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Lower limb biomechanics and habitual mobility among mid-Holocene populations of the Cis-Baikal

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ABSTRACT

The mid-Holocene hunter–gatherer populations of the Cis-Baikal represent long-term occupation by the Early Neolithic Kitoi Culture (6800–4900 B.C.) and the Middle Neolithic and Bronze Age Isakovo, Serovo and Glazkovo (ISG) cultures (4200–1000 B.C.). While there is considerable evidence for cultural and genetic discontinuity between these populations, differences in habitual activity between these periods remain poorly understood. The current study uses cross sectional geometric (CSG) properties of the femur and tibia in the lower limb, to investigate variation in mechanical loading and terrestrial locomotion between the Kitoi and ISG cultural groups. The results demonstrate a significant decrease in femoral rigidity and a trend towards more circular femoral diaphyses among the later ISG groups which suggests that there was a significant decrease in terrestrial mobility across this transition. This trend is accompanied by significant declines in tibial rigidity among females, resulting in greater sexual dimorphism among the ISG than the Kitoi. This indicates a shift towards a sexual division of labour which involved greater sedentism of the ISG than Kitoi women. Overall, the results suggest that shifts in habitual activity throughout the mid-Holocene of the Cis-Baikal involved both increased sedentism, and an increase in sexual differences in logistical mobility.

1. Introduction

The mid-Holocene in the Cis-Baikal is characterized by a long archaeological chronology of hunter–gatherer populations (Weber, 1995). While there is evidence for the early colonization of Siberia by late Pleistocene hunter–gatherers, the long-term colonization of the Cis-Baikal by larger populations of hunter–gatherers dates to the Early Neolithic Kitoi Culture, represented by sites such as Lokomotiv and Shamanka II. These sites consist of large cemeteries of relatively well preserved burials, dating to between 6800 and 4900 B.C (Weber, 1995; Weber et al., 2002). Subsequent human occupation of region by the Middle Neolithic and Bronze Age Isakovo, Serovo and Glazkovo (ISG) cultures, dates to between 4200 and 1000 B.C. (Weber, 1995; Weber et al., 2002). Although this represents a relatively continuous chronology of occupation in the Cis-Baikal region, it is worthy of note that there is a hiatus of approximately 700 years between the Early Neolithic and Middle Neolithic periods. The 'Neolithic' populations on either side of this Hiatus followed a hunting-gathering and fishing subsistence strategy. This subsistence is associated with pottery and the bow and arrow rather than cultivated plants or domestic livestock, so they do not represent early farmers as the term 'Neolithic' might suggest in other contexts. Despite the long-term continuity of a hunting and gathering subsistence strategy in the region, there is significant evidence for both cultural (Weber, 1995; Weber et al., 2002) and biological discontinuity (Mooder et al., 2005, 2006) across this hiatus.

On a very broad level, relative to other hunter–gatherers worldwide, there was considerable homogeneity in the habitual behaviour of Cis-Baikal hunter–gatherers throughout the Holocene. Both pre and post-hiatus populations practiced a hunting and gathering subsistence strategy with the exploitation of a mixture of terrestrial and aquatic resources (Lieverse et al., 2011). While there was a general warming trend throughout the Holocene (Prokopenko et al., 2007; White et al., 2008) which led to a northward expansion of coniferous forests, the Holocene climate was more stable than the preceding Pleistocene. Despite these broad similarities in behaviour and ecology between the Kitoi and ISG, detailed comparisons of skeletal biology and stable isotopes between the periods provide some evidence for differences in habitual behaviour. Evidence from musculo-skeletal stress markers

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suggests that watercraft use was an important component of mobility throughout both periods, and was undertaken by most community members (Lieverse et al., 2011). This interpretation is supported by evidence from long-bone cross-sectional geometry. A comparison of humeral 35% total subperiosteal area (*TA*) relative to femoral midshaft *TA* provides an indicator of upper limb relative to lower limb strength, and by extension, an indicator of the relative importance of watercraft. In this context, Kitoi (Early Neolithic) humeri are particularly robust relative to femora among both women and men suggesting that watercraft use was an important component of Kitoi logistical mobility (Lieverse et al., 2011). This morphological pattern remained among ISG males, suggesting a continued importance of watercraft use after the hiatus. A significant reduction in humeral robusticity among ISG females suggests a shift in the sexual division of labour. This is accompanied by changes in the shape of the femoral diaphysis which provide some evidence for a decrease in terrestrial mobility between the Kitoi and ISG periods (Lieverse et al., 2011). Subtle differences in habitual behaviour between the groups may be a result of local variation in ecology and site distributions which influence regional differences in subsistence activity, rather than specific cultural variation (Lieverse et al., 2007a, 2007b).

In addition to the morphological evidence for habitual behaviour, there is isotopic evidence for variation in diet between the Kitoi and ISG periods. Stable carbon isotopes reflect variation in marine sources rather than terrestrial plants in the Baikal region, however stable nitrogen isotopes provide an index of the relative importance of terrestrial mammals and aquatic species such as fish or seals (Katzenberg et al., 2010). The available isotopic evidence suggests that high trophic level fish and seals provided an important component of the diet throughout the Holocene, although there is some evidence for a shift from shallow water to more open water fish from the Kitoi to ISG periods (Lieverse et al., 2011). This further suggests that watercraft use may have increased in importance in concert with this dietary change. Strontium isotope analyses have provided some additional perspective on mobility, with evidence for inter-site variation in both the Kitoi and ISG periods (Lieverse et al., 2011). This may be linked to either different regions of logistical foraging between groups, or technological limitations which delimited the range of foraging and watercraft use in both periods.

While there now considerable evidence for temporal and spatial differences in the interaction of people with their environments between the Kitoi and ISG periods, the general question as to the relative intensity of terrestrial mobility remains relatively poorly understood.

The very rich archaeological evidence from Kitoi period cemeteries suggests that these communities were larger than the subsequent ISG, with considerable logistical mobility but lower residential mobility (Weber et al., 2002). Under this interpretation, Kitoi mobility was predominantly undertaken by males for the purpose of the acquisition of large terrestrial mammals such as ruminants, and through fishing and the use of watercraft. At present the evidence for logistical mobility and sedentism is challenging to interpret, and one might predict that both logistical and residential mobility were relatively high throughout the mid-Holocene. Further analyses of lower limb biomechanical properties of the Kitoi and ISG populations may shed light on longer-term trends in terrestrial mobility in the region.

1.1. Skeletal biomechanics

Variation in the morphology of the human skeleton is influenced by a wide range of factors (Stock et al., 2011). Skeletal robusticity, or relative bone strength, is largely responsive to patterns of habitual activity during life, leading to a correlation between bone morphology and patterns of activity (Ruff, 2008). The underlying biological mechanism for bone functional adaptation is complex (Pearson and Lieberman, 2004), however there is significant evidence that mechanical loading influences the distribution of cortical bone in long bone diaphyses (Robling et al., 2000; Ruff et al., 2006; Shaw and Stock, 2009a, 2009b; Stock et al., 2013). The most commonly used method of analysis of long bone robusticity uses engineering formulae for hollow beams to estimate the mechanical performance of bones based on the distribution of cortical bone in diaphyseal cross-sections to calculate strength properties which are standardized to body mass prior to comparison (Larsen, 1997; Ruff, 2000).

Variation in long bone robusticity has frequently been used to infer patterns of activity in the past (Ruff et al., 1984; Bridges, 1989; Stock, 2006; Macintosh et al., 2014a), with particular emphasis on the relationship between lower limb robusticity and terrestrial mobility (Ruff, 1987, 1994; Larsen, 1995; Holt, 2003; Stock and Pfeiffer, 2004; Stock, 2006; Stock et al., 2011; Pomeroy, 2013; Shaw and Stock, 2013; Davies et al., 2014; Macintosh et al., 2014b). Comparisons of lower limb robusticity across cultural transitions in North America have noted that femoral diaphyses among agricultural populations tend to be more circular with smaller total subperiosteal areas, which suggests decreased mobility following the adoption of agriculture (Ruff et al., 1984; Ruff, 1987; Ruff and Larsen, 1990). In contrast, the hunter–gatherer morphological pattern is characterised by greater robusticity and antero-posterior strengthening of the femur midshaft, which may be associated with greater terrestrial mobility. As the most repetitive weight bearing activities are likely to have the greatest influence on skeletal morphology among prehistoric populations, antero-posterior loading of the lower limb in response to terrestrial mobility is thought to stimulate cortical bone hypertrophy in the antero-posterior plane leading to greater antero-posterior (I_x) to mediolateral (I_y) bending strength ratios.

A general reduction in cross-sectional geometric properties, and hence rigidity, of the lower limb has been noted across longer term cultural transitions associated with the transition to agriculture in both Northeast Africa (Stock et al., 2011) and Central Europe (Macintosh et al., 2014b). In other contexts where changes in modes of production have been associated with continued high mobility, such as the adoption of pastoralism, femoral shape indices remained high across the Pleistocene–Holocene boundary (Marchi et al., 2006). While this research suggests that sedentism associated with food production and domestication may lead to gracilization of the lower limb, there is also evidence for variation in lower limb diaphyseal morphology among hunter–gatherers which may reflect variation in mechanical loading and hence terrestrial mobility. Variation in femoral and tibial robusticity are also found between groups of hunter–gatherers with significantly different patterns of mobility (Stock and Pfeiffer, 2001; Stock, 2006). Khoisan foragers with very high terrestrial mobility were found to have greater torsional strengths of the femur and tibia, and more antero-posteriorly thickened diaphyses when compared to more sedentary and marine based hunter–gatherers (Stock and Pfeiffer, 2001). Similarly, regional variation among closely related foragers was identified between groups in the forest and fynbos biomes of southern Africa (Stock and Pfeiffer, 2004). This may reflect ecological influences on the relative mobility of closely related populations. A relationship between femoral antero-posterior bending strength and archaeological evidence for declining mobility has also been identified from the Upper Palaeolithic to Mesolithic in Europe (Holt, 2003). These studies suggest that lower limb robusticity can be used to interpret more subtle patterns variation in mobility between hunter–gatherer populations. While

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differences in terrain may influence the biomechanical loading of the lower limb (Ruff, 1999), the people of the Kitoi and Isakovo-Serovo-Glazkovo periods occupied the similar landscapes and hence differences in terrain are not likely to have influenced lower limb variation among these groups.

Comparisons of skeletal robusticity may be used to detect general, population level variation in habitual activity, but patterns of sexual dimorphism may also be useful indicators of the division of labour in the past (Ruff, 1987). Although hormonal, genetic and developmental differences may underpin much of the pattern of sexual dimorphism in our species, reduced sexual dimorphism has been linked with lower levels of gender-based task specialization (Ruff, 1987, 1999; Collier, 1993). Previous comparisons of femoral robusticity among the mid Holocene populations of the Cis-Baikal suggest that the ISG have more circular femoral diaphyses than the earlier Kitoi, indicative of a general reduction in terrestrial mobility through time (Stock et al., 2010; Lieverse et al., 2011). Recent analyses, however, suggest that analyses of pattern of variation in skeletal robusticity of tibia may provide more important information about terrestrial mobility than those of the femur (Davies and Stock, 2014a,b; Macintosh et al., 2014b), as the energetic demand of locomotion may place selective pressure on tissue optimization in distal elements of the limbs (Stock, 2006).

In this study we examine variation in lower limb robusticity among the populations of the middle Holocene Cis-Baikal to investigate whether there is evidence for variation in terrestrial mobility between the Kitoi and ISG groups. We hypothesize that the earlier Kitoi populations will have more robust femora and tibiae, consistent with greater habitual mechanical loading related to high levels of logistical mobility. We also hypothesize that the Kitoi will have greater antero-posterior hypertrophy of the long-bone diaphyses and, in particular, of the tibia.

2. Materials and methods

Skeletal remains used in this study represent femora and tibiae of adult skeletal remains (Table 1) from the Kitoi period cemeteries of Lokomotiv/Raisovet and Shamanka II (M = 31, F = 19), and primarily the ISG cemeteries of Ust'Ida and Khuzhir-Nuge XIV, but also several individuals from Verkholensk, Zakuta and Silinskaia (M = 18, F = 12); (see Lieverse et al., 2011; Lieverse et al., 2015, in press). Sex was determined using standard observational methods which evaluate sexual dimorphism in the pelvis (Buikstra and Ubelaker, 1994). Long bone diaphyseal robusticity was quantified at the femoral and tibial midshaft locations using silicone moulds of periosteal contours (Stock, 2002; Stock and Shaw, 2007). The periosteal contours are used to estimate cross sectional properties of long-bone diaphyses (Table 2) which are highly correlated with values derived from methods which consider both the periosteal and endosteal contours (Stock and Shaw, 2007). Second moments of area (I) represent an estimate of the bending rigidity about a particular plane. They are commonly calculated as maxima (I_{max}) and minima (I_{min}), as well as in the antero-posterior (I_x) and mediolateral (I_y) planes. The polar second moment of area (J) represents an estimate of the torsional rigidity of a diaphysis, calculated as the sum of any two perpendicular second moments of area (I_{max} and I_{min}; I_x and I_y). Ratios of these bending rigidities (I_{max}/I_{min}; I_x/I_y) can be used as an indicator of the cross-sectional shape of diaphyses as reflected by the distribution of cortical bone about the centroid. Total subperiosteal area (*TA*) is a measure of the total area of a section within the periosteal contour, and while area measures are often considered to correspond with compressive strength, their high correlation with J values suggests that they are a good indicator of overall bone diaphysis rigidity ($r^2 = 0.996$), (Stock and Shaw, 2007).

Table 1
Cis-Baikal skeletal population details.

Population	Approximate date (cal. BP)	Cemetery	Individuals (males/females)
Kitoi (Early Neolithic)	**8000–6800 cal. BP**	**Total**	**50 (31/19)**
		Lokomotiv	28 (14/14)
		Raisovet	5 (3/2)
		Shamanka	17 (14/3)
Isakovo/Serovo/Glazkovo (Late Neolithic – Bronze Age)	**6000/5800–4000 cal. BP**	**Total**	**30 (18/12)**
		Ust'Ida	22 (13/9)
		Verknolensk MK	1 (0/1)
		Zakuta	2 (1/1)
		Khuzhir-Nuge XIV	4 (4/0)
		Silinskaia	1 (0/1)

All material curated at Irkutsk State University.

Table 2
Descriptions of cross-sectional geometry properties and shape ratios.

Variable	Formula	Biomechanical or morphological relevance
Total subperiosteal area (*TA*)	–	External quantification of combined cortical bone and medullary area, highly correlated with J
Second moment of area about:		
Maximum axis	I_{max}	Maximum bending rigidity
Minimum axis	I_{min}	Minimum bending rigidity
Anteroposterior (A-P) axis	I_x	A-P bending rigidity
Mediolateral (M-L) axis	I_y	M-L bending rigidity
Polar second moment of area (J)	$I_{max} + I_{min}$	Torsional and twice average bending rigidity in any two perpendicular planes
Shape ratio	I_{max}/I_{min}	Distribution of bone about the major and minor axes of a cross section
Shape ratio	I_x/I_y	Distribution of bone about the A-P and M-L axes of a cross section

$TA = mm^2$; all second moments of area and polar second moment of area $= mm^4$; descriptions from Ruff and Hayes (1983), Ruff (2008).

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Table 3
Femur length and body mass estimates of the Kitoi and Isakovo/Serovo/Glazkovo groups (adapted from Stock et al., 2010).

Variable	Kitoi				Isakovo/Serovo/Glazkovo		
	Sex	N	Mean	S.D.	N	Mean	S.D.
Femur max length	♂	28	432.98	12.58	17	443.47	16.43
	♀	19	412.34	14.49	8	420.94	11.31
	Total	50	425.29	17.74	25	436.26	18.23
Body Mass	♂	31	66.33	3.64	16	70.16	5.45
	♀	19	58.00	4.11	8	60.84	5.28
	Total	50	63.17	5.57	24	67.05	6.93

The effect of body size differences on lower limb cross-sectional geometry was controlled for by standardizing *TA*, *J*, and all second moments of area to appropriate measures of body size, following the method of Ruff (2008): *TA*/estimated body mass, *J*/(estimated body mass*(maximum bone length^2)). Maximum bone lengths parallel to the long axis of the diaphysis were recorded using an osteometric board, and body mass was estimated from an average of left and right superoinferior femoral head breadths utilizing the average of equations of Ruff and colleagues (1991), McHenry (1992) and Grine et al. (1995). Mean femur lengths and estimated body masses are presented in Table 3. Although the people of the ISG period were slightly taller with greater body mass than the earlier Kitoi period, their body sizes are broadly similar relative to other

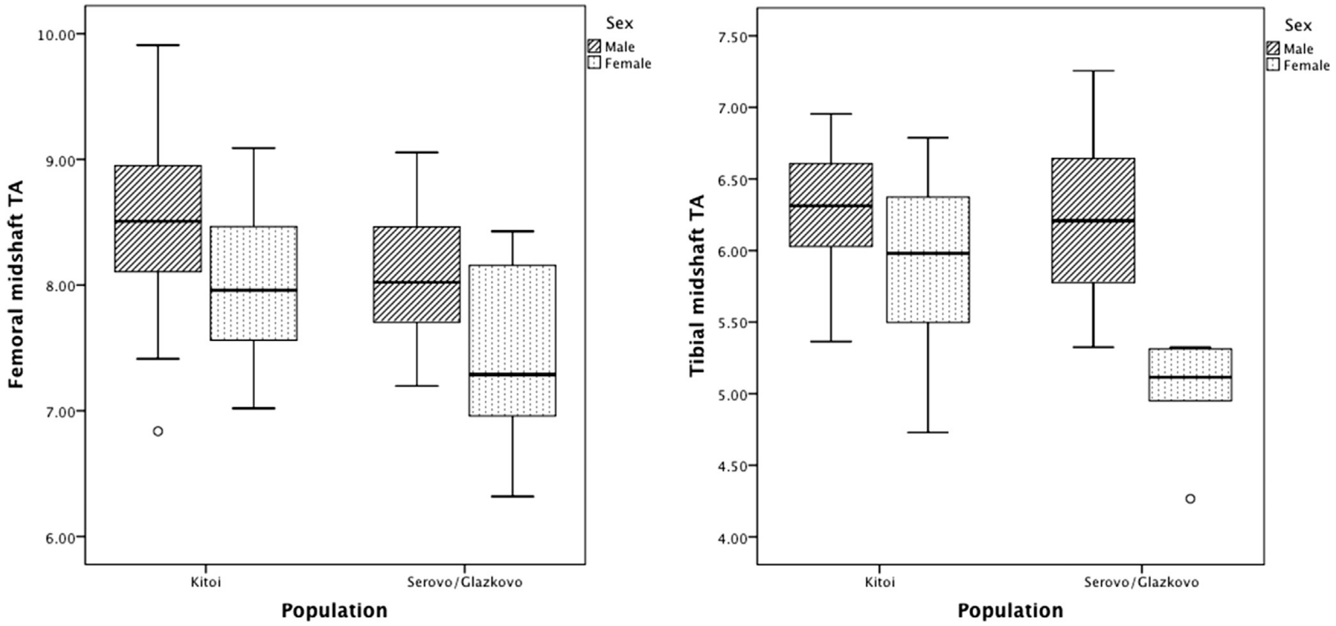

Fig. 1. Variation in femoral and tibial midshaft total subperiosteal areas (*TA*).

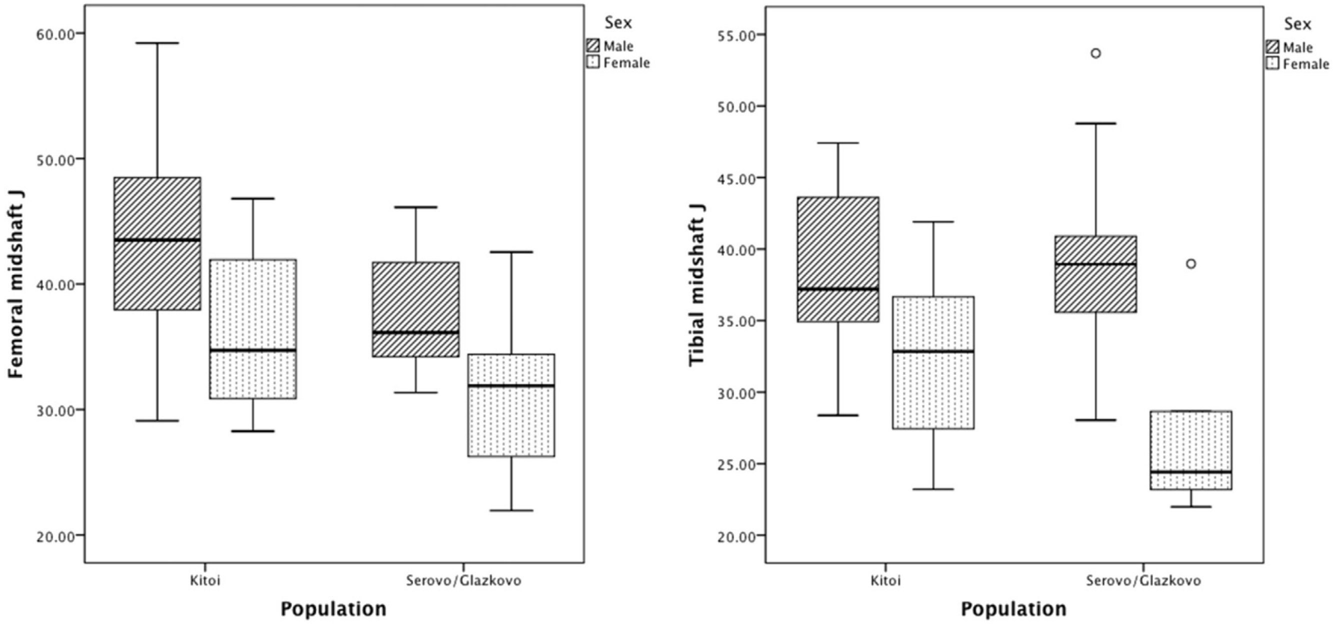

Fig. 2. Variation in femoral and tibial midshaft polar second moment of area (*J*).

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populations (Stock et al., 2010), so it is not anticipated that the choice of body mass estimation equations would bias the results derived from the use of size-standardized cross-sectional properties. All outliers greater than three standard deviations from the mean were removed from the data prior to analyses. Femoral and tibial midshaft cross-sectional areas and second moments of area were compared between Kitoi and Isakovo/Serovo/Glazkovo individuals by sex using independent samples *t*-tests. Indices of cross-sectional shape, I_x/I_y and I_{max}/I_{min}, being skewed in their distributions within the samples, were compared using Mann–Whitney non-parametric tests. These were also used to examine sexual dimorphism within each group. Statistical analyses were conducted in SPSS v20.

3. Results

Summary statistics for midshaft CSG properties by population and sex are presented for the femur (Table 4) and tibia (Table 5). Results of *t*-tests between means of CSG properties between the Kitoi and ISG groups, for both males and females, are presented in Table 6. Comparisons between Kitoi and ISG midshaft total subperiosteal areas among both males and females are presented in Fig. 1. Both Kitoi males and females have significantly higher femoral midshaft *TA* than the ISG males and females, respectively. At the tibial midshaft, there is no significant difference between Kitoi and Serovo/Glazkovo males, however the Kitoi females have significantly higher tibial midshaft *TA* values than the ISG females. Comparisons of midshaft polar second moments of area (*J*) between the Kitoi and ISG (Fig. 2) reveal a similar pattern to that observed for *TA*. Values of *J* are significantly lower in the ISG than the Kitoi at the femoral midshaft among both males and females. Significantly lower *J* values are also found among the females at the tibial midshaft, but there is no reduction in tibial *J* among males. These results suggest that the post-hiatus populations are generally more gracile in lower limb robusticity than the pre-hiatus Kitoi.

Investigation of the pattern of midshaft bending rigidities in the femur (Fig. 3) helps to investigate the underlying variation that is reflected in differences in *TA* and *J* values. Here we can see that there are significant differences in I_{max} values among both males and females between the Kitoi and ISG populations, but no significant differences in I_{min}. The significant differences are also reflected in I_x values, but not I_y, which suggests that the majority of the variation present is reflected in greater hypertrophy in the antero-posterior plane among the earlier Kitoi populations. This suggests that minimum and medio-lateral bending rigidities are similar between the populations, but that the earlier Kitoi femora are characterized by greater antero-posterior rigidity.

A similar comparison of bending rigidities at the midshaft of the tibia (Fig. 4) provides a somewhat different picture. Here there are no differences in tibial midshaft I_{max} or I_x among males, but a slight and non-significant increase in I_{min} and I_y values. A comparison of Kitoi and ISG women, however, reveals a statistically significant decrease in I_x, I_{max} and I_{min} values. These results are suggestive of differences in both diaphyseal shape between populations, as well as sexual dimorphism. These will be investigated further below.

Overall the observed trends in diaphyseal bending rigidities suggest that variation in diaphyseal shape indices between populations and sexes may underpin much of the observed morphological variation. Comparisons of diaphyseal shape properties demonstrate a statistically significant reduction in I_{max}/I_{min} ratios between both the Kitoi and ISG males and females (Fig. 5) at the femoral midshaft, but no differences in I_{max}/I_{min} ratios of the tibial midshaft between the periods. While I_{max}/I_{min} ratios provide an index of diaphyseal shape that is independent of orientation of planes of loading, I_x/I_y ratios provide a measure of antero-posterior relative to medio-lateral rigidity of the diaphyses. In this measure there is evidence for a significant reduction in relative antero-posterior rigidity of the femur midshaft between the Kitoi and ISG males and females (Fig. 6). In contrast, there is no significant variation in I_x/I_y ratios of the tibial midshaft between the periods.

Table 4
Femoral midshaft summary statistics by population and sex.

	N	*TA*		*J*		I_{max}		I_x		I_{min}		I_y		I_{max}/I_{min}		I_x/I_y	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Males																	
Kitoi	31	8.53	0.654	43.35	6.942	25.90	4.719	25.00	4.678	17.46	2.620	18.36	2.927	1.49	0.172	1.37	0.196
Serovo/Glazkovo	18	8.06	0.556	37.64	4.701	21.47	2.944	19.52	3.611	16.18	2.321	18.12	2.421	1.35	0.171	1.08	0.235
Females																	
Kitoi	19	8.01	0.596	36.27	6.229	20.47	4.116	19.93	4.068	15.79	2.395	16.33	2.689	1.29	0.155	1.22	0.176
Serovo/Glazkovo	12	7.43	0.685	31.39	6.660	17.14	3.709	15.12	3.322	14.25	3.215	16.27	3.903	1.22	0.152	0.94	0.155

N: number of bones included in analyses; SD: standard deviation; *TA*: total subperiosteal area (mm^2); *J*: polar second moment of area (mm^4); *I*: bending rigidity.

Table 5
Tibial midshaft summary statistics by population and sex.

	N	*TA*		*J*		I_{max}		I_x		I_{min}		I_y		I_{max}/I_{min}		I_x/I_y	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Males																	
Kitoi	24	6.28	0.460	38.58	5.055	28.88	3.973	26.32	3.629	9.69	1.512	12.26	2.138	2.98	0.377	2.19	0.362
Serovo/Glazkovo	13	6.26	0.554	39.09	6.843	28.91	5.545	26.08	5.260	10.18	1.770	13.01	2.163	2.86	0.389	2.02	0.324
Females																	
Kitoi	16	5.94	0.576	32.31	5.478	22.71	3.729	20.45	3.987	9.60	2.167	11.86	2.132	2.43	0.441	1.75	0.326
Serovo/Glazkovo	7	4.99	0.435	24.53	2.518	17.66	1.665	15.08	1.343	7.36	1.546	10.04	1.973	2.62	0.322	1.64	0.255

N: number of bones included in analyses; SD: standard deviation; *TA*: total subperiosteal area (mm^2); *J*: polar second moment of area (mm^4); *I*: bending rigidity.

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Table 6
Results of *t*-tests and Mann–Whitney tests for femoral and tibial temporal change and sexual dimorphism.

	TA	J	I_{max}	I_x	I_{min}	I_y	I_{max}/I_{min}[a]	I_x/I_y[a]
Femur								
Males	<0.018	<0.004	<0.001	<0.001	–	–	<0.026	<0.001
Females	<0.019	<0.048	<0.030	<0.002	–	–	–	<0.001
Sexual Dimorphism								
Kitoi	<0.008	<0.001	<0.001	<0.001	<0.028	<0.018	<0.001	<0.011
Serovo/Glazkovo	<0.011	<0.006	<0.002	<0.002	–	–	<0.035	–
Tibia								
Males	–	–	–	–	–	–	–	–
Females	<0.003	<0.007	<0.009	<0.001	<0.032	–	–	–
Sexual Dimorphism								
Kitoi	<0.049	<0.001	<0.001	<0.001	–	–	<0.001	<0.001
Serovo/Glazkovo	<0.001	<0.001	<0.001	<0.001	<0.004	<0.011	–	<0.014

[a] Mann–Whitney nonparametric test results, as I_{max}/I_{min} and I_x/I_y ratios are not normally distributed, all other results represent t-tests values indicate significance to at least $p < 0.05$; dash indicates lack of significance at $p < 0.05$; all significant results indicate higher values in the Kitoi relative to Serovo/Glazkovo (temporal change) and in males relative to females (sexual dimorphism).

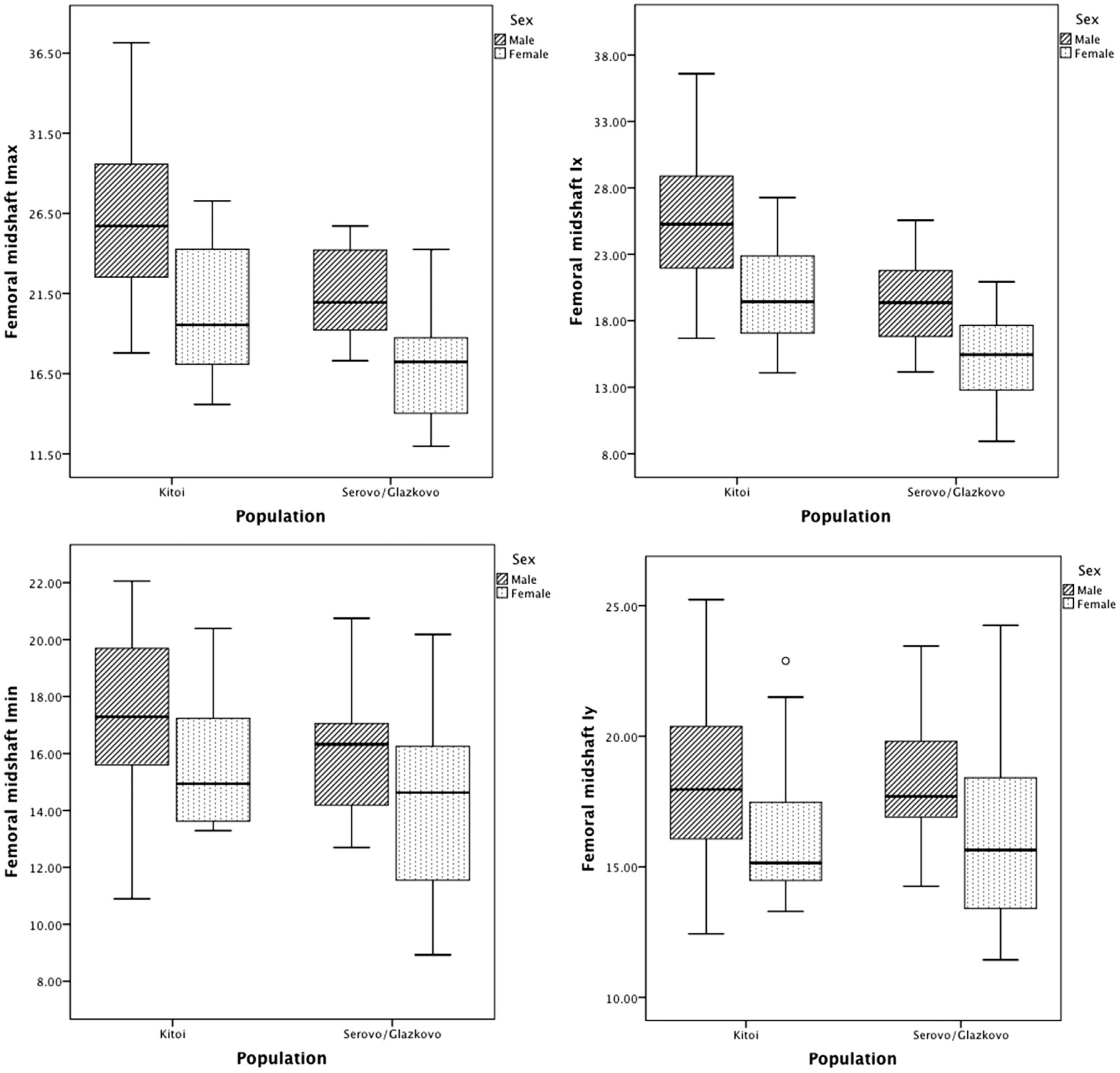

Fig. 3. Variation in femoral midshaft bending rigidities (I_{max}, I_{min}, I_x, I_y).

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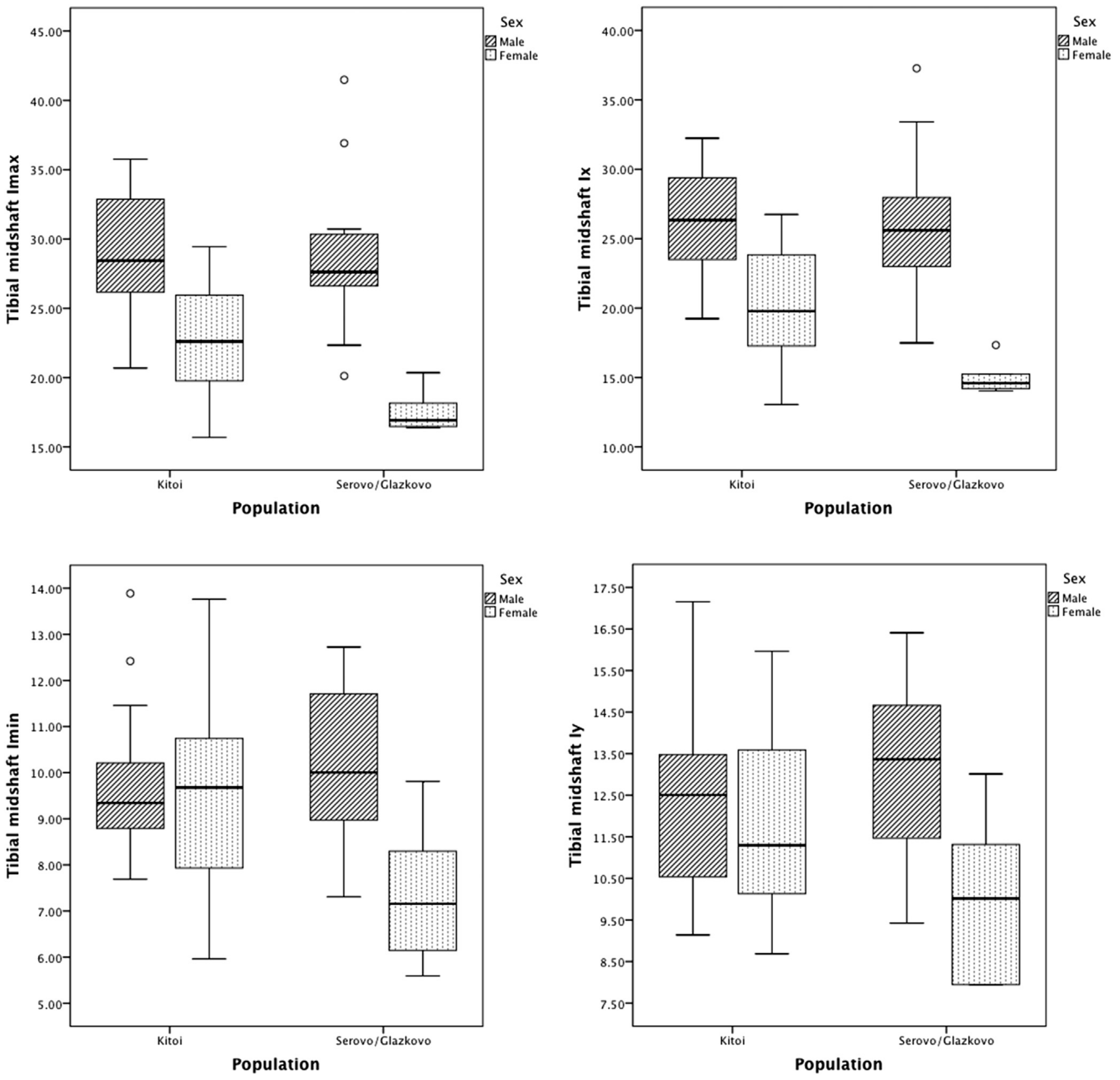

Fig. 4. Variation in tibial midshaft bending rigidities (I_{max}, I_{min}, I_x, I_y).

While there is a general pattern of greater *TA* and *J* values among males than females, accompanied by less circular diaphyses, specific comparisons between males and females within the Kitoi and ISG periods can provide more insight into the pattern of sexual dimorphism and variation in the division of labour. Sexual dimorphism is high in femoral CSG properties among the Kitoi, with significantly higher values for all properties in males relative to females. Among the Serovo/Glazkovo, males also have significantly higher values of *TA*, *J*, I_{max}, I_x, and I_{max}/I_{min} than females. Kitoi males also have significantly less circular femoral diaphyses (higher midshaft I_{max}/I_{min}).

Sexual dimorphism remains high in the tibia as well as the femur, though it is particularly pronounced in the Serovo/Glazkovo, where males have significantly higher values of all properties relative to females, with the exception of I_{max}/I_{min}. Among the Kitoi, males have significantly higher values of tibial midshaft *TA*, *J*, I_{max}, I_x, and both shape ratios than Kitoi females.

4. Discussion

Overall, this study has identified a number of differences in the biomechanical properties of lower limb diaphyses between the Kitoi and ISG populations of the mid-Holocene Cis-Baikal. These differences can be interpreted as indicative of variation in habitual loading, and thus activity, between these groups. Analyses of measures of lower limb bone quantity (*TA*, *J*) suggest that the pre-hiatus Kitoi are generally more robust than post-hiatus ISG populations. These results provide evidence for a reduction in lower limb compressive and torsional rigidity between the periods, which can be interpreted as evidence for a decline in terrestrial mobility.

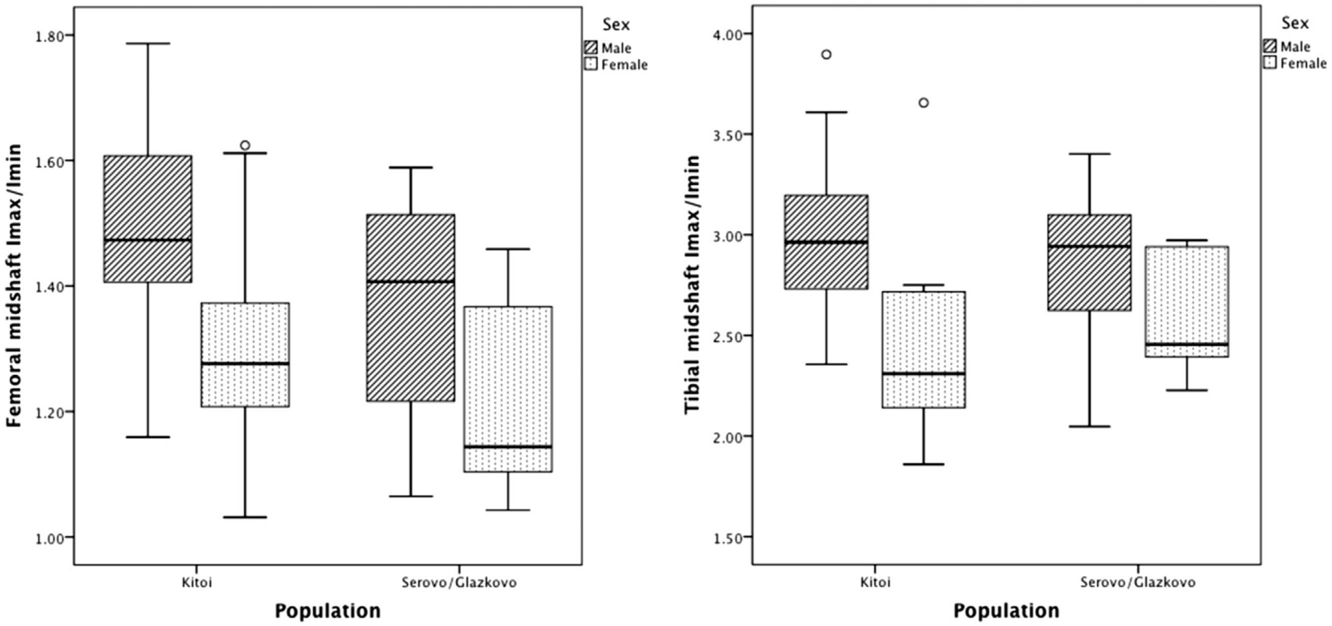

Fig. 5. Variation in femoral and tibial midshaft I_{max}/I_{min} ratios.

As general robusticity of cortical bone in the lower limb reflects mechanically induced remodeling over a long period of time, given the pace of bone remodeling, it is more conservative to interpret cross-sectional variation in long bone diaphyses as indicative of general patterns of loading and mobility rather than specifically logistical or residential mobility.

While this study notes somewhat different patterns of variation in total bone rigidity (TA, J) versus diaphyseal shape (I_{max}/I_{min}, I_x/I_y) between the femur and tibia, this is not entirely unexpected. There is now some evidence to suggest that tibial midshaft TA and J values may be a particularly useful indicator of general mobility (Stock, 2006; Davies and Stock, 2014a,b; Macintosh et al., 2014b). In these indicators there is a significant decrease among the ISG females, which result in particularly high levels of sexual dimorphism. This may reflect differences in the sexual division of labour between the Kitoi and ISG. A plausible explanation for this trend would be a decrease in logistical mobility among ISG women, although this interpretation would be strengthened with verification by other lines of evidence.

The general decrease in femoral TA and J values between the Kitoi and ISG populations is reflected by differences in most measures of bending rigidity (I_x, I_y, I_{max}, I_{min}). These are suggestive of a general decrease in mechanical loading of the femur. When tibial bending rigidities were compared, the primary differences were identified as significant decreases among the ISG women. These provide some additional support for the interpretations of a general

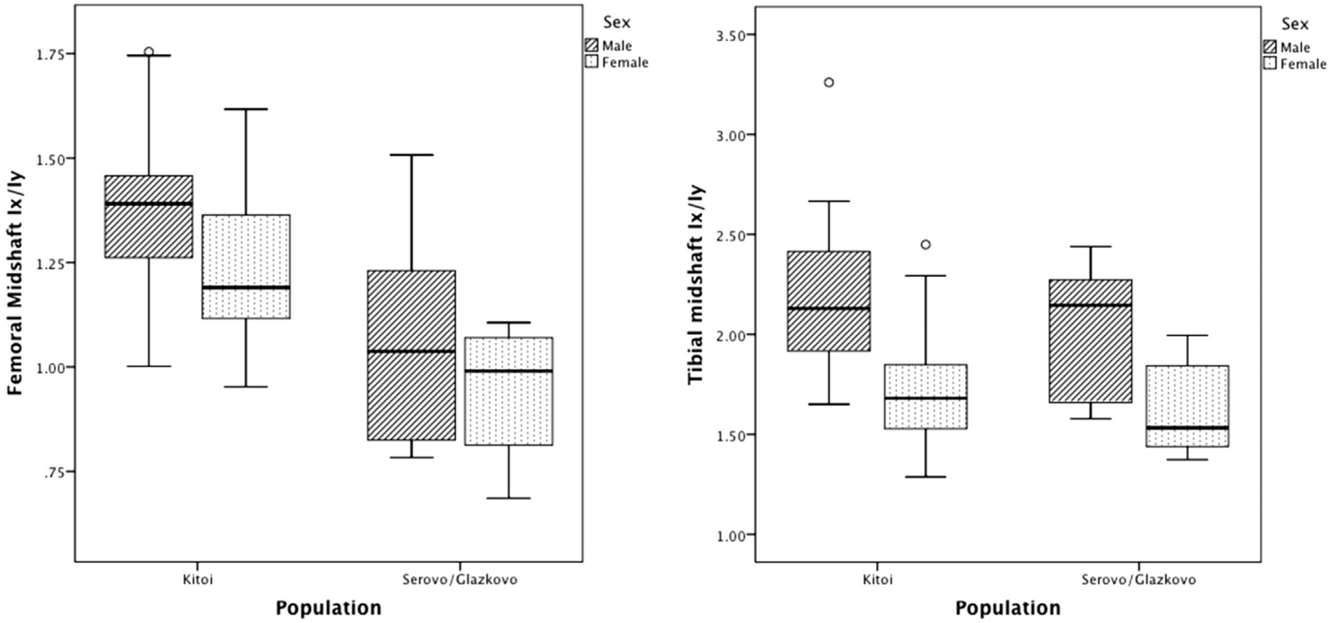

Fig. 6. Variation in femoral and tibial midshaft I_x/I_y ratios.

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decrease in mobility between the Kitoi and ISG, which is particularly pronounced among women. It is interesting to note that the differences in shape indices of the tibial midshaft are non-significant. There is some evidence that diaphyseal shape indices of the tibia are less sensitive to variation in terrestrial mobility than tibial midshaft rididity (Stock and Pfeiffer, 2001; Holt, 2003; Stock, 2006; Sládek et al., 2006a,b; Marchi, 2008; Marchi et al., 2011). This may relate to the added mechanical complexity of the tibial and fibular complex (Marchi et al., 2011; Sparacello et al., 2014). Lower limb shape indices do not seem to be influenced by limb lengths or proportions (Shaw and Stock, 2011), but do correlate with inferred patters of mobility (Stock, 2006). The results of the current study provide further evidence for these trends and are suggestive of a decrease in terrestrial mobility from the Kitoi to the ISG periods. While there is no direct way of determining whether this reflects logistical or residential mobility from biomechanical signature of the skeleton, it is reasonably to suggest that logistical mobility may provide the most regular and habitual component of total mobility, and hence should be reflected in lower limb biomechanics.

When we place the current results within the context of previous work on the mid-Holocene archaeology of the Cis-Baikal, there is evidence that the Kitoi period groups had greater population sizes than the subsequent ISG, with very high levels of logistical mobility but lower residential mobility (Weber et al., 2002). This interpretation suggests that male logistical mobility was particularly high due to hunting of ruminants and fishing. Patterns of sexual dimorphism are somewhat difficult to interpret on their own, due to the different hormonal profiles between men and women which influence the pattern of bone remodeling and thus the 'norm of reaction' to habitual loading. However, the relatively high levels of sexual dimorphism among both the Kitoi and ISG is consistent with high levels of male logistical mobility. A more surprising result is the relatively pronounced level of sexual dimorphism found among the ISG, where the women show a considerable reduction in tibial midshaft J. This suggests that mobility remains high among ISG men, but that women became more sedentary during this period. This may reflect a fundamental shift in the division of labour, the balance between logistical and residential mobility, and/or underlying ecological variation in the site distributions. Further research is required to differentiate these.

Previous research has noted differences in the evidence for habitual activity between the Kitoi and ISG groups, on the basis of the prevalence of osteoarthritis (Lieverse et al., 2007a). The current study suggests that these differences are accompanied by changes in terrestrial mobility, and in particular, the sexual division of labour surrounding mobility. Stable isotopic analysis of some of the same remains suggests that diets were dominated by locally available combinations of terrestrial mammals and aquatic species (Katzenberg et al., 2010), although in there is evidence to suggest that there was a shift from shallow to open water fish from the Kitoi to ISG periods (Lieverse et al., 2011). When we consider that this trend is accompanied by a reduction in female humeral (Lieverse et al., 2011) and lower limb robusticity (this paper), it appears as there was a significant shift towards more sedentary activity among females in the ISG groups.

5. Conclusions

The current study provides skeletal biomechanical evidence for a decrease in terrestrial mobility between the Kitoi and later ISG populations of the mid-Holocene Cis-Baikal. In particular, there were significant decreases in femoral midshaft J and I_x/I_y, combined with an increase in sexual dimorphism in the ISG, driven largely by tibial *TA* and J values. Further analyses of limb biomechanical properties of the Kitoi and ISG populations may shed light on longer-term trends in terrestrial mobility in the region. New research suggests that microarchitecture of cortical and trabecular bone, in combination with gross morphological analyses, may provide more subtle understanding of loading in the past (Faccia et al., 2015, in this volume). While previous research which integrates multiple lines of evidence (Lieverse et al., 2011) has helped to delimit our understanding of habitual activity among these populations, future research incorporating more subtle variation in skeletal morphology within an archaeological framework may further refine our understanding of mobility in the past.

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