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Subsistence strategy changes: The evidence of entheseal changes

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ABSTRACT

Changes in subsistence strategy have caused some of the profoundest changes to the structure and health of humans. This study aims to test whether these changes have reduced work-load as assessed by entheseal changes. Entheseal changes, formerly called musculoskeletal stress markers, are thought to reflect muscle usage throughout life, although it is widely agreed that they have a multifactorial origin. This paper uses a meta-analysis of comparable published data to plot trends in time by muscle, enthesis type and sex. The results show that agriculturalists have the lowest scores for entheseal changes, with hunte–gatherers next highest and those working in industry the highest. These findings are the same for males and females, for most muscles and muscle groups. However, entheseal changes are highly correlated with increased age and the age distributions of the samples analysed could not be compared. It is, therefore, possible that differences in age distribution of the samples are one of the reasons for this finding. Recommendations are provided to reduce this and other limitations for future meta-analyses.

Introduction

Humans evolved as hunter–gatherers and, as such, our genetic make-up and physiology should be best adapted to this lifestyle (Bellisari, 2007; Chakravarthy and Booth, 2004; Cordain et al., 2007; Eaton and Eaton, 2003). Anthropological research, particularly using generalised indicators of activity,

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e.g. cross-sectional geometry, predominantly indicates that levels of physical activity have reduced Q2 through time due to subsistence strategy changes (Larsen, 1994; Ruff, 1987; Sparacello and Marchi, 2008). This reduction in mobility alongside other lifestyle changes has increased morbidity (Larsen, 1995; Steckel and Rose, 2002b), i.e. humans are poorly adapted to more recent subsistence strategy changes. This is a clear oversimplification of evolutionary biology (Eaton et al., 2002), of the energy expenditure involved in agriculture (Bellisari, 2007), and biocultural differences in the activities involved in subsistence strategy in different environments (Bridges, 1992). However, the generalised trends do seem to support it. This paper aims to use more specific indicators of physical activity, i.e. supposed markers of muscle use, to study the effect of subsistence strategy in general and for each muscle.

The increase in morbidity is supported anthropologically by the decline in health, which has been documented with the adoption of agriculture (e.g. Larsen, 1995; Steckel and Rose, 2002b). The Global History of Health project has used evidence from degenerative joint disease (DJD) to study the effect of lifestyle (e.g. subsistence strategy and industrialisation), and region (including altitude) on activity-levels (Steckel and Rose, 2002a). Studies using DJD have found an increase in activity in industrial populations (Steckel et al., 2002), but the trends are not uniform for changes associated with the adoption of agriculture (Cohen and Armelagos, 1984; Bridges, 1992; Larsen, 2002). This is unsurprising given the multi-factorial aetiology of these changes (Jurmain, 1999). A recent study of DJD (Cardoso, 2008) using identified skeletons found no association with occupation once the effect of age was taken into account. It is, therefore, possible that different age structures in the samples may have been one of the factors causing the lack of uniformity in results. However, it has now been acknowledged that DJD is not an appropriate stand-alone method for studying activity-related stress (Jurmain et al., 2012).

Entheseal changes (EC) are changes to the normal surface structure of muscle, tendon and ligament attachments to bone. EC are thought to occur primarily due to activity-related stress, particularly repetitive movement (Hawkey and Merbs, 1995; Henderson et al., 2013). Consequently, they have been widely and systematically recorded to study activity-levels and activity-patterns since the mid-1990s (reviews: Henderson and Alves Cardoso, 2013; Jurmain et al., 2012). Activity-pattern is defined here to mean which types of activities, based on muscle usage, were most common. Recent research has questioned this simplistic interpretation, as disease and age along with one-off trauma (e.g. soft tissue ruptures when falling) are all associated with these changes and cannot, currently, be distinguished (Jurmain et al., 2012; Henderson and Alves Cardoso, 2013; Henderson, 2013; Villotte and Knüsel, 2013). Nevertheless, there is a large body of literature which has systematically reported the results of activity-patterns in archaeological and identified skeletal collections (reviews: Henderson and Alves Cardoso, 2013; Jurmain et al., 2012).

One study has compared EC between hunter–gatherers and agriculturalists (Eshed et al., 2004). These authors found a reduction with the adoption of agriculture. However, this study has a relatively small sample size and is focussed on one limited geographic area. The aim of this paper is to review the body of literature to explore the effect of subsistence strategy on EC. The hypothesis to be tested is that hunter–gatherers are best adapted to their environment and lifestyle and that mean scores of entheseal changes will increase from hunter–gatherers, to agriculturalists and be highest industrial populations who have had the least time to adapt to their working life.

Materials and methods

This meta-analysis uses papers found using Google Scholar and Web of Science between 1995 and the end of June 2012. The cut-off dates were chosen based on the publication of the method (Hawkey and Merbs, 1995) and the end date was chosen as the point at which data were collected. The search criteria were the citation of the original publication (Hawkey and Merbs, 1995). While meta-analyses in medical journals may suffer from publication bias, i.e. only favourable results are published, most of the studies on EC are exploring results, therefore publication bias is unlikely to be a limitation of this study.

The method developed by Hawkey (1988) has been very widely used (Chapman, 1997; Hawkey, 1998; Hawkey and Merbs, 1995; Lovell and Dublenko, 1999; Peterson, 1998; Steen and Lane, 1998), but was developed prior to recent developments in anatomical knowledge summarised in Jurmain et al.

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(2012). Specifically, there is no differentiation in scoring system between fibrous and fibrocartilaginous entheses which is vital as their normal appearance on skeletal remains differs significantly. Fibrous entheses are generally found on the diaphyses of long bones where the soft tissue attaches to the bone either directly or via the periosteum (Benjamin et al., 2002). These entheses normally have a slightly roughened appearance and are poorly demarcated on the bone (Benjamin et al., 2002; Henderson et al., 2013). Fibrocartilaginous entheses are located in close proximity to joints and, in contrast, are normally smooth with well defined margins, due to the mediation of two layers of fibrocartilage between the soft and hard tissues (Benjamin et al., 2002). Not only is this difference not taken into account by this recording method, the normal appearance, i.e. the roughened surface of fibrous entheses, is one of the key features of the recording method. This is a key limitation and one which is rarely addressed by those using this method. The point at which normal fibrous enthesis roughness ends and abnormal roughness begins is also currently under discussion and no consensus has been reached (Henderson et al., 2013). This leads on to a further problem with the data analysis commonly used in these publications. Often enthesis scores are ranked to determine which muscles were used most frequently. However, the recording method may create an inherent bias towards higher scores for fibrous entheses. For these reasons, new methods are being developed to avoid these issues (Henderson, 2013; Henderson et al., 2013; Villotte, 2006). To mitigate against this issue, the results were analysed by sex, side, enthesis, and pooled into fibrous and fibrocartilaginous groups. Only those entheses recorded by all researchers were pooled to ensure comparability between the subsistence strategies. Data were not pooled by joint due to the limited number of studies which recorded the same entheses. The problem of the increase in EC with age could not be taken into account due to the limited data and the problems associated with ageing skeletons.

Scores of EC recorded using this method range from 0 to 5 and are reported as presenting an increase in severity (Hawkey and Merbs, 1995). To ensure comparability the following data had to be present in the report: mean enthesis score presented by side and sex. Where available, data on sample size were also collected. Subsistence strategy and economy were recorded based on the interpretation of the archaeology presented in the paper. All missing data were removed. As the data collected are means of ordinal data, which are not normally distributed, no inferential statistics were used to analyse the data. Box plots with standard errors of means were plotted in the 64 bit version of the statistics package R version 2.15.1. Effect sizes were calculated to determine whether any differences between groups were meaningful (Bond et al., 2003; Field and Gillett, 2010). Two effect sizes were calculated using Eqs. (1)–(3) where the control is the hunter–gatherer sample for all comparisons except that between agricultural and industrial samples, for which the agricultural sample is used as the control. The sample size used was that of the number of sites, and not the number of skeletons. This is because the data sets are based on the mean from each site, which was the only information available from all papers:

$$\text{Glass's}\quad \Delta = \frac{(x_1 - x_2)}{s_1} \tag{1}$$

$$\text{Cohen's}\quad d = \frac{(\bar{x}_1 - \bar{x}_2)}{\sqrt{\left(\frac{\left((n_1-1)s_1^2+(n_2-1)s_2^2\right)}{(n_1+n_2-2)}\right)}} \tag{2}$$

$$d_{\text{unbiased}} = d_{\text{Cohen's}\ d}\left[1 - \left(\frac{3}{(4(n_1+n_2)-1)}\right)\right], \tag{3}$$

where $\bar{x}_1 =$ mean of control, n_1 = sample size of control, s_1 = standard deviation of control.

Results

Twenty three publications (Cardoso, 2008; Chapman, 1997; Clapper, 2006; Doying, 2010; Eshed et al., 2004; Hawkey, 1998; Hawkey and Merbs, 1995; Lieverse et al., 2009; Lovell and Dublenko, 1999; Molnar, 2006, 2008; Molnar et al., 2009; Niinimäki, 2012; Pany, 2005; Papathanasiou, 2005; Peterson,

Table 1
List of papers used for the meta-analysis subsistence strategy and geographic location. Original data can be found in the Appendix A.

Reference	Country or region	Period	Subsistence strategy
Chapman (1997)	Mexico	Pre-contact	Agricultural
		Post-contact	Agricultural
Doying (2010)	New Mexico	Post-medieval	Industrial
Eshed et al. (2004)	Levant	Natufian	Hunter–gatherer
		Neolithic	Agricultural
Hawkey and Merbs (1995)	Hudson Bay	Early period	Hunter–gatherer
		Late period	Hunter–gatherer
Pany (2005)	Austria	Early iron age – salt mine	Industrial
Peterson (1998)	Levant	Natufian	Hunter–gatherer
Steen and Lane (1998)	Alaska	Pre-historic	Hunter–gatherer
		300-80BP	Hunter–gatherer
Weiss (2007)	California	2180-250BP	Hunter–gatherer
Wysocki and Whittle (2000)	England	Neolithic	Transitional
Zabecki (2009)	Eqypt	Pre-dynastic	Agricultural
		Old Kingdom	Agricultural
		Middle Kingdom	Agricultural

1998; Steen and Lane, 1998; Toyne, 2008; Weiss, 2003, 2007; Weiss et al., 2010; Wysocki and Whittle, 2000; Zabecki, 2009) were found which recorded skeletons using this method, but of these only 11 reported the mean scores by sex, side and entheses (listed in Table 1 with the eleventh paper, Lieverse et al., 2009). All bar one of these (Lieverse et al., 2009), reported data on the right side, therefore only ten reports could be compared and these are listed in Table 1. Of these only two reports (Doying, 2010; Pany, 2005) discuss industrial societies, but it should be noted that there are large temporal and geographic differences (as well as differences in daily activities) between these two. One site is reported by the archaeologists as representing a transitional economy between hunting, gathering and growing crops (Wysocki and Whittle, 2000), therefore these data were placed in a separate category (Table 1). Sample sizes were small for most studies with a mean sample size of 18.6, standard deviation of 14 and a range of 1 to 77. It should be noted that all sample sizes of zero were excluded from this analysis. The original data can be found in Appendix A.

Males and females and fibrous and fibrocartilaginous entheses all demonstrated the same trends in scores, with the agriculturalists having the lowest mean scores, hunter–gathers higher scores and industrial societies the highest scores (Table 2 and Figs. 1–3), while the transitional scores fall between the two groups. Glass's Δ demonstrates large effect sizes, but this does not take into account sample size, the unbiased *d* (Eq. (3)) presents smaller but still important effect sizes. The small sample size and its non-normal distribution mean that these results have to be interpreted with caution but they highlight that the differences seen in the means are real. Only one paper directly compared hunter–gather and agricultural populations living in the same geographic location (Eshed et al., 2004). Data from this publication were compared to the other results, to ascertain whether inter-observer error is solely responsible for these results. However, the same trend—agriculturalists had lower scores than hunter–gatherers—was found with meaningful effect sizes (Table 3).

Outliers were found (Appendix A), but the majority corresponded to small sample sizes ($n < 20$). Only one outlier with a larger sample size was found for the females. This was the *latissimus dorsi* enthesis for a Californian hunter–gatherer site which had a very low score (Weiss, 2007). Interestingly, the same was found for males from this site. Other male entheses with outliers were the *biceps brachii*, deltoid and *pectoralis major* insertions from a Natufian site, which had low scores compared to the other hunter–gatherers (Eshed et al., 2004). The final male outlier in this category was the *subclavius* insertion from an early period Hudson Bay site, which had a higher score than other hunter–gatherers (Hawkey and Merbs, 1995).

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Table 2
Scores of entheseal changes by sex and subsistence strategy. All insertion sites unless otherwise stated. Cut-off points for effect sizes (presented here as absolute values): small <0.50, medium <0.80, large >0.80 (Cohen, 1988).

Enthesis	Sex	Hunter–gatherer						Agricultural					
		Mean	Min	Max	St. Dev.	*n* (site)	*n* (skel)	Mean	Min	Max	St. Dev.	*n* (site)	*n* (skel)
Anconeus	Male	1.54	0.90	1.90	0.41	5	86	0.57	0.27	1.00	0.38	3	67
	Female	1.31	1.00	1.60	0.25	5	66	0.47	0.13	1.10	0.55	3	61
Biceps brachii	Male	1.96	0.80	2.71	0.66	6	144	1.25	0.88	1.59	0.25	6	83
	Female	1.52	0.80	2.22	0.51	6	124	0.92	0.70	1.23	0.22	6	96
Brachialis	Male	1.93	1.40	2.40	0.40	6	110	1.40	0.88	2.00	0.47	6	114
	Female	1.72	1.10	2.00	0.36	5	84	1.09	0.43	1.90	0.61	6	130
Common extensor (O)	Male	1.93	1.45	2.41	0.68	2	35	0.84	0.60	0.94	0.14	5	64
	Female	1.56	1.11	2.00	0.63	2	22	0.83	0.43	1.13	0.28	5	77
Common flexor (O)	Male	1.85	1.30	2.17	0.48	3	43	0.82	0.60	0.98	0.16	5	87
	Female	1.35	0.91	1.79	0.62	2	25	0.79	0.48	1.18	0.34	5	71
Conoid ligament	Male	1.59	1.40	1.83	0.22	3	39	1.12	0.67	1.80	0.44	5	79
	Female	1.72	1.44	2.00	0.40	2	30	0.96	0.63	1.88	0.53	5	109
Coracobrachialis	Male	1.07	1.00	1.17	0.09	3	46	0.07	0.04	0.09	0.04	2	69
	Female	1.13	1.08	1.18	0.07	2	34	0.07	0.04	0.10	0.05	2	74
Costoclavicular ligament	Male	3.14	1.60	4.24	0.92	6	84	2.20	0.60	3.00	1.13	4	38
	Female	1.93	0.80	2.50	0.66	5	63	1.90	1.00	2.71	0.71	4	58
Deltoid	Male	2.17	1.20	2.74	0.51	7	170	1.20	0.56	1.80	0.54	6	96
	Female	1.83	1.40	2.14	0.25	6	171	1.07	0.59	1.60	0.39	6	102
Extensors and supinators(O)	Male	1.67	0.80	2.40	0.81	3	39	1.50	1.50	1.50	0.00	1	2
	Female	1.13	0.80	1.30	0.29	3	34	1.20	1.20	1.20		1	5
Infraspinatus	Male	1.40	0.94	1.80	0.44	4	49	0.97	0.96	0.98	0.01	2	52
	Female	1.01	0.75	1.38	0.33	3	36	0.95	0.94	0.95	0.01	2	46
Infraspinatus and supraspinatus	Male	1.20	0.50	1.90	0.99	2	17	2.00	2.00	2.00	0.00	1	1
Latissimus dorsi	Male	1.47	0.73	2.20	0.44	7	143	0.59	0.15	1.60	0.52	6	97
	Female	0.98	0.16	1.20	0.41	6	141	0.37	0.12	0.60	0.16	6	115
Pectoralis major	Male	3.17	2.20	5.29	0.99	7	161	1.65	0.73	3.30	0.85	7	106
	Female	2.16	1.80	2.89	0.48	6	149	1.47	1.06	2.40	0.51	6	140
Pectoralis minor	Male	1.36	0.96	2.00	0.44	6	61	0.53	0.53	0.53	0.00	1	16
	Female	1.53	1.00	1.83	0.39	4	41	0.80	0.56	1.00	0.22	3	20
Pronator quadratus	Male	1.00	0.40	1.80	0.54	5	57	0.35	0.08	0.80	0.40	3	66
	Female	0.66	0.07	1.30	0.62	3	45	0.20	0.00	0.50	0.26	3	67
Pronator teres	Male	1.40	0.60	2.00	0.52	6	68	0.74	0.40	1.40	0.57	3	66
	Female	0.94	0.30	1.30	0.39	5	50	0.55	0.29	1.00	0.39	3	72
Subclavius	Male	1.26	0.60	2.00	0.46	6	96	0.69	0.40	1.40	0.37	6	89
	Female	1.07	0.40	1.46	0.40	5	71	0.45	0.14	1.20	0.39	6	117
Supinator	Male	1.04	0.30	1.70	0.50	6	72	0.34	0.00	0.80	0.27	6	97
	Female	0.89	0.80	1.10	0.13	5	62	0.28	0.04	0.70	0.24	6	114
Supinator(O)	Male	1.03	0.90	1.16	0.18	2	62	0.51	0.19	1.00	0.43	3	77

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Table 2 (*Continued*)

Enthesis	Sex	Hunter–gatherer						Agricultural					
		Mean	Min	Max	St. Dev.	*n* (site)	*n* (skel)	Mean	Min	Max	St. Dev.	*n* (site)	*n* (skel)
	Female	0.70	0.60	0.79	0.13	2	63	0.65	0.19	1.40	0.65	3	73
Supraspinatus	Male	1.29	1.10	1.64	0.24	4	33	0.85	0.83	0.87	0.03	2	49
	Female	1.07	0.62	1.50	0.44	3	38	0.78	0.78	0.78		1	16
Teres major	Male	2.18	0.80	3.44	0.98	6	139	1.31	0.62	2.10	0.55	6	89
	Female	1.74	0.40	3.40	1.07	6	135	1.18	0.83	2.14	0.50	6	104
Teres minor	Male	1.42	0.00	3.86	1.34	6	52	0.95	0.91	1.00	0.05	3	34
	Female	0.91	0.33	1.40	0.54	3	42	0.72	0.17	1.30	0.57	3	46
Trapezius	Male	1.63	1.17	2.20	0.37	6	59	0.91	0.90	0.92	0.01	2	50
	Female	1.32	1.20	1.40	0.08	4	36	1.31	0.43	2.20	1.26	2	25
Trapezoid ligament	Male	1.86	1.60	2.00	0.22	3	40	0.56	0.31	1.00	0.28	5	70
	Female	1.61	1.54	1.67	0.09	2	29	0.87	0.41	2.63	0.98	5	93
Triceps brachii	Male	1.45	0.80	1.90	0.44	6	118	0.73	0.18	1.60	0.49	6	105
	Female	1.04	0.35	1.43	0.42	6	110	0.32	0.12	0.60	0.21	6	113

Enthesis	Sex	Industrial							Agriculture & Hunter		Industry & Hunter		Industry & Agriculture	
		Mean	Median	Min	Max	St. Dev.	*n* (site)	*n* (skel)	Glasses delta	Unbiased *d*	Glasses delta	Unbiased *d*	Glasses delta	Unbiased *d*
Anconeus	Male						0	0	−2.37	**−2.11**				
	Female			0.00	0.00		0	0	−3.37	**−1.94**		0.00		0.00
Biceps brachii	Male	4.14	4.14	4.00	4.28	0.20	2	63	−1.07	**−1.31**	3.31	**3.13**	11.38	**10.24**
	Female	4.19	4.19	3.97	4.40	0.30	2	38	−1.17	**−1.40**	5.23	**4.81**	15.16	**12.21**
Brachialis	Male	4.36	4.36	4.36	4.36	0.00	1	25	−1.34	**−1.13**	6.12	**5.15**	6.31	**5.31**
	Female	4.57	4.57	4.57	4.57		1	14	−1.73	**−1.12**	7.81	**6.25**	5.74	**4.84**
Common extensor (O)	Male	2.80	2.80	2.80	2.80	0.00	1	10	−1.61	**−2.80**	1.28	**1.03**	14.04	**11.23**
	Female	1.71	1.71	1.71	1.71		1	7	−1.15	**−1.61**	0.25	0.00	3.12	**2.49**
Common flexor (O)	Male	3.08	3.08	3.08	3.08	0.00	1	12	−2.16	**−2.95**	2.55	**2.04**	14.50	**11.60**
	Female	1.67	1.67	1.67	1.67		1	9	−0.89	**−1.14**	0.51	0.00	2.61	**2.09**
Conoid ligament	Male	2.45	2.45	2.45	2.45	0.00	1	11	−2.16	**−1.08**	3.93	**3.14**	3.02	**2.41**
	Female	3.13	3.13	3.13	3.13		1	8	−1.92	**−1.27**	3.56	0.00	4.11	**3.29**
Coracobrachialis	Male						0	0	−11.52	**−9.82**				
	Female			0.00	0.00		0	0	−14.98	**−10.10**				
Costoclavicular ligament	Male	5.00	5.00	5.00	5.00	0.00	1	15	−1.01	**−0.84**	2.02	**1.47**	2.47	**1.80**
	Female	3.50	3.50	3.50	3.50		1	6	−0.05	−0.04	2.40	**1.92**	2.27	**1.65**
Deltoid	Male	3.88	3.88	3.88	3.88	0.00	1	40	−1.91	**−1.73**	3.36	**2.83**	4.95	**4.16**

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Table 2 (*Continued*)

Enthesis	Sex	Industrial							Agriculture & Hunter		Industry & Hunter		Industry & Agriculture	
		Mean	Median	Min	Max	St. Dev.	*n* (site)	*n* (skel)	Glasses delta	Unbiased *d*	Glasses delta	Unbiased *d*	Glasses delta	Unbiased *d*
	Female	4.00	4.00	4.00	4.00		1	29	−3.04	**−2.16**				
Extensors and supinators(O)	Male						0	0	−0.21					
	Female			0.00	0.00		0	0	0.23	0.13				
Infraspinatus	Male	3.40	3.40	3.40	3.40	0.00	1	15	−0.97	**−0.89**	4.54	0.00	228.96	0.00
	Female	2.43	2.43	2.43	2.43		1	7	−0.19	−0.17	4.31	**2.47**	174.89	0.00
Infraspinatus and supraspinatus	Male						0	0	0.81	**0.00**		0.00		
Latissimus dorsi	Male	3.79	3.79	3.79	3.79	0.00	1	14	−2.00	**−1.70**	5.27	**4.44**	6.10	**5.14**
	Female	3.00	3.00	3.00	3.00		1	3	−1.48	**−1.80**	4.97	**4.19**	16.45	**13.85**
Pectoralis major	Male	3.85	3.85	3.80	3.90	0.07	2	55	−1.53	**−1.54**	0.69	0.66	2.59	**2.49**
	Female	3.74	3.74	3.33	4.14	0.57	2	37	−1.42	**−1.28**	3.25	**2.74**	4.46	**3.79**
Pectoralis minor	Male						0	0	−1.88	**−1.59**				
	Female			0.00	0.00		0	0	−1.91	**−1.88**				
Pronator quadratus	Male						0	0	−1.22	**−1.15**				
	Female			0.00	0.00		0	0	−0.74	−0.77				
Pronator teres	Male						0	0	−1.28	**−1.10**				
	Female			0.00	0.00		0	0	−0.99	**−0.86**				
Subclavius	Male						0	0	−1.22	**−1.25**				
	Female			0.00	0.00		0	0	−1.51	**−1.40**				
Supinator	Male						0	0	−1.41	**−1.62**				
	Female			0.00	0.00		0	0	−4.58	**−2.83**				
Supinator(O)	Male						0	0	−2.81	**−1.02**				
	Female			0.00	0.00		0	0	−0.30	−0.05				
Supraspinatus	Male						0	0	−1.83	**−1.69**				
	Female			0.00	0.00		0	0	−0.66	−0.38				
Teres major	Male	4.11	4.11	4.09	4.12	0.02	2	51	−0.89	**−1.01**	1.97	**1.87**	5.11	**4.87**
	Female	3.74	3.74	3.09	4.38	0.91	2	37	−0.52	−0.61	1.88	**1.67**	5.13	**3.78**
Teres minor	Male						0	0	−0.35	−0.37				
	Female			0.00	0.00		0	0	−0.35	−0.28				
Trapezius	Male	2.63	2.63	2.63	2.63	0.00	1	8	−1.93	**−1.84**	2.68	0.00	121.62	0.00
	Female	2.00	2.00	2.00	2.00		1	6	−0.03	0.00	8.21	**5.97**	0.55	0.00
Trapezoid ligament	Male						0	0	−5.82	**−4.29**				
	Female			0.00	0.00		0	0	−7.95	−0.70				
Triceps brachii	Male	3.43	3.43	2.93	3.92	0.70	2	54	−1.67	**−1.44**	4.52	**3.50**	5.47	**4.40**
	Female	3.27	3.27	2.50	4.04	1.09	2	42	−1.70	**−1.98**	5.28	**3.30**	13.79	**5.29**

Bold effect sizes indicate large differences, but only presented for the most conservative estimate. Data for which no effect size could be calculated have been removed. O = origin; *n* (site) = number of sites; and *n* (skel) = number of skeletons.

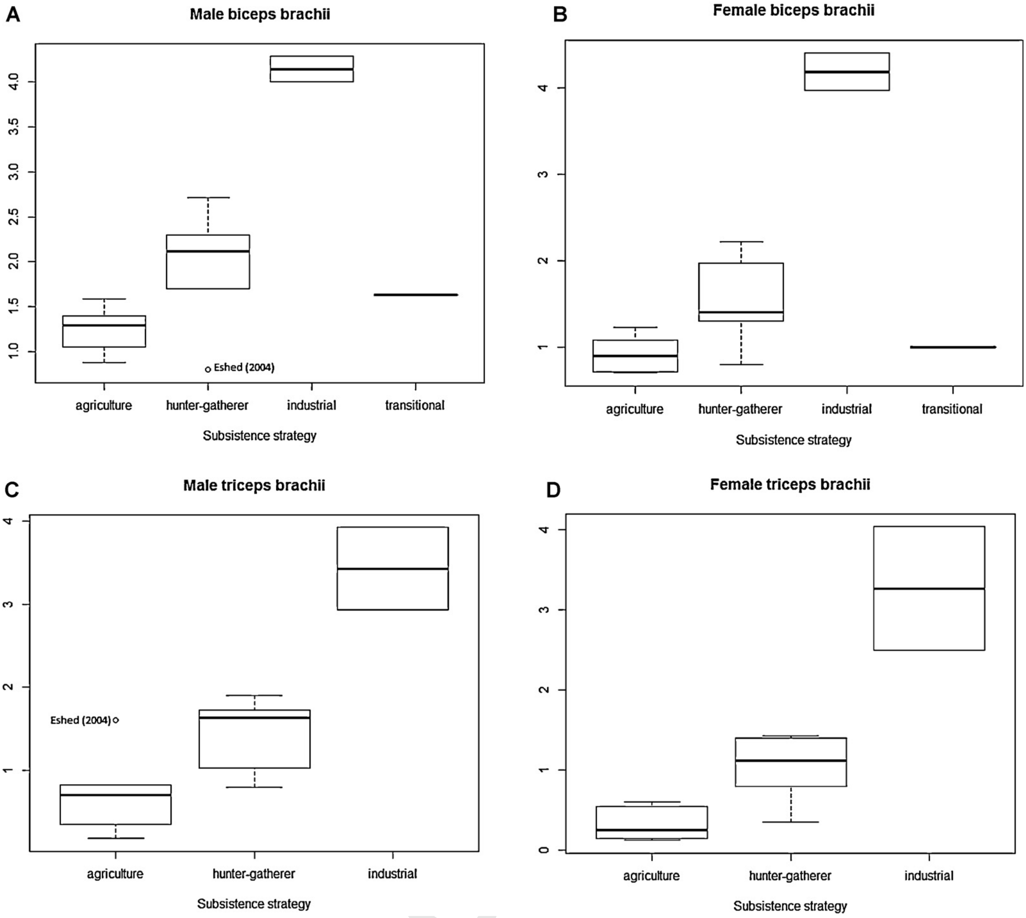

Fig. 1. Boxplots (whiskers represent the data within the 1.5 interquartile range) for the most commonly recorded fibrocartilaginous entheses, outliers are marked by reference. (A) *Male biceps brachii*; (B) Female *biceps brachii*; (C) Male *triceps brachii*; (D) Female *triceps brachii*. Y-axis presents the score (max is 6).

Table 3
Effect sizes for comparison of hunter–gatherer (HG) and agriculturalists (A) using pooled fibrocartilaginous (FC) and fibrous entheses (Eshed et al., 2004).

Sex	Anatomy	Difference of mean	Standard deviation HG	Standard dev A	*n* HG	*n* A	Glass's delta	Cohen's *d*	Unbiased *d*
Female	FC[a]	−0.25	0.15	0.57	4	4	−1.67	−0.60	−0.52
Female	Fibrous[b]	−0.36	0.51	0.49	12	12	−0.70	−0.71	−0.69
Male	FC[c]	−0.68	0.30	0.39	6	6	−2.28	−1.96	−**1.80**
Male	Fibrous[d]	−0.52	0.54	0.70	13	13	−0.95	−0.83	−**0.80**

Difference of mean calculated as A minus HG, n = number of entheses in the pool. Cut-off points for effect sizes (presented here as absolute values): small <0.50, medium <0.80, large >0.80 (Cohen, 1988). Bold effect sizes for the unbiased d indicate large differences.

[a] *biceps brachii*, *brachialis*, *triceps brachii* and the combined *extensor* and *supinator* origin.

[b] *anconeus*, *costoclavicular ligament*, *deltoid*, *latissimus dorsi*, *pectoralis major*, *pronator quadratus* (origin), *pronator teres*, *subclavius*, *supinator* (origin), *supinator*, *teres major* and the combined *brachioradialis* and *extensor carpi radialis longus* (origin).

[c] *biceps brachii*, *brachialis*, combined *infra-* and *supraspinatus*, *teres major*, *triceps brachii* and the combined *extensor* and *supinator* origin.

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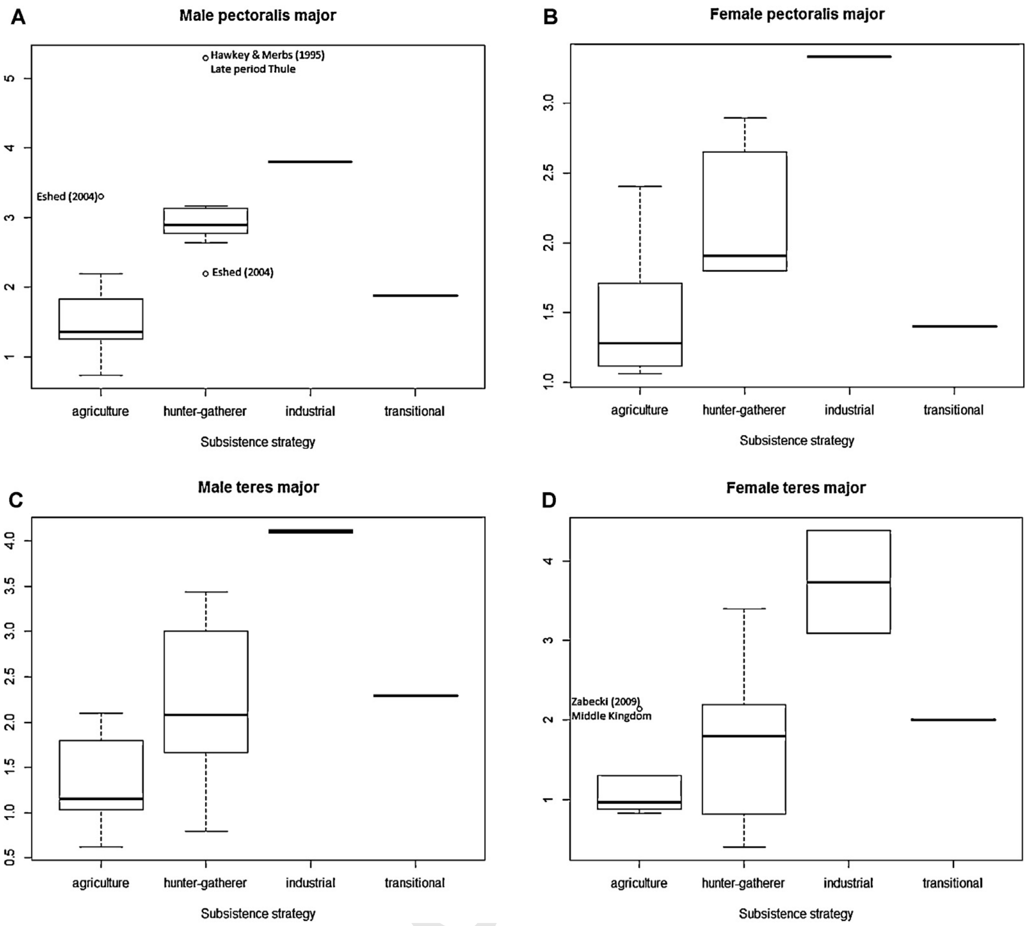

Fig. 2. Boxplots (whiskers represent the data within the 1.5 interquartile range) for the most commonly recorded fibrous entheses, outliers are marked by reference. (A) Male *pectoralis major*; (B) Female *pectoralis major*; (C) Male *teres major*; (D) Female *teres major*. Y-axis presents the score (max is 6).

Discussion

The aim of this paper was to present a meta-analysis of published data on EC recorded using the most commonly used method, that developed by Hawkey (1988) to determine whether differences in EC patterns due to subsistence strategies can be found. The results highlight that there are general trends which hold for all entheses and both sexes, with agricultural populations having the lowest mean scores and industrial populations the highest. The hypothesis that hunter–gatherers are best adapted to the physical demands of life is not supported, but the high scores of the industrial samples do support the idea that these populations have had the least time to adequately adapt to their workload.

This study has some very serious limitations, there are only ten papers to draw data from and, as there is no consensus on which entheses to record, this reduced the data set further. Recommendations need to be drawn up by the working groups on entheseal changes, set up in 2009 (Henderson, 2012; Perréard Lopreno et al., 2012; Santos et al., 2011), to decide which minimum set of entheses should be recorded to enable meta-analyses to be performed. These working groups will also standardise the methods for recording to ensure that fibrous and fibrocartilaginous entheses are recorded appropriately. As discussed in the introduction, the method used in this study is not biologically appropriate,

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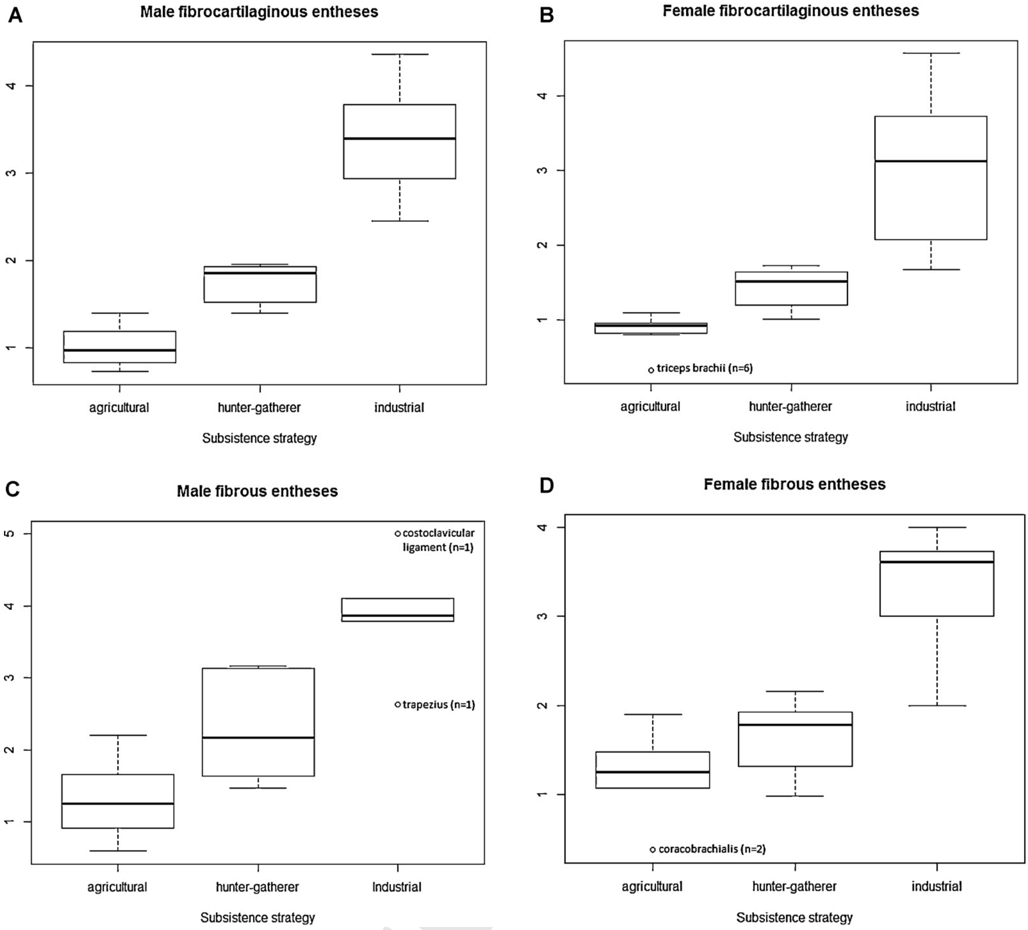

Fig. 3. Boxplots (whiskers represent the data within the 1.5 interquartile range) for the pooled means of the pooled entheses, outliers are marked by enthesis. Y-axis presents the score (max is 6). (A) Male fibrocartilaginous with unbiased effect sizes (unbiased *d*) between hunter–gatherer and agriculturalists = −2.82; hunter–gather and industrialists = 4.28; agriculturalists and industrialists = 6.20. (B) Female fibrocartilaginous with unbiased effect sizes (unbiased *d*) between hunter–gatherer and agriculturalists = −2.07; hunter–gather and industrialists = 2.52; agriculturalists and industrialists = 3.90. (C) Male fibrous with unbiased effect sizes (unbiased *d*) between hunter–gatherer and agriculturalists = −1.46; hunter–gather and industrialists = 2.12; agriculturalists and industrialists = 4.14. (D) Female fibrous with unbiased effect sizes (unbiased *d*) between hunter–gatherer and agriculturalists = −0.92; hunter–gather and industrialists = 3.26; agriculturalists and industrialists = 3.72.

which is one of the primary limitations for this analysis. Furthermore, researchers should publish means or medians (whichever is appropriate for the recording method), sample sizes, standard deviations and effect sizes to enable meta-analyses to be performed. Recommendations on the type of data to present should be made by the authors of all new methods, ideally with raw data provided as supplementary data where appropriate.

It is unlikely that all those researchers who have recorded agricultural populations routinely score lower than those recording hunter–gatherers, but inter-observer error must be considered. The original report (Hawkey and Merbs, 1995) presented low intra- and inter-observer error, but a recent study (Davis et al., 2013) found higher error rates. These are likely to be caused by the difficulty of using photographs to learn a recording method (Davis et al., 2013). Similarly, there are inter-observer

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differences in how pathological changes are defined and which conditions lead to exclusion from the sample. Pathological conditions, e.g. ankylosing spondylitis, are associated with changes to entheses which cannot currently be differentiated from other causes (Henderson, 2008; Villotte and Knüsel, 2013). It is possible that evidence for one-off trauma, e.g. fractures, should also be taken into account. Further research is required to ensure suitable recommendations for dealing with other factors can be made. However, it is unlikely that large numbers of individuals will be affected by these diseases, except in some unusual circumstances e.g. endemic fluorosis (Littleton, 1999), and this is unlikely to have biased the present study.

While the problems associated with the methods are important they are not the most significant limitations. The large temporal and geographic distribution of the samples, but the small number of samples may have an effect. Climate is also a significant factor, as individuals are more likely to injure themselves working in cold conditions (Kroemer, 1989). All these factors will also affect the detail of the subsistence strategies, how much energy is required to find food, what can be found or grown and how it is processed. These differences might explain the presence of outliers. However, it was not the aim of this study to look at the effect of detailed resource usage but to look at the overall wider effect of subsistence strategy change.

However, the most serious limitations relate to the sample sizes of the original studies and their age distributions, which are caused by the nature of archaeological sites and biased preservation of skeletons. Sample sizes were small and, although these grew once the data were pooled, the underlying biased nature of the original datasets cannot be ignored. Means calculated from the small samples are unlikely to reflect the living population and the biased nature of cemetery assemblages is a well-known problem. This biased nature leads on to the final limitation: the age distribution of the samples. Increasing age is highly correlated with EC (Alves Cardoso and Henderson, 2013; Alves Cardoso and Henderson, 2010; Milella et al., 2012; Niinimäki et al., 2013; Villotte et al., 2010) and is more important than occupation when using the recording method utilised in this meta-analysis (Cardoso, 2008). This leads to the conclusion that the most significant effect on the results is likely to be differences in age distributions of the samples between the three subsistence strategies, rather than true differences in activity-patterns. Studies of age distribution have highlighted a decrease in mean age with the adoption of agriculture (Cohen and Armelagos, 1984). A previous study (using different recording methods) demonstrated a significant increase in EC over the age of forty (Villotte et al., 2010). Therefore the lower scores found in the agricultural sample may be caused by a lower mean age. However, the methods for ageing skeletons are not good at identifying older individuals. Further analysis on identified skeletal collections is needed to determine whether using a cut-off at young adult (defined as per Roksandic and Armstrong, 2011) reduces the impact of degenerative processes, thus allowing activity-patterns to be analysed. Another method to reduce the effect of age is to study bilateral asymmetry within individuals (Villotte pers. comm.).

Due to these very serious limitations it is impossible to determine whether the trends observed in the data are a result of activity or are caused by other factors, particularly differences in age distributions affected by different subsistence strategies (and by different environmental stressors). Nevertheless this is an interesting research question which can be explored in the future with improvements in methods and reporting of data.

In conclusion, this research demonstrated trends in data which were reflected for all entheses and were similar for males and females. The limitations are important and mean that the hypothesis cannot be properly tested. Future research must aim to determine whether other methods of recording entheseal changes can be applied to this problem. In particular, research must determine whether entheses have a greater specificity than other methods for recording activity related stress.

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Appendix A.

Original data used. Data with sample size 0 have been removed. NB data sorted alphabetically and in reverse chronological order. Bold numbers indicate outliers.

Enthesis	Sex	Chapman (1997)				Doying (2010)		Eshed et al. (2004)				Hawkey and Merbs (1995)				Pany (2005)	
		Agriculture				Industrial		Agriculture		Hunter–gatherer		Hunter–gatherer				Industrial	
		Postcontact		Precontact		Postmedieval		Neolithic		Natufian		Late Period		Early Period		Early Iron Age	
		Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n
Anconeus	**F**	0.13	19	0.18	34			1.10	8	1.00	7			1.43	15		
	M	0.42	26	0.27	31			1.00	10	0.90	19			1.47	18		
Biceps brachii	**F**	0.71	21	0.70	22	3.97	28	0.80	7	0.80	3			1.31	18	4.40	10
	M	1.05	19	0.88	20	4.28	39	1.30	8	**0.80**	**20**			2.00	32	4.00	24
Brachialis	**F**	1.50	20	1.46	48			1.90	9	**1.10**	**6**			2.00	32	4.57	14
	M	1.73	30	1.66	35			2.00	11	1.40	24	1.50	6	2.07	29	4.36	25
Brachioradialis	**F**	0.23	11	0.20	23												
	M	0.24	21	0.43	22												
Brachioradialis and extensor carpi radialis longus (O)	**F**							1.50	12	1.10	7						
	M							1.10	10	1.60	22						
Common extensor (O)	**F**	0.93	15	1.00	18									2.00	13	1.71	7
	M	0.94	18	0.83	18									2.41	16	2.80	10
Common flexor (O)	**F**	1.14	11	1.18	19									1.79	14	1.67	9
	M	0.98	26	0.91	33							2.17	6	2.09	17	3.08	12
Conoid ligament	**F**	0.69	21	0.63	32									1.44	18	3.13	8
	M	0.86	18	0.67	24							1.40	5	1.55	11	2.45	11
Coracobrachialis	**F**	0.04	26	0.10	48									1.08	20		
	M	0.09	32	0.04	37							1.00	4	1.05	22		
Costoclavicular ligament	**F**							1.00	7	**0.80**	**3**			2.13	16	3.50	6
	M							2.20	6	1.60	18	3.50	4	4.24	17	5.00	15
Deltoid	**F**	0.88	16	0.59	22	4.00	29	1.60	13	1.90	7			1.94	48		
	M	0.62	21	0.56	25	3.88	40	1.80	11	**1.20**	**23**	2.13	8	2.10	44		
Extensors and supinators (O)	**F**							1.20	5	0.80	4						
	M							1.50	2	0.80	15						
Infraspinatus	**F**	0.95	21	0.94	25									1.38	20	2.43	7
	M	0.98	24	0.96	28							1.80	5	1.75	22	3.40	15
Infraspinatus and supraspinatus	**F**							1.20	3								
	M							2.00	1	0.50	4						

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Appendix A (*Continued*)

Enthesis	Sex	Chapman (1997)				Doying (2010)		Eshed et al. (2004)				Hawkey and Merbs (1995)				Pany (2005)	
		Agriculture				Industrial		Agriculture		Hunter–gatherer		Hunter–gatherer				Industrial	
		Postcontact		Precontact		Postmedieval		Neolithic		Natufian		Late Period		Early Period		Early Iron Age	
		Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n
Latissimus dorsi	**F**	0.46	24	0.33	26			0.60	12	1.00	4			1.13	30	3.00	3
	M	0.56	26	0.42	31			**1.60**	**9**	1.30	19	1.57	7	1.64	33	3.79	14
Pectoralis major	**F**	1.27	24	1.29	47	4.14	28	2.40	14	1.80	5			2.65	33	3.33	9
	M	1.33	20	1.36	37	3.90	40	**3.30**	**11**	**2.20**	**26**	**5.29**	**7**	3.17	36	3.80	15
Pectoralis minor	**F**	0.56	8	0.83	9			1.00	3					1.00	7		
	M	0.53	16							1.00	9	1.10	5	0.96	13		
Pronator quadratus	**F**	0.00	20	0.11	41			0.50	6					0.07	15		
	M	0.16	29	0.08	31			0.80	6	0.40	10	1.20	5	0.69	16		
Pronator quadratus (O)	**F**							1.80	8	1.20	3						
	M							1.50	8	0.90	10						
Pronator teres	**F**	0.29	24	0.37	42			1.00	6	0.30	2			1.00	11		
	M	0.40	26	0.42	30			1.40	10	0.60	14	2.00	3	1.69	16		
Rhomboid lig	**F**	1.07	14	1.10	15												
	M	1.53	20	1.05	21												
Subclavius	**F**	0.55	22	0.35	33			**1.20**	**6**	**0.40**	**4**			1.46	24		
	M	0.60	21	0.62	25			**1.40**	**4**	0.60	17	1.00	6	**2.00**	**24**		
Subscapularis	**F**	1.06	18	0.98	32												
	M	1.11	22	1.09	27												
Supinator	**F**	0.38	24	0.26	38			0.70	6	0.80	3			0.80	15		
	M	0.35	24	0.27	30			0.80	8	0.30	12	0.75	4	1.29	14		
Supinator (O)	**F**	0.38	20	0.19	45			1.40	8	0.60	4						
	M	0.35	31	0.19	35			1.00	11	0.90	19						
Supraspinatus	**F**	0.78	16											1.50	18		
	M	0.87	23	0.83	26							1.25	4	1.64	11		
Teres major	**F**	0.94	16	1.00	21	4.38	26	1.30	13	0.40	4			3.40	35	3.09	11
	M	1.03	20	1.04	24	4.12	40	2.10	12	0.80	21			3.44	40	4.09	11
Teres minor	**F**	0.17	19	0.69	24			1.30	3					0.33	9		
	M	0.91	17	0.94	16			1.00	1	1.00	5	**3.86**	**7**	0.57	14		
Trapezius	**F**	0.43	20					2.20	5					1.33	12	2.00	6
	M	0.92	25	0.90	25					1.40	9	1.67	3	1.17	9	2.63	8
Trapezius (Clavicle)	**F**	0.15	17	0.08	24												
	M	0.19	18	0.13	30												
Trapezoid ligament	**F**	0.41	16	0.43	27									1.67	18		
	M	0.44	17	0.38	20							2.00	6	1.97	15		
Triceps brachii	**F**	0.15	17	0.12	37	4.04	29	0.60	7	0.80	6			1.43	14	2.50	13

Appendix A (*Continued*)

Enthesis	Sex	Chapman (1997)				Doying (2010)		Eshed et al. (2004)				Hawkey and Merbs (1995)				Pany (2005)	
		Agriculture				Industrial		Agriculture		Hunter–gatherer		Hunter–gatherer				Industrial	
		Postcontact		Precontact		Postmedieval		Neolithic		Natufian		Late Period		Early Period		Early Iron Age	
		Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n
Triceps brachii (long head)	**M**	0.35	27	0.18	33	3.92	40	1.60	7	0.80	17			1.72	18	2.93	14
	F															3.62	13
	M															4.29	14

Enthesis	**Sex**	**Peterson 1998**		**Steen and Lane 1998**				**Weiss 2007**		**Wysocki and Whittle 2000**		**Zabecki 2009**					
		Hunter–gatherer		Hunter–gatherer				Hunter–gatherer		Transitional foraging/ agriculture		Agriculture					
		Natufian		300-80BP		Prehistoric		2180-250BP		Neolithic		Middle Kingdom		Old Kingdom		Predynastic	
		Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n
Anconeus	**F**	1.10	10	1.40	20	1.60	14			1.00	4						
	M	1.53	18	1.90	16	1.90	15			1.63	8						
Biceps brachii	**F**	2.22	9	1.50	19	1.30	16	1.97	59	1.00	4	1.00	7	1.08	13	1.23	26
	M	2.24	21	2.30	14	1.70	14	2.71	43	1.63	8	1.40	5	1.29	14	1.59	17
Brachialis	**F**	1.91	11	1.70	21	1.90	14			1.75	4	0.43	7	0.72	18	0.54	28
	M	2.02	20	2.20	15	2.40	16			2.38	8	1.25	4	0.88	17	0.88	17
Brachioradialis	**F**																
	M																
Brachioradialis and extensor carpi radialis longus (O)	**F**																
	M																
Common extensor (O)	**F**	1.11	9									0.43	7	1.13	8	0.66	29
	M	1.45	19									**0.60**	**5**	0.88	8	0.93	15
Common flexor (O)	**F**	0.91	11									0.57	7	0.60	5	0.48	29
	M	1.30	20									0.60	5	0.71	7	0.88	16
Conoid ligament	**F**	2.00	12									**1.88**	**8**	0.67	18	0.93	30
	M	1.83	23									1.80	5	1.00	14	1.28	18
Coracobrachialis	**F**	1.18	14							0.75	3						

Appendix A (*Continued*)

Enthesis	**Sex**	**Peterson 1998**		**Steen and Lane 1998**				**Weiss 2007**		**Wysocki and Whittle 2000**		**Zabecki 2009**					
		Hunter–gatherer		Hunter–gatherer				Hunter–gatherer		Transitional foraging/ agriculture		Agriculture					
		Natufian		300-80BP		Prehistoric		2180-250BP		Neolithic		Middle Kingdom		Old Kingdom		Predynastic	
		Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n
	M	1.17	20							0.57	7						
Costoclavicular ligament	**F**	2.50	11	2.20	20	2.00	13			3.16	6	2.71	7	1.80	15	2.07	29
	M	2.58	19	3.60	14	3.30	12			4.80	5	3.00	5	0.60	10	3.00	17
Deltoid	**F**	2.14	14	1.90	23	1.40	20	1.72	59	1.50	6	1.43	7	0.81	16	1.11	28
	M	2.43	23	2.60	13	2.00	16	2.74	43	1.88	13	1.80	5	1.21	19	1.20	15
Extensors and supinators (O)	**F**			1.30	16	1.30	14										
	M			2.40	11	1.80	13										
Infraspinatus	**F**	0.75	2			0.90	14										
	M	0.94	8			1.10	14										
Infraspinatus and supraspinatus	**F**			1.10	20												
	M			1.90	13												
Latissimus dorsi	**F**	1.17	6	1.20	22	1.20	20	**0.16**	**59**	0.50	6	0.33	6	**0.12**	**17**	0.40	30
	M	1.36	14	**2.20**	**13**	1.50	14	**0.73**	**43**	1.63	8	0.60	5	0.23	13	0.15	13
Pectoralis major	**F**	2.89	9	2.00	23	1.80	20	1.82	59	1.40	5	1.71	7	1.12	17	1.06	31
	M	2.90	21	2.90	13	3.10	15	2.64	43	1.88	8	2.20	5	1.47	17	1.19	16
Pectoralis minor	**F**	1.83	3	1.50	23	1.80	8										
	M	1.81	8	2.00	13	1.30	13										
Pronator quadratus	**F**			1.30	18	0.60	12										
	M			1.80	11	0.90	15										
Pronator quadratus (O)	**F**																
	M																
Pronator teres	**F**	1.19	8	1.30	19	**0.90**	**10**			1.50	5						
	M	1.41	11	1.70	13	1.00	11			1.20	8						
Rhomboid lig	**F**																
	M																
Subclavius	**F**	1.07	14	1.10	17	1.30	12					0.14	7	0.33	18	0.16	31
	M	1.25	24	1.30	12	1.40	13					0.40	5	0.73	15	0.42	19
Subscapularis	**F**	1.37	4														
	M	1.70	10														
Supinator	**F**	0.94	8	1.10	21	0.80	15					0.14	7	0.15	13	0.04	26
	M	1.32	11	1.70	15	0.90	16					0.00	5	0.46	13	0.18	17

Appendix A (*Continued*)

Enthesis	**Sex**	**Peterson 1998**		**Steen and Lane 1998**				**Weiss 2007**		**Wysocki and Whittle 2000**		**Zabecki 2009**					
		Hunter–gatherer		Hunter–gatherer				Hunter–gatherer		Transitional foraging/ agriculture		Agriculture					
		Natufian		300-80BP		Prehistoric		2180-250BP		Neolithic		Middle Kingdom		Old Kingdom		Predynastic	
		Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n	Mean MSM score	n
Supinator (O)	**F**							0.79	59								
	M							1.16	43								
Supraspinatus	**F**	0.62	4			1.10	16										
	M	1.17	6			1.10	12										
Teres major	**F**	2.19	8	2.00	23	1.60	6	0.82	59	2.00	4	**2.14**	**7**	0.88	17	0.83	30
	M	1.67	15	3.00	13	2.50	7	1.67	43	2.29	7	1.80	5	1.27	15	0.62	13
Teres minor	**F**			1.40	20	1.00	13										
	M			1.80	12	1.30	10										
Trapezius	**F**	1.33	3	1.40	16	1.20	5			1.83	6						
	M	1.45	10	1.90	16	2.20	12			2.20	5						
Trapezius (Clavicle)	**F**																
	M																
Trapezoid ligament	**F**	1.54	11									**2.63**	**8**	0.47	15	0.44	27
	M	1.60	19									1.00	5	0.67	12	0.31	16
Triceps brachii	**F**	0.94	9	1.30	12	1.40	10	0.35	59			0.14	7	0.35	17	0.54	28
	M	1.57	20	1.90	11	1.70	9	1.03	43			0.75	4	0.82	17	0.65	17
Triceps brachii (long head)	**F**																
	M																

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