
Light labour	0.868	0.276	0.174/0.380	−3.885	−8.911/1.139	13
Right hand	0.461	0.128	0.076/0.179	4.435	1.841/7.028	91
Left hand	0.561	0.157	0.111/0.204	1.779	−0.655/4.110	100
Males	0.545	0.146	0.098/0.193	3.289	0.944/5.635	89
Females	0.648	0.147	0.058/0.235	0.558	−4.296/5.412	19
All	0.536	0.139	0.097/0.182	3.112	0.988/5.236	108

Heavy and light labour groups are side averaged, sexes are pooled, right and left side information include pooled sexes and pooled labour. Males and females are side averaged and include individuals performing heavy and light labour.

Table 5. Muscle size (radial tuberosity area) adjusted LSQ-equations

Variable	Slope	Intercept
Heavy labour	<0,001	0,017
Light labour	0,001	−0,006
Right hand	<0,001	0,021
Left hand	0,001	0,010
Males	<0,001	0,016
Females	<0,001	0,014

Table 6. Analysis of covariance table for variables explaining combined MSM score

Parameter	B	Std. error	t	Sig.	95% Interval
Intercept	−2.296	1.949	−1.178	0.241	−6.161/1.569
Age	0.126	0.021	6.060	<0.001	0.085/0.168
Muscle size	0.022	0.007	3.263	0.001	0.009/0.036

Reliability of regression equation $R^2 = 0{,}337$.

individuals in female group and 13 individuals in light labour group. Average ages were similar in groups with statistical significance (t-test, critical alpha at 0.01). Humeral size was found to be statistically significantly different between males and females but similar between labour groups and left and right side (t-test, critical alpha at 0.01).

Table 7. Analysis of covariance table for variables explaining combined MSM score without radial tuberosity size

Parameter	B	Std. Error	t	Sig.	95% Interval
Intercept	−13.079	6.630	−1.973	0.051	−26.225/0.068
Humerus	0.177	0.072	2.473	0.015	0.035/0.319
Age	0.138	0.021	6.606	0.000	0.096/0.179

Reliability of regression equation $R^2 = 0{,}326$.

Combined MSM score correlated moderately and significantly ($p < 0{,}01$) with age and muscle size in this study (Table 4). Muscle size and size were also correlated strongly and significantly, which is to be expected because larger body needs larger muscles to maintain same functional efficiency. Because males and females were sexually dimorphic in size, sex specific correlation coefficients are provided (Table 5). There were two main differences in sex specific correlations: muscle size was correlated strongly and significantly with age and MSM in females but not in males, and muscle size and size were correlated moderately but significantly in males but not in females (Table 5). This implies that male muscle size is dependent on size whereas muscle size in females depends on encaged activities and age.

The variables explaining combined MSM score were explored using ANCOVA. The model was customized for best predictors for MSM from a set of covariates (age, size, and muscle size), fixed factors (sex, labour intensity) and all possible interactions between these variables. If a covariate, fixed factor or an interaction did not have power in explaining the dependent variable or if it did not enhance the reliability of the model it was excluded from the model.

Sex and labour intensity were not relevant factors explaining combined MSM score. The only significant covariates were age and muscle size (Table 6) where combined MSM scores are elevated with advancing age and increasing muscle size. Muscle size correlates with size and age (Table 2), and therefore I tested whether size also affects combined MSM. ANCOVA was repeated with all other covariates, fixed factor and all possible interactions except muscle size and its interactions. For this test significant factors explaining muscle ruggedness scores were age and size (Table 7). Therefore size is a factor to be considered when interpreting MSM.

Group comparisons of age effects on MSM were made by comparing LSQ-equation parameter estimates (slopes and intercepts). Differences between sexes in the parameter estimates showed that males have higher MSM scores, but the increase per year is similar in both sexes (Table 4). When combined MSM scores were adjusted for muscle size the differences between males and females disappeared (Table 5). This suggests that higher MSM scores in males are due to their bigger sizes and not more intense muscle use.

Labour differences in the slope and intercept measures indicated that heavy physical labour elevates MSM in early life where combined MSM score is high, but the elevation per year is lower than in light labour group (Table 2). Therefore my primary hypothesis of higher elevations in combined MSM score in the heavy labour group was rejected. This also means that in later years of life heavy and light physical labour cannot be separated simply by looking at MSM (Figure 1). The point after which the intensity of labour cannot be separated by higher MSM scores is in the late 50s or early 60s since the two regression lines intersect at 59 years. Males and females were pooled to study for labour intensity effects. There were only nine females with known type of activity, three individuals with heavy labour and six with light labour. Heavy-light labour differences were the same whether including or excluding females. This should be the case if the differences between sexes are due to differences in size (Tables 4 and 5). Size did not account for the differences between heavy and light labour, because

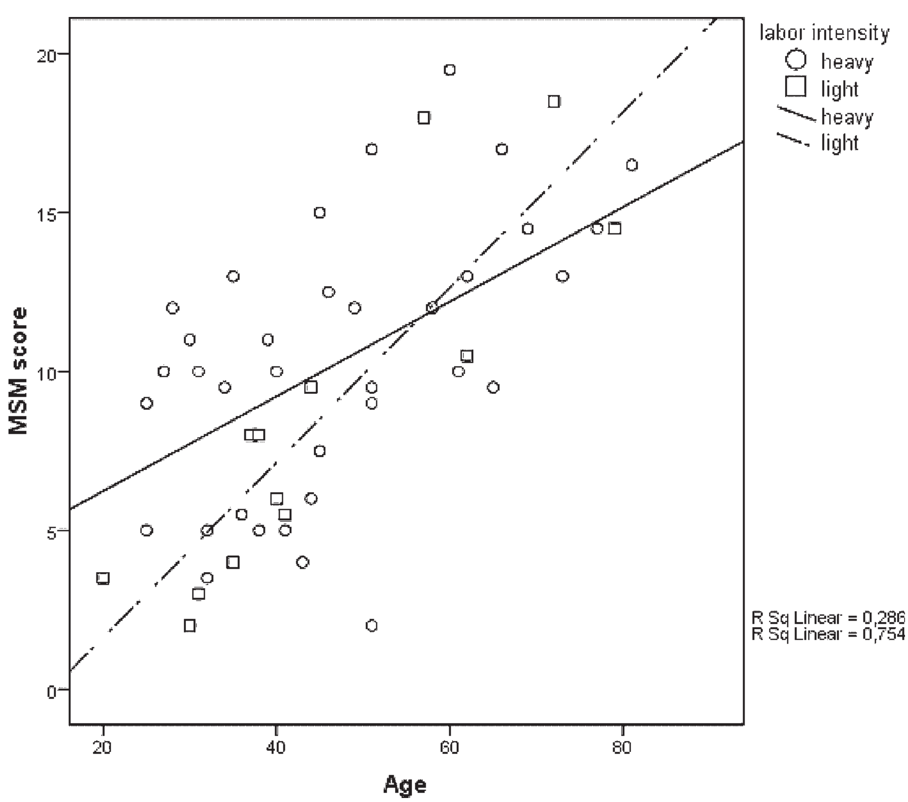

Figure 1. Heavy and light labour group differences in age and combined MSM correlation.

the slopes and intercepts were similar in trend even after muscle size adjustment (Table 5).

Left-right side comparison showed that the intercept on the left side was smaller than the right side, but slopes were steeper in the left than right. The combined MSM score was higher in the right than the left in early life but MSM increased faster in the left than the right, which was similar to the difference in MSM between heavy and light labour (Table 4). Size adjustment eliminated left-right differences as it did between sexes.

Discussion

The main result of this study is that age and size affect the interpretation of labour intensity and that MSM seems incapable of separating labour intensity in later life. This may be due to accumulative effects of age on MSM sites. Also, individuals performing heavy labour have developed their MSM in early life, and it may be that additional stress to MSM site does not show in traditional visual surface scoring very well. It may be that bone has also other mechanisms to respond to muscle induced stress, such as bone distribution in bone shafts and bone mineral density.

In this material actual age was known for all individuals. This made it possible for me to study the effects of age by year rather than comparing age groups as in other studies where age has been assessed by osteometric protocol.

The results of ANCOVA revealed that the main factors affecting MSM are age and muscle size. Both advancing age and increasing muscle size elevate MSM. Muscle size is partially independent of the age because certain muscle size is needed for a given body size to maintain the same functional efficiency regardless of age, but muscle attachment areas also grow with advancing age, but probably only up to a point. Size, as indicated by humeral size in this study, was found to be an important variable together with age. Therefore size does influence MSM. This is in accordance with previous studies (Zumwalt *et al.*, 2000; Mariotti *et al.*, 2004; Molnar, 2006; Zumwalt, 2006; Weiss, 2003, 2004, 2007) where size and/or age have been found to affect MSM. Also muscle insertion areas had been found to correlate with age in earlier studies by Churchill and Morris (1998) and Wilzcak (1998).

Sex was not an important variable explaining MSM. Parameter estimates of males and females showed that MSM scores and thus muscle ruggedness increases at the same rate in both sexes, which would mean that factors affecting muscle scoring function is similar in both sexes, as could be expected. Starting ruggedness was higher in males, which should be a result of bigger muscle sizes in males needed to work with larger bodies. This seems to be true, because male-female differences in MSM disappeared after adjusting for muscle size. This is in agreement with the results of Weiss (2003, 2004, 2007) where sexes did not differ after controlling for size.

Labour intensity and side dominance were also not important factors explaining MSM. Comparison of labour group parameter estimates revealed that MSM scores are high in early life in heavy labour group when muscle markers start to develop after longitudinal growth has ended, but with advancing age the differences in MSM sites between different labour intensities seem to level off. Similar development was found between left and right side, where MSM scores were higher in the right side, which is usually the dominant side. The muscle use of the dominant arm is more in precision tasks whereas heavy manipulation usually employs both hands (Wilzcak, 1998).

Conclusions

Age thus affects MSM, but is this because as one gets older, he/she has done more repetitions, or does older bone tend to develop more surface area to strengthen bone-muscle attachment against decreasing bone density? It has been noted before that bone density decreases (Forbes, 1987; Anderson, 2001), and cortical bone grows thinner and bone shaft diameter increases with age (Mays, 2000).

Higher MSM scores at young age in males, heavy labour group and the right side (interpreted as the dominant arm) could be seen as a result of already stronger muscles (be it due to more repetitions/ loadings or larger muscles required by larger size) attaching to their final position after longitudinal growth has ended (Enlow, 1990) and MSM starts to form. More forceful and/or frequent muscle pulls have induced greater stress to the bone already (which should be shown in higher cross-sectional strength).

MSM did not elevate as much under heavy labour as they did under light labour. This could mean that bone is unable to react to continuous heavy loadings merely on its surface structure and that the increase of MSM scores may slow down after a certain level of stress is reached. Labour group differences were not due to size, because the differences remained after size adjustment.

Labour intensity and side dominance affects the intensity at which muscle ruggedness scores elevate, but these effects can be seen as external whereas age and size could be seen affecting internally. Ageing process and individuals' size are largely independent from engaged activities, but labour intensity and side preference influence the skeleton externally depending on the amount of activity engaged by an individual. Size gives a fixed set of stress depending on overall size and robusticity which sets the requirement for a certain level of muscle mass for a certain body size.

Why is it impossible to tell apart heavy and light labour in old age? It may be that age levels out any differences between the labour groups. As was suggested by Robb (1998), it may be that in old individuals bone may have reached its limits to react to stress and the effects of age are levelled off. Intense use of muscles in heavy labour produces higher scores in early years of life right after longitudinal growth has stopped. Could heavy-light labour separation in later years of life also be impossible because of decreased physical activity and intensity (due to retirement and weakening muscles)? This is not likely to be so, because if both groups stop working, these groups would still have the same mechanisms in which bone density decreases. The heavy labour group should have denser bones and stronger muscles which would wither similarly than the bones and muscles of light labour group, but because the light labour group should have already less bone density and weaker muscles, the decrease should seem more dramatic in the light labour group and the difference in labour intensity should also be seen in later years of life. The mechanisms underlying MSM formation are yet unknown, and bone density studies combined with labour intensity and MSM studies could give a new insight on this matter. Other features could also be used for scoring MSM to separate labour intensity also in old age. I would hypothesize that intense use of muscles could show more in cross-sectional properties and bone density, because bone surface seems to be incapable of reacting to continuing heavy stress.

What does the ruggedness of MSM tell us? It has been shown before and also in this study that larger size and advancing age affect MSM, so labour intensity is the last thing that the scoring system can tell us. For this reason, controlling for age and size is crucial. When comparing labour intensity, it was found that age affects the scorings where differences in labour intensity can only be separated in young individuals, or that the bone surface has limited possibilities to react to heavy stress. Also, it may be that there are other changes in bone at the MSM sites which traditional visual surface scoring systems cannot record. Muscle scoring system can track which muscles are used, but differences in labour intensity can only be separated in young age before levelling the effects of age.

Acknowledgements

I would like to thank Sami Kivelä, David Carrasco, Markku Niskanen and Arja Kaitala for their comments on this paper. This research was funded by Finnish Cultural Foundation.

References

Albrecht GH, Gelvin BR, Hartman SE. 1993. Ratios as size adjustment in morphometrics. *American Journal of Physical Anthropology* **91**: 441–468.

Anderson JJB. 2001. Calcium requirements during adolescence to maximize bone health. *Journal of the American College of Nutrition* **20**: 186S–191S.

Chaffin DB. 1981. Functional assessment for heavy physical labor. *Occupational Health and Safety* **50**(1): 24–32, 64.

Chapman M. 1997. Evidence for Spanish influence on activity induced musculoskeletal stress markers at Pecos Pueblo. *International Journal of Osteoarchaeology* **7**: 497–506.

Churchill SE, Morris AG. 1998. Muscle marking morphology and labor intensity in prehistoric Khoisan Foragers. *International Journal of Osteoarchaeology* **8**: 390–411.

Cook DC, Dougherty SP. 2001. Row, row, row your boat: activity patterns and skeletal robusticity in a series from Chirikof Island, Alaska. *American Journal of Physical Anthropology* **32**: 53 (abstract).

Enlow D. 1990. *Facial Growth*. W.W. Saunders: Philadelphia.

Eshed V, Gopher A, Galili E, Hershkovitz I. 2004. Musculoskeletal stress markers in Natufian hunter-gatherers and neolithic farmers in the Levant: the upper limb. *American Journal of Physical Anthropology* **123**: 303–315.

Forbes GB. 1987. *Human Body Composition: Growth, Ageing, Nutrition, and Activity*. Springer-Verlag. New York.

Havelková P, Villotte S. 2007. Enthesopathies: test of the reproducibility of the new scoring system based on current medical data. *Slovenská antropológia* **10**: 51–57.

Hawkey DE, Merbs CF. 1995. Activity-induced musculoskeletal stress markers (MSM) and subsistence strategy changes among ancient Hudson Bay Eskimos. *International Journal of Osteoarchaeology* **5**: 324–338.

Hopsu RH, Hämäläinen LH. 1957. On variations in the scapula in persons in Finland performing light and heavy work. *Annales Academiae Scientiarum Fennicae. Series A, Volume V. Medica-Anthropologica* 65.

Kannus P, Haapasalo H, Sankelo M, Sievänen H, Pasanen M, Heinonen A, Oja P, Vuori I. 1995. Effect of starting age of physical activity on bone mass in the dominant arm of tennis and squash players. *Annals of Internal Medicine* **123**: 27–31.

Kennedy KAR. 1989. Skeletal markers of occupational stress. In *Reconstruction of Life from the Skeleton*, Iscan M, Kennedy K (eds). Alan R. Liss: New York; 129–160.

Kennedy KAR. 1998. Markers of occupational stress: conspectus and prognosis of research. *International Journal of Osteoarchaeology* **8**(5): 305–310.

Lieberman DE, Osbjorn M, Pearson JD, Polk BD, Crompton AW. 2003. Optimization of bone growth and remodeling in response to loading in tapered mammalian limbs. *Journal of Experimental Biology* **206**: 3125–3138.

Mariotti V, Facchini F, Belcastro MG. 2004. Enthesopathies—proposal of a standardized scoring method and applications. *Collegium Antropologicum* **28**: 145–159.

Mays S. 2000. Age-dependent cortical bone loss in women from 18th and early 19th century London. *American Journal of Physical Anthropology* **112**: 349–361.

Molnar P. 2006. Tracing prehistoric activities: musculoskeletal stress markers of a stone-age population on the island of Gotland in the Baltic Sea. *American Journal of Physical Anthropology* **129**: 12–23.

Nagy BLB. 1998. Age, activity, and musculoskeletal stress markers. *American Journal of Physical Anthropology* **26**: 168–169 (abstract).

Nagy BLB. 1999. Bioarchaeological evidence for atl-atl use in prehistory. *American Journal of Physical Anthropology* **28**: 208 (abstract).

Nagy BLB, Hawkey DE. 1995. Musculoskeletal stress markers as indicators of sexual division of labor: multivariate analyses. *American Journal of Physical Anthropology* **20**: 158 (abstract).

Niskanen M, Junno J-A. 2009. Estimation of African apes' body size from postcranial dimensions. *Primates* **50**: 211–220.

Robb JE. 1998. The interpretation of skeletal muscle sites: a statistical approach. *International Journal of Osteoarchaeology* **8**: 363–377.

Ruff C. 2003. Growth in bone strength, body size, and muscle size in juvenile longitudinal sample. *Bone* **33**: 317–329.

Ruff C, Holt B, Trinkaus E. 2006. Who's afraid of the big bad Wolff? "Wolff's Law" and bone functional adaptation. *American Journal of Physical Anthropology* **129**: 484–498.

Telkkä A. 1950. On the prediction of the human stature from the long bones. *Acta Anatomica* **9**: 103–117.

Villotte S. 2006. Connaissances médicales actuelles, cotation des enthésopathies: nouvelle méthode. *Bulletins et Mémoires de la Société d'Anthropologie de Paris* **18**: 65–85.

Weiss E. 2003. Understanding muscle markers: aggregation and construct validity. *American Journal of Physical Anthropology* **121**: 230–240.

Weiss E. 2004. Understanding muscle markers: lower limbs. *American Journal of Physical Anthropology* **125**: 232–238.

Weiss E. 2007. Muscle markers revisited: activity pattern reconstruction with controls in a Central California Amerind population. *American Journal of Physical Anthropology* **133**: 931–940.

Wescott DJ, Cunningham DL. 2006. Temporal changes in Arikara humeral and femoral cross-sectional geometry associated with horticultural intensification. *Journal of Archeological Science* **33**: 1022–1036.

Wilzcak C. 1998. Consideration of sexual dimorphism, age, and asymmetry in quantitative measurements of muscle insertion sites. *International Journal of Osteoarchaeology* **8**: 311–325.

Zumwalt A. 2006. The effect of endurance exercise on the morphology of muscle attachment sites. *Journal of Experimental Biology* **209**: 444–454.

Zumwalt A, Ruff C, Wilczak C. 2000. Primate muscle insertions: what does size tell you? *American Journal of Physical Anthropology* **30**: 331 (abstract).

Appendix 1. Occupation and labour intensity

Occupation	(males/females)	Intensity
Workman	(34/2)	heavy
Carpenter	(1/0)	heavy
Bricklayer	(1/0)	heavy
Seaman	(4/0)	heavy
Fireman	(1/0)	light
Shoemaker	(2/0)	light
Painter	(2/0)	light
Landlord	(2/0)	light
Servant	(0/4)	light
Housemaid	(0/1)	light
Foreman	(1/0)	light
Office worker	(1/0)	light
Driver	(1/0)	light
Businessman	(1/0)	light
Seamstress	(0/1)	light
Upholsterer	(1/0)	light
Bookbinder	(1/0)	light
Taylor	(1/0)	light
Prisoner	(27/1)	unknown
Vagabond	(1/1)	unknown
Unmarried	(1/0)	unknown
Wife	(0/1)	unknown
Widow	(1/2)	unknown
Daughter	(0/2)	unknown
Senior citizen	(2/1)	unknown
Unknown	(40/17)	unknown