Lower Limb Activity in the Cis-Baikal: Entheseal Changes Among Middle Holocene Siberian Foragers

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ABSTRACT Lower limb enthesal changes are evaluated in order to reconstruct activity levels and more fully understand cultural and behavioral variation among the middle Holocene (ca. 9,000–3,000 years BP) foragers of Siberia’s Cis-Baikal region. The four cemetery samples examined span a period of diachronic change characterized by an 800- to 1,000-year discontinuity in the use of formal cemeteries in the region. Two of the cemetery samples represent the early Neolithic Kitoi culture, dating from 8,000 to 7,000/6800 cal. BP; the other two represent the late Neolithic-early Bronze Age Isakovo-Serovo-Glazkovo (ISG) cultural complex, dating from 6,000/5,800 to 4,000 cal. BP. Findings suggest a dynamic pattern of cultural variability in the Cis-Baikal, with spatial distribution (i.e., site location within particular microregions) appearing to be just as important a factor as cultural/temporal affiliation in explaining intersample differences in enthesal morphology. In addition, intrasample comparisons reveal increasing sexual disparity with advancing age at death, emphasizing the influence of sex-related activities on lower limb enthesal changes. Finally, results from the separate fibrous and fibrocartilaginous datasets appear to be largely congruous, implying that activity patterns in the Cis-Baikal may have similar effects on the morphology of both types of entheses. Am J Phys Anthropol 000:000–000, 2013. ©2013 Wiley Periodicals, Inc.

In the anthropological literature, activity-induced changes to the bony attachments for muscles, tendons, and ligaments have been most commonly referred to as enthesopathies or musculoskeletal stress markers (MSM). Unfortunately, both terms are inaccurate: the former implying a pathological condition and the latter presupposing its etiology (Jurmain and Villotte, 2010). For this reason, we use the more neutral term “enthesal changes,” as suggested at the Coimbra workshop in 2009 (Jurmain and Villotte, 2010), because it addresses the current understanding of underlying etiologies. Over the last several decades, enthesal changes (however they have been termed) have been used to reconstruct past activities based on the common, but perhaps somewhat misleading, assumption that they directly reflect the extent of muscle and/or ligament use over the course of individuals’ lives (e.g., Dutour, 1986; Angel et al., 1987; Kelley and Angel, 1987; Owsley et al., 1987; Lai and Lovell, 1992; Hawkey and Merbs, 1995; Chapman, 1997; Churchill and Morris, 1998; Hawkey, 1998; Peterson, 1998; al-Oumoui et al., 2004; Eshed et al., 2004; Molnar, 2006; Weiss, 2007; Alves Cardoso and Henderson, 2010; Maroti and Belcastro, 2011; Molnar et al., 2011; Schrader, 2012; Stefanović and Porčić, 2011). Various approaches to this research have been employed (e.g., Hawkey and Merbs, 1995; Eshed et al., 2004; Weiss, 2003, 2004; Alves Cardoso and Henderson, 2010; Villotte et al., 2010; Niinimäki, 2011, 2012), most of which have been based on the principle of bone functional adaptation [sometimes referred to as Wolff’s Law (Wolff, 1892)], maintaining that bone form reflects the cumulative effects of intra vitam mechanical loading or strain (Ruff et al., 2006). The use of enthesal changes to reconstruct past activity is not without its limitations. Some scholars have been unable to document bony modifications associated with intra vitam activity among experimental or known-occupation samples (e.g., Zumwalt, 2006; Alves Cardoso and Henderson, 2010), suggesting that the relationship between enthesal morphology and activity patterns is far from straightforward. Further complicating the matter is the fact that changes to muscle and ligament attachment sites are not only associated with activity, but also with age at death, sex (e.g., hormonal differences), body size, and/or pathological status. For example, older, male, and larger-bodied individuals tend to have more robust entheses than younger, female, and smaller-bodied ones, respectively (Hawkey and Merbs, 1995; Robb, 1998; Steen and Lane, 1998; Wilczak, 1998; Eshed...
et al., 2004; Molnar, 2006; Weiss, 2003, 2004, 2007; Jurmain and Roberts, 2008; Lieverse et al., 2009; Alves Cardoso and Henderson, 2010; Villotte et al., 2010; Milella et al., 2012; Weiss et al., 2012). While age-at-death distinctions are often interpreted as evidence for the cumulative effects of skeletal loading over time (Robb, 1998; Wilczak, 1998; Ruff et al., 2006), in many cases, apparent sexual disparity may merely reflect relative body size. These biasing factors must be taken into account when using enthesal changes to understand and reconstruct past activities.

Despite the challenges, entheses can still be useful tools for reconstructing past mobility patterns and habitual behaviors, in a general sense, as long as their limitations are kept in mind (Villotte et al., 2010). Here, we investigate lower limb entheses in order to understand more fully the spatial and temporal variation among the middle Holocene (ca. 9,000–3,000 years BP) foragers of the Cis-Baikal region (Fig. 1) of Siberia (Russian Federation). The Cis-Baikal exhibits a rich archaeological record documenting more-or-less continuous human occupation for at least the last 20,000 years (Weber, 1995; Goebel, 1999), with large collections of human remains representing parts of the middle and late Holocene (see Table 1). The notable exception to this sequence is a period of considerable cultural

**Fig. 1.** Map of the Cis-Baikal and location of micro-regions and cemetery sites. Lokomotiv and Shamanka II represent the early Neolithic Kitoi culture; Ust’-Ida I, Khuzhir-Nuge XIV, and Kurma XI represent the late Neolithic-early Bronze Age Isakovo-Serovo-Glazkovo (ISG) cultural complex.
change during the middle Neolithic period (ca. 7,000/6,800–6,000/5,800 cal. BP), reflected archaeologically by the absence of formal cemeteries and, therefore, a lack of human skeletal material. Equally noteworthy is the fact that the populations lying on either side of the middle Neolithic—that is early Neolithic (8,000–7,000/6,800 cal. BP) Kitoi peoples and the late Neolithic–early Bronze Age (6,000/5,800–4,000 cal. BP) Isakovo–Serovo–Glazkovo (or ISG) groups—are biologically distinct (Moore et al., 2005, 2006). In this article, for the sake of brevity, the early Neolithic and late Neolithic–early Bronze Age groups are referred to as prehiatus and posthiatus, respectively. While the middle Neolithic is referred to as the hiatus, it is important to emphasize that all that is meant here is the discontinuity in the use of formal cemeteries, the other processes and characteristics defining the cultural pattern of the period remaining unclear.

Continuing research into the nature of hunter-gatherer behavioral variability during the middle Holocene has allowed us to further refine our understanding of foraging adaptations on either side of the middle Neolithic hiatus. Data suggest a dynamic pattern of cultural variability, both temporally and spatially (Weber and Bettinger, 2010; Weber et al., 2011), with interesting similarities and distinctions documented between and within the pre- and posthiatus groups. Using the archaeological, osteological, genetic, and geochemical data from formal cemeteries as proxies for population parameters, prehiatus Kitoi communities appear to have been larger but concentrated predominately in two microregions, the Angara River Valley and South Baikal (Fig. 1), typically near major river mouths (Weber and Bettinger, 2010). Conversely, while the posthiatus ISG population seems to have been larger as a whole, people were more evenly distributed across the entire region in smaller but more numerous individual groups. Much of the ISG population expansion may reflect growth in the Little Sea microregion, an area that appears to have received the majority of migrants from other parts of the Cis-Baikal, most notably the upper Angara River, during this time (Weber et al., 2011; Weber and Goriunova, 2012).

Bone chemistry data indicate that prehiatus Kitoi and posthiatus ISG populations essentially followed the same general subsistence strategy: that of relying on game, fish, and seasonally available plant foods that were local to their particular microregions (Weber et al., 2011). A possible temporal shift in subsistence regimes is only observable for the Angara River Valley (Fig. 1), with a probable decreased emphasis on fishing during the later ISG interval relative to the earlier Kitoi period (Weber et al., 2011). The lack of a similar temporal shift in the other microregions may reflect, at least in part, incomplete datasets for these regions, as well as the variable incorporation of Baikal seal (Pusa sibirica) into the Little Sea diet (Weber and Bettinger, 2010; Weber et al., 2011; Weber and Goriunova, 2012). On the other hand, it may also reflect reality: in fact, there is no reason to assume that similar patterns of temporal change would have occurred in the other microregions. Fishing in the Little Sea, in particular, seems to have remained steady and of low intensity throughout the middle Holocene, in contrast to its shifting emphasis in the Angara River Valley (Loosey et al., 2008; Weber and Bettinger, 2010).

Skeletal and dental morphological data reveal points of both contrast and consistency between pre- and posthiatus groups. The overriding trend appears to be one of general good health for all middle Holocene occupants of the Cis-Baikal, but with higher weaning ages and some evidence of increased physiological stress among the prehiatus Kitoi (Lieverse, 2010; Lieverse et al., 2007b, Waters-Rist, 2011; Waters-Rist et al., 2011). Regarding lower limb activities—the focus of this article—several lines of inquiry suggest higher activity and/or mobility among the Kitoi, particularly Kitoi males. In work conducted by Stock (Stock et al., 2010; Lieverse et al., 2011), significantly greater anteroposterior femoral hypertrophy, indicative of higher anteroposterior loading, was documented among the Kitoi when compared the ISG. This pattern of femoral loading has been found to be compatible with a biomechanical signature of increasing terrestrial mobility documented for other hunter-gatherer populations (Stock, 2006), providing compelling evidence for higher mobility and greater lower limb strain during the prehiatus period. An investigation of osteoarthritic data disclosed uniformly high levels of activity during both periods, but unique distribution patterns that suggested significantly more knee degeneration among Kitoi males, likely reflecting increased lower limb strain (Lieverse et al., 2007a; Lieverse, 2010). Finally, an examination of postcranial nonmetric traits also revealed possible evidence for higher mobility among the Kitoi, particularly males, consistent with locomotion over steep/uneven terrain while carrying heavy loads (Macintosh, 2011).

Here we explore Kitoi and ISG activity further, focusing on lower limb entheseal morphology in order to gain new insights into temporal and spatial variation in foraging behavior during the middle Holocene. By examining skeletal remains from four cemetery samples—representing both pre- and posthiatus groups and three distinct geographical micro-regions (Fig. 1)—we will test the hypothesis that significant variation in lower limb activity patterns existed throughout the middle Holocene, reflecting differences not only in sex and age at death, but also in spatial distribution (i.e., site location within particular micro-regions), and temporal and cultural affiliation.

### Table 1. Culture history model of the middle Holocene Cis-Baikal

<table>
<thead>
<tr>
<th>Period</th>
<th>Mortuary complex</th>
<th>Calibrated age BP</th>
<th>Cemeteries included in this study</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early Neolithic</td>
<td>Kitoi and others</td>
<td>8,000–7,000/6,800</td>
<td>Lokomotiv, Shamanka II</td>
</tr>
<tr>
<td>Middle Neolithic</td>
<td>None</td>
<td>7,000/6,800–6,000/5,800</td>
<td></td>
</tr>
<tr>
<td>Late Neolithic</td>
<td>Isakovo, Serovo</td>
<td>6,000/5,800–5,200/5,000</td>
<td>Ust’-Ida I</td>
</tr>
<tr>
<td>Bronze Age</td>
<td>Glazkovo</td>
<td>5,200/5,000–4,000</td>
<td>Ust’-Ida I, Khuzhir-Nuge XIV*, Kurma XI*</td>
</tr>
</tbody>
</table>

* Samples from Khuzhir-Nuge XIV and Kurma IX were combined into one Little Sea (LS) sample for analyses.
In this article, we examine four collections of human remains from five cemeteries and three Cis-Baikal micro-regions. While the Cis-Baikal actually contains four main geographical micro-regions, the fourth—the upper Lena River from its source in the mountains west of Lake Baikal to the mouth of the Kirenga River (Fig. 1)—is not included in this study because it is not well known, archaeologically (Weber and Bettinger, 2010). The cemeteries of Lokomotiv (n = 60) and Shamanka II (n = 67) both represent the early Neolithic period (8,000–7,000/6,800 cal. BP) and belong to the class Kitoi mortuary tradition. Lokomotiv is located in the Angara River Valley microregion spanning the distance between the river’s headwaters at Lake Baikal to its confluence with the Ilim River about 990 km to the north (Fig. 1). Shamanka II is situated in the South Baikal microregion that includes the delta of the Selenga River and the area west to the southern tip of Lake Baikal (Fig. 1). The Ust’-Ida I cemetery (n = 26), also situated in the Angara River Valley microregion but located about 150 km north of Lokomotiv, includes individuals dating to the late Neolithic (6,000/5,800–5,200/5,000 cal. BP) and early Bronze Age (5,200/5,000–4,000 cal. BP). Since late Neolithic and early Bronze Age subsistence strategies in the Angara micro-region appear to be essentially the same (Weber et al., 2011), the Ust’-Ida I materials have been combined into one analytical unit.

Finally, the Khuzhir-Nuge XIV (n = 18) and Kurma XI (n = 15) cemeteries are situated about 15 km apart in the Little Sea (or Ol’khon) microregion, located in the middle section of Lake Baikal’s northwest coast, across from its largest island, Ol’khon (Fig. 1). Both date to the early Bronze Age. In the Little Sea, however, two different subsistence strategies have been identified based on the variable use of Baikal seal (Pusa sibirica)—the so-called game-fish and game-fish-seal diets—both of which are represented at Khuzhir-Nuge XIV and Kurma XI. Unfortunately, at present it is not possible to divide our Little Sea sample into two separate units based on this dietary distinction. The matter is complicated by the fact that, while all those associated with the game-fish diet appear to have been born in the upper Lena River microregion, about half of those consuming the game-fish-seal diet appear to have been born in the Little Sea and half on the upper Lena (Haverkort et al., 2008; Weber and Gorinova, 2012). Furthermore, it is unclear at which point in their lives the individuals born on the upper Lena moved into the Little Sea microregion. To keep the matter simple and manageable, both collections from the Little Sea have been combined into one analytical unit. Overall then, the available materials have been grouped into four spatio-temporal units of analysis: two are early Neolithic (Lokomotiv and Shamanka II), one is late Neolithic—early Bronze Age (Ust’-Ida I), and one is early Bronze Age (Khuzhir Nuge XIV and Kurma XI combined), with three out of four archaeological micro-regions represented in this study.

Of the total of 432 individuals represented by these four cemetery collections, 186 were deemed suitable for observation of lower limb entheseal and included in this study. Suitability was based on five main criteria: cultural and temporal affiliation, age at death, sex determination, skeletal condition, and absence of pathology. Because several cemeteries yielded human remains dating to cultural periods other than the dominant one (e.g., 11 early Bronze Age individuals were excavated from Shamanka II and three early Neolithic individuals were excavated from Kurma XI), only those associated with the principal archaeological culture or period were included. Furthermore, only adult individuals (those 20 years of age at death and older) and those of determinable sex were considered for documentation and analyses. Any individual fitting these criteria and exhibiting at least one lower limb element (femur or tibia) with at least one clearly observable enthesis (of the 10 documented, see Table 2) was included unless the observed element(s) and/or limb(s) were deemed to be pathological. Pathological elements, including those with fractures and severe osteoarthritis, were excluded from this study. In addition, non-pathological elements from individuals exhibiting any evidence of abnormal bone growth or remodeling were omitted in order to eliminate any potential cases of seronegative spondyloarthropathy, DISH, and/or acromegaly, conditions known to influence entheseal morphology (Matteucci, 1995; Belanger and Rowe, 2001; Benjamin and McGonagle, 2001; Colao et al., 2004).

Sex assessment and age at death estimation were based largely on the standards presented by Buikstra and Ubelaker (1994; p 16–21), with as many techniques as possible being applied to each individual. Sex assessment focused predominately on pelvic and cranial morphology (e.g., Phenice, 1969; Acsádi and Nemeskéri, 1970; Buikstra and Mielke, 1985; Milner, 1992), and age estimation on changes to pubic symphyseal and auricular surface morphology, as well as cranial and palatal suture closure (Suchey and Katz, 1986; Mann et al., 1987; Meindl and Lovejoy, 1985, 1989; Brooks and Suchey, 1990). Unfortunately, sex and age at death determinations were often compromised by poor preservation and/or incomplete element representation, particularly among the posthiatus sample from the Little Sea (Khuzhir-Nuge XIV and Kurma XI). As a result, all adults of undetermined sex had to be excluded from analyses, while adult males and females for whom age at death could not be more specifically determined could only be included in basic analyses that did not control for age. For this reason, the sums of young (20–35 years) and older (36+) adult males and females for some populations do not necessarily correspond to the total numbers of observable males or females indicated.

Ten lower limb entheseal sites were documented: four muscle origin sites and six muscle insertion sites (Table 2). Data were originally collected (between 2007 and 2010) using the graded visual reference system developed by Hawkey (1988) and outlined by Hawkey and

### Table 2. List of the 10 lower limb enthese documented

<table>
<thead>
<tr>
<th>Element</th>
<th>Enthesis</th>
<th>Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Femur</td>
<td>Gluteus maximus insertion</td>
<td>Fibrous</td>
</tr>
<tr>
<td>Femur</td>
<td>Adductor magnus (posterior insertion on linea aspera)</td>
<td>Fibrous</td>
</tr>
<tr>
<td>Femur</td>
<td>Vastus medialis origin</td>
<td>Fibrous</td>
</tr>
<tr>
<td>Femur</td>
<td>Vastus lateralis origin</td>
<td>Fibrous</td>
</tr>
<tr>
<td>Tibia</td>
<td>Soleus origin</td>
<td>Fibrous</td>
</tr>
<tr>
<td>Femur</td>
<td>Gluteus medius insertion</td>
<td>Fibrocartilaginous</td>
</tr>
<tr>
<td>Femur</td>
<td>Gluteus minimus insertion</td>
<td>Fibrocartilaginous</td>
</tr>
<tr>
<td>Femur</td>
<td>Obturator externus insertion</td>
<td>Fibrocartilaginous</td>
</tr>
<tr>
<td>Femur</td>
<td>Gastrocnemius (origin of medial head)</td>
<td>Fibrocartilaginous</td>
</tr>
<tr>
<td>Femur</td>
<td>Illiacus insertion</td>
<td>Fibrocartilaginous</td>
</tr>
</tbody>
</table>
Merbs (1995): absent (0), faint (1), moderate (2), and strong (3) robusticity. Following the lead of Alves Cardoso and Henderson (2010), these robusticity scores were modified in order to account for the known differences (reflecting tissue type present at the site of attachment) between the two main groups of entheses: fibrous and fibrocartilaginous (Benjamin and Ralphs, 1997, 1998; Hems and Tillmann, 2000; Benjamin and McGonagle, 2001; François et al., 2001; Miltz et al., 2001; Benjamin et al., 1992, 2002). Because fibrous entheses tend to have large roughened surfaces with poorly delimited margins, absence of lesions included robusticity scores of 0 and 1, with scores of 2 and 3 being rescored as 1 and 2, respectively. For naturally smooth and clearly defined fibrocartilaginous entheses, on the other hand, absence included robusticity scores of 0 only, with scores of 1 to 3 remaining unchanged. Fibrous and fibrocartilaginous entheses were analyzed separately (as aggregates, see below).

In the interest of maximizing sample sizes, scores were documented for all observable lower limb entheses with the intent of using left and right scores interchangeably (or averaging them if both had been recorded) for analyses. However, bilateral asymmetry was first examined in order to assess the appropriateness of combining sides. For the five fibrous and five fibrocartilaginous entheses used in aggregate analyses (see below), Wilcoxon sign-rank tests for paired design (appropriate for ordinal data) were conducted for all bilaterally recorded attachment sites in order to test for right versus left side usage. Additionally, because some scholars have documented relationships between entheseal morphology and body size (e.g., see Weiss, 2003, 2004), the effects of this on the Cis-Baikal data were examined. Two femoral measurements—maximum length and maximum diameter of the femoral caput (defined by Buikstra and Ubelaker, 1994; p 83)—and one tibial measurement—maximum length (defined by Buikstra and Ubelaker, 1994; p 83)—and one iliac measurement—maximum length (defined by Buikstra and Ubelaker, 1994; p 83)—served as a proxy for body size and the basis for analyses. Similar to the procedures employed by Weiss (2004), the three measurements were summed (aggregated) for each individual, being averaged if both left and right side values were available. Again, bilateral asymmetry was examined in advance, this time with the use of paired t-tests (appropriate for the continuous nature of the metric aggregate data) or, if samples were small (generally less than 10) and/or failed to meet the parameters of normality, Wilcoxon sign-rank tests for paired design. Two different sets of analyses were conducted to test for the effects of body size differences. First, the metric aggregates were compared both among and within (i.e., male vs. female) the cemetery populations, again using t-tests or, for small samples (generally less than 10), Mann–Whitney U tests for unmatched design. The second set of analyses utilized Spearman’s correlation tests to compare the metric aggregates with those generated for 1) fibrous and 2) fibrocartilaginous entheses (see below).

Statistical analyses focused on comparing lower limb entheseal scores both among and within the four cemetery samples, as well as between pooled Kitoi and ISG samples, in order to discern any significant differences and/or patterns of differences. Sex was controlled for in every case and age at death in most cases; as discussed below (see Results), body size was not directly controlled for. All analyses utilized aggregate scores similar to the method employed by Weiss (2003, 2004, 2007). The use of aggregate variables can decrease error, increase reliability, and may even reduce the effects of body size on entheseal morphology (Weiss, 2003, 2004, 2007; see Weiss, 2003, for a detailed discussion of the appropriateness and advantages of aggregate usage). Scores for five fibrous entheses—the gluteus maximus (insertion), adductor magnus (posterior insertion on linea aspera), vastus medialis (origin), vastus lateralis (origin), and solus (origin)—were aggregated (or summed) into one composite fibrous variable for each observable individual. Likewise, scores for five fibrocartilaginous entheses—the gluteus medius (insertion), gluteus minimus (insertion), obturator externus (insertion), gastrocnemius (origin of medial head), and iliacus (insertion)—were aggregated into one composite fibrocartilaginous variable for each individual. Because missing data were inevitable, absent values were substituted with the average of all remaining values comprising the composite for each individual (after Weiss, 2003, 2007). While substitution rates were low on average (8.13%), any individual with more than two substitutions in his/her aggregate score was excluded from analyses. Kruskal–Wallis tests, appropriate for ordinal data, were used to compare aggregates scores both within (i.e., male vs. female, young adult vs. older adult) and among the cemetery groups. Fibrous and fibrocartilaginous scores were examined separately. In addition, correlation analyses (Spearman’s tests) were conducted between the fibrous and fibrocartilaginous aggregates in order to gauge any significant associations between the two and to shed light on the appropriateness (if applicable) of giving preference to one type of enthesis over the other in this study. For all analyses, significance levels were set at 0.05.

RESULTS

Bilateral asymmetry

An examination of bilateral asymmetry among fibrous and fibrocartilaginous entheses revealed no statistically significant side differences in lower limb morphology (Supporting Information Table S1). For this reason, left and right entheseal scores were used interchangeably in constructing the aggregates, being averaged if both sides had been recorded. Likewise, an examination of bilateral asymmetry among lower limb metric data also failed to reveal any statistically significant side differences (Supporting Information Table S2), warranting our interchangeable use of left and right data to construct the metric aggregates (summarized in Supporting Information Table S3) that are used as proxies for body size.

Effects of body size

Comparisons of metric aggregate data failed to identify any significant body size differences among the four cemetery populations or between males and females within each group (Supporting Information Tables S4 and S5). Similarly, Spearman’s tests between the metric and entheseal (fibrous and fibrocartilaginous) aggregates revealed no statistically significant correlations (Supporting Information Table S6). Taken together, these results provide no evidence for substantive body size differences among or within groups and no significant correlations between body size and entheseal morphology. Because of this, analyses did not directly control for body size.

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Fibrous aggregates

Aggregate scores for fibrous lower limb entheses, separated by sex and adult age at death, are summarized in Table 3 and Figure 2 and suggest a very general pattern of male, older adult (36+ years), and prehiatus (Kitoi) individuals exhibiting higher scores than female, young adult (20–35 years), and posthiatus (ISG) individuals, respectively. Results of intersample comparisons and pooled (i.e., Kitoi vs. ISG) sample comparisons, also presented in Table 3, partially support these initial observations. With few exceptions (most notably, young adult males), all individuals from the Kitoi cemetery of Lokomotiv exhibit significantly higher aggregate scores than individuals from the other three cemetery samples, including those from the other Kitoi cemetery of ShamaANKa II. While aggregate scores for Shamanka II are higher overall than those of the two posthiatus samples, statistical significance was noted only between older adult males and those from the Little Sea. No significant differences were found between the two posthiatus samples from Ust’-Ida I and the Little Sea. Comparisons of pooled Kitoi and ISG samples also largely support the observed pattern: with the exception of young adult males, aggregate scores are significantly higher among prehiatus Kitoi individuals than their posthiatus successors.

Table 3 presents results of intrasample comparisons as well, specifically young adults versus older adults and males versus females. The general trend of increasing aggregate scores with advancing age at death appears to be largely supported, being statistically significant for all males and Lokomotiv (Kitoi) females. Likewise, the overall tendency of males to exhibit higher entheseal scores than females is supported statistically, for “all” individuals and older adults in particular. The notable exception concerns young adults, with no significant sex-based differences documented in this age category for any of the cemetery samples.

Fibrocartilaginous aggregates

Aggregate scores for fibrocartilaginous lower limb entheses, also separated by sex and adult age at death, are summarized in Table 4 and Figure 3 and again suggest an overall pattern of higher scores among male, older adult, and prehiatus (Kitoi) individuals compared to female, young adult, and posthiatus (ISG) individuals, respectively. Table 4 also presents results of intersample and pooled (i.e., Kitoi vs. ISG) sample comparisons, many of which are similar to those obtained from the fibrous aggregate data (above). The Kitoi cemetery of Lokomotiv continues to stand apart, with “all” and older adult males exhibiting significantly higher scores than those from Shamanka II (Kitoi), older adult males and “all” females exhibiting significantly higher scores than those from Ust’-Ida I (ISG), and all individuals other than young adult males exhibiting significantly higher scores than those from the Little Sea (ISG). Results also distinguish the second Kitoi cemetery of Shamanka II somewhat from the Little Sea, with females from the former site exhibiting significantly higher aggregate scores than those from the latter. As seen above with the fibrous data, no statistically significant differences were found between the two posthiatus cemeteries of Ust’-Ida I and the Little Sea. Results of pooled Kitoi and ISG sample comparisons agree partially with initial
observations, indicating significantly higher aggregate scores among older adult males, “all” females, and young adult females from the prehiatus Kitoi samples when compared to their ISG counterparts.

Results of intrasample comparisons—young adults versus older adults and males versus females—are presented in Table 4 as well. A general trend of increasing aggregate scores with advancing age at death is observable, being supported statistically for males from the two Kitoi cemeteries of Lokomotiv and Shamanka II. The tendency of males to exhibit higher scores than females is seen mostly clearly among ISG individuals, an assertion that is also supported statistically. Significant sex differences in aggregate scores are discerned among “all” individuals from both ISG samples and young adult individuals from the Little Sea. It is worth noting that this significant sex difference among Little Sea young adults is the only fibrocartilaginous result that is incongruous with those obtained from the fibrous aggregate data above.

**Fibrous versus fibrocartilaginous aggregates**

Results of the Spearman’s tests between the fibrous and fibrocartilaginous aggregates are presented in Table 5. The overwhelming trend, for males in particular, is that of statistically significant correlations, or co-variations, between aggregate scores obtained from these two entheseal types. The significant r coefficients for pooled samples (all Lokomotiv [Kitoi] individuals, all Shamanka II [Kitoi] individuals, and all ISG [Ust-IIda I and Little Sea combined] individuals) lie consistently between 0.623 and 0.671.

**DISCUSSION**

Results presented here (Tables 3 and 4) largely support our initial hypothesis that significant variation in lower limb activity patterns existed throughout the middle Holocene, reflecting differences not only in sex and age at death, but also in spatiotemporal distribution. In fact, intersample entheseal comparisons suggest additional dimensions of variation in lower limb activity than has been indicated by earlier studies, with spatial distribution appearing to play just as important a role as temporal or cultural affiliation. While a very general trend suggests higher entheseal robusticity among prehiatus groups (Tables 3 and 4), intersample comparisons—of both fibrous and fibrocartilaginous aggregate scores—draw particular attention to the prehiatus Kitoi cemetery of Lokomotiv, located in the Angara River Valley. With the exception of young adult males, all age and sex groups from this site exhibit significantly higher aggregate scores than analogous groups from at least one other analyzed sample, including the other Kitoi cemetery of Shamanka II, located in South Baikal. Several intersample comparisons indicate higher aggregate scores for Shamanka II relative to the prehiatus groups, but these distinctions are less compelling than those revealed for Lokomotiv.

With evidence of fewer but larger local communities during the prehiatus period, it is possible, and even likely, that local resources would have been depleted more rapidly (compared to the later posthiatus period), prompting logistical foraging outside of the immediate habitation vicinity (Weber and Bettinger, 2010). Conducted by both males and females, these forays may account for the substantially (and often significantly) higher entheseal scores documented among prehiatus individuals. Additionally, population densities may have been particularly high in parts of the Angara River Valley, with several smaller and at least two other large prehiatus populations (represented by the Kitoi and Ust’-Belaia cemeteries) located within 85 km of Lokomotiv (see Weber and Bettinger, 2010). This would have led to increasing competition for resources in this micro-
region and to more reliance on logistical foraging. In South Baikal, on the other hand, there seems to be less evidence for higher population densities and resultant intergroup competition. Finally, the higher reliance on fishing (Weber et al., 2011) during the prehiatus period may have acted to tether already large groups to specific waterways for longer periods of time, further exacerbating the intensity, duration, and/or frequency of logistical foraging. Together, these circumstances may explain the generally higher aggregate scores documented for the prehiatus samples, and the especially high scores characterizing Lokomotiv, in particular.

Another interesting pattern emerging from the intersample comparisons of fibrous and fibrocartilaginous aggregates pertains to the posthiatus ISG population from the Little Sea. Even though sample sizes are small for this group, aggregate scores are consistently the lowest documented (Tables 3 and 4), being significantly lower than most of those from Lokomotiv (Kitoi) and several of those from Shamanka II (also Kitoi). Posthiatus communities are characterized as having been smaller, more numerous, and more evenly distributed across the entire Cis-Baikal (Weber and Bettinger, 2010), a scenario that is further complicated in the Little Sea by extensive seasonal travel between the upper Lena and Little Sea (see Fig. 1) microregions and the variable incorporation of Baikal seal (*Pusa sibirica*) into the diets of the upper Lena migrants (Weber and Bettinger, 2010; Weber et al., 2011; Weber and Gorunova, 2012). In addition, fishing in the microregion, as elsewhere in Cis-Baikal, was of relatively low intensity and remained so throughout the middle Holocene (Losey et al., 2008; Weber and Bettinger, 2010). The fact that individuals or small groups from the upper Lena continued to return to the Little Sea for at least part of their seasonal rounds, coupled with evidence for sealing and low-intensity fishing, suggests that resources in the region were relatively rich and/or stable. This may account, at least in part, for the apparently reduced levels of lower limb activity in the Little Sea compared to contemporaneous populations elsewhere in the Cis-Baikal (i.e., Ust’-Ida I).

Intrasample comparisons further expand our understanding of lower limb activity, and variation in activity, throughout the middle Holocene. For both fibrous and fibrocartilaginous entheses, higher aggregate scores are generally associated with more advanced age at death (Tables 3 and 4). This trend, documented in numerous other studies (e.g., Hawkey and Merbs, 1995; Robb, 1998; Wilczak, 1998; Mariotti et al., 2004; Molnar, 2006; Ruff et al., 2006; Alves Cardoso and Henderson, 2010; Niinimäki, 2011; Weiss et al., 2012), is typically attributed to the cumulative effects of muscle and ligament strain over the course of individuals' lives. It was largely expected among the Cis-Baikal groups, having already been observed on the upper limbs of these same populations (Lieverse et al., 2009), but its disproportionate representation among the sexes was not. Older males consistently exhibit significantly higher enthesal scores than their young adult counterparts; with only one exception (the Kitoi cemetery of Lokomotiv), older adult females do not. This suggests that, in general, females engaged in activities that were not intense/frequent enough to significantly alter enthesial morphology over time, or that they altered their activity patterns as they aged. While these results may reflect, at least in part, smaller female sample sizes, the fact that they are sup-
ported by intrasite sex comparisons (see below) implies
that they are more than simply artifacts of sample bias.
For both fibrous and fibrocartilaginous entheses, male
scores are generally higher than those of females (Tables
3 and 4), being statistically significant nearly half of the
time. It is interesting to note that, with one exception
(fibrocartilaginous scores of young adults from the post-
hiatus Little Sea sample), no significant sex differences
in entheseal morphology are documented among young
adult individuals, despite being relatively common
among "all" and older adults. These observations again
point to sex-based discrepancies: lower limb activities
employed by most males and females in the Cis-Baikal
appear to have been distinct enough, whether in type or
intensity/duration, to eventually (i.e., by older adulthood)
warrant significant differences in entheseal morphology.

Taken together, results of lower limb intrasample age
and sex comparisons provide compelling evidence for
increasing sexual disparity with advancing age at death
throughout the Cis-Baikal, regardless of geographical
location or temporal/cultural affiliation. While the magni-
tude of this disparity may have varied somewhat among
the groups considered—possibly being reduced at prehia-
tus Lokomotiv due to the considerably higher levels of ac-
tivity apparently experienced by both males and females—its presence is supported by both fibrous and
fibrocartilaginous data. This increasing disparity may be
interpreted in several ways, including 1) the reflection of slight differences in sex-based roles that are only observ-
able as their effects accumulate over time, or 2) an actual
shift in male and/or female activity patterns over the
course of individuals' lives, with male activities generally
rising in frequency/intensity and/or female ones generally
declining. The relationship between greater sexual dispar-
ity and advancing age at death may also lend credence to
our explanation that sex (or, specifically, activities linked
to sex), rather than relative body size, accounts for many
of male-female differences documented here. If, for exam-
ple, discrepancies in body size (males being generally
larger bodied than females) are responsible for much or
all of the observed variation in lower limb entheseal mor-
phology, then we should not expect these differences to
change significantly with increasing age. On the other
hand, if they reflect underlying variation in lower limb
activities, changes over the course of individuals' lives are
not only feasible but, perhaps, even probable.

Results obtained separately from fibrous and fibrocar-
tilaginous entheseal data have been found to be largely
congruent. While there is some variation in the data
themselves, with differences among fibrous aggregates
being more likely to be statistically significant, similar
conclusions can be drawn from both datasets. This obser-
vation is further supported by the results of correlation
analyses (Spearman's tests), presented in Table 5. Anato-
mical differences between the types of entheses are
well documented in the literature, fibrous entheses being
naturally rough with poorly defined margins and fibro-

TABLE 5. Summary of correlation results for fibrous aggregate
scores versus fibrocartilaginous aggregate scores

<table>
<thead>
<tr>
<th></th>
<th>Lokomotiv (Kitoi)</th>
<th>Shamanka II (Kitoi)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
</tr>
<tr>
<td>n</td>
<td>30</td>
<td>21</td>
</tr>
<tr>
<td>r</td>
<td>0.614</td>
<td>0.298</td>
</tr>
<tr>
<td>P</td>
<td>0.000</td>
<td>0.190</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Ust'-Ida I (ISG)</th>
<th>Little Sea (ISG)</th>
<th>All</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
<td>Males</td>
</tr>
<tr>
<td>n</td>
<td>11</td>
<td>7</td>
<td>17</td>
</tr>
<tr>
<td>r</td>
<td>0.613</td>
<td>0.593</td>
<td>0.609</td>
</tr>
<tr>
<td>P</td>
<td>0.045</td>
<td>0.160</td>
<td>0.009</td>
</tr>
</tbody>
</table>

n, number of individuals; r, Spearman correlation coefficient; P, P value (bold font indicates statistical significance).
cartilaginous ones being naturally smooth with clearly delineated margins (Benjamin et al., 1992, 2002; Hems and Tillmann, 2000; François et al., 2001; Miltz et al., 2001). Moreover, fibrocartilaginous entheses seem to be more susceptible to overuse injuries (Benjamin et al., 2002), making them an attractive choice for scholars seeking to reconstruct past activity (e.g., Villotte et al., 2010; Schrader, 2012), despite the fact that they may be less likely to preserve archaeologically due to their location on long bone epiphyses and apophyses. While it is clearly important to consider the two enthesal types separately in analyses, results from this study support the assertion that activity patterns influencing the morphology of one type of enthesis will, more than likely, have a similar (in direction, not necessarily in scale) effect on the morphology of the other type, at least in respect to the lower limbs. In the Cis-Baikal, where poor skeletal preservation is a serious issue with some samples (e.g., the posthiatus Little Sea cemeteries in the current study), adequate lower limb activity-based data may be obtainable from fibrous entheses only, an approach that has not been commonly employed in the anthropological literature.

SUMMARY AND CONCLUSIONS

The examination of lower-limb enthesal data from four large middle Holocene cemetery samples in the Cis-Baikal region supports our previous findings and reveals several new and important insights about the nature and patterning of ancient foraging activities. While a very general trend suggests increased lower limb activity during the prehiatus period, possibly reflecting the larger size of local populations and subsequent engagement in more frequent and/or intensive logistical foraging, results also point to the importance of spatial distribution (i.e., site location within particular micro-regions) in explaining differences in enthesal morphology. Of particular note is the uniqueness of the prehiatus Kitoi site of Lokomotiv, located in the Angara River Valley, which exhibits considerably—and often significantly—higher aggregate scores than most of those from the other three cemetery samples. This distinction may be accounted for by the particularly high population densities in the microregion that could have further increased competition over resources. The posthiatus ISG sample from the Little Sea is situated at the opposite end of the spectrum, being consistently characterized by the lowest aggregate scores, a number of which are significantly lower than those of the other sites. Again, these (apparently reduced) activity levels may reflect peculiarities of the microregion, particularly available food resources such as rich fisheries and seasonal access to seals. The other two samples included in analyses, Shamanka II (prehiatus) and Usť'-Ida I (posthiatus), are more average but exhibit aggregate scores that are generally closest to their contemporaries, Lokomotiv and Little Sea, respectively.

Intrasample comparisons geared toward discerning age at death and sex differences in enthesal morphology reveal generally higher aggregate scores among males and older adults compared to females and young adults, respectively, but also increasing male-female discrepancy with advancing age at death. This observed increase in sexual disparity with age among both the Kitoi and the ISG may reflect the cumulative effects of slight activity differences over time or actual shifts in male and/or female roles throughout adulthood. It also acts to discount the influence of body size, per se, on enthesal morphology, lending support to our interpretations that sex differences (i.e., differences in sex-specific activities) account for much of the male-female disparity observed in the region.

A final observation worthy of note is the fact that data from fibrous and fibrocartilaginous entheses are largely congruous in this study. Not only can similar conclusions being drawn from both datasets, but correlation analyses also indicate statistically significant co-variation between the two entheseal types for most of the groups examined. While the considerable anatomical differences between fibrous and fibrocartilaginous entheses require that they be analyzed separately, these results suggest that, at least in the Cis-Baikal, their morphology may have been similarly affected by the same physical activities or patterns of such activities.

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