

Skeletal Growth in Early and Late Neolithic Foragers from the Cis-Baikal Region of Eastern Siberia

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ABSTRACT Skeletal growth is explored between Early Neolithic (EN) (8000 to 6800 BP) and Late Neolithic (LN) (6000 to 5200 BP) foragers from the Cis-Baikal region of Eastern Siberia. Previous studies suggest that increased systemic stress and smaller adult body size characterize the EN compared to LN. On this basis, greater evidence for stunting and wasting is expected in the EN compared to LN. Skeletal growth parameters assessed here include femoral and tibial lengths, estimated stature and body mass, femoral midshaft cortical thickness, total bone thickness, and medullary width. Forward selection was used to fit polynomial lines to each skeletal growth parameter relative to dental age in the pooled samples, and standardized residuals were compared between groups using *t* tests. Standardized residuals of body mass and femoral length were significantly

lower in the EN compared to LN sample, particularly from late infancy through early adolescence. However, no significant differences in the standardized residuals for cortical thickness, medullary width, total bone thickness, tibial length, or stature were found between the groups. Age ranges for stunting in femoral length and wasting in body mass are consistent with environmental perturbations experienced at the cessation of breast feeding and general resource insecurity in the EN compared to LN sample. Differences in relative femoral but not tibial length may be associated with age-specific variation in growth-acceleration for the distal and proximal limb segments. Similarity in cortical bone growth between the two samples may reflect the combined influences of systemic and mechanical factors on this parameter. *Am J Phys Anthropol* 153:377–386, 2014. © 2013 Wiley Periodicals, Inc.

This study uses a variety of skeletal growth parameters to explore differences in stress between Early and Late Neolithic foragers from the Cis-Baikal region of Eastern Siberia. Stress is defined as an external perturbation that disrupts physiological homeostasis (Seyle, 1936; Goodman et al., 1988). Skeletal growth is disrupted by external stressors when nutritional thresholds are breached and reallocated from growth in body size to provide energetic support to the continued growth and maintenance of essential tissues (Leary et al., 2006; Barbiro-Michaely et al., 2007; Giussani, 2011; Pomeroy et al., 2012). These consequences represent physiological trade-offs in the developing organism, whereby investments in survival limit future energetic investments in growth, maintenance, and productivity (Worthman and Kuzara, 2005; Kuzawa, 2007).

It is well established that populations experience reduced rates of growth or faltering in age-specific size when environmental perturbations exact a significant cost on energy metabolism (Bogin, 1998). Bioarchaeological studies find slowed growth and age-specific stunting in long bones among skeletal samples where the physiological cost of maintenance was increased (Johnston, 1962; Cook, 1984; Jantz and Owsley, 1984; Mensforth, 1985; Lovejoy et al., 1990; Okazaki, 2004; Pinhasi et al., 2005, 2006; Schillaci et al., 2011; Temple, 2011). Evidence for wasting in cortical width is also reported in environments with greater systemic stress levels (Humert, 1983; Van Gerven et al., 1985; Mays et al., 2009; Cowgill, 2010). This process is surface-specific with endosteal wasting found in samples from nutritionally deprived environments (Garn et al., 1964, 1967; Garn, 1970; Van Gerven et al., 1985). Catch-up growth in cortical

bone width is not, however, reported, suggesting that disruptions in cortical bone growth can be observed into adulthood (Garn et al., 1964, 1967; Antoniadis et al., 2003). More recent studies advocate for comparisons of body mass and stature as these parameters allow for broad comparisons between skeletal and living growth samples (Ruff, 2007). Indeed, evidence for body mass wasting and faltering in stature is reported from nutritionally deprived environments (Cowgill, 2010; Robbins Schug, 2011; Ruff et al., 2013).

Growth differences in height and weight during infancy and childhood are attributed to the physiological cost of maintenance, while those in adolescence are associated with ancestry in samples of contemporary humans from documented nutritional environments and genetic histories (Habicht et al., 1974; Johnston et al., 1975, 1976; Frisancho et al., 1980; Gratice and Gentry, 1981). The environmental influence on growth during infancy and childhood reflects a relatively strong response to demands for maintenance early in development that diminish energetic resources allocated for growth (Hochberg and Albertsson-Wikland, 2008; Hochberg, 2009). These findings are of particular importance to bioarchaeological

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research as age-specific variation in stature and body mass may help explain the relative environmental contribution to skeletal growth in genetically divergent populations (Ruff et al., 2013).

Hunter-gatherers from the Cis-Baikal region of Eastern Siberia have formalized cemeteries beginning in the Early Neolithic (8000 to 6800 BP) and are associated with Kitoi culture (Bazaliiskii, 2010; Weber and Bettinger, 2010). Early Neolithic Kitoi cemeteries are geographically concentrated in the upper section of the Angara River and Southwestern Cis-Baikal. Early Neolithic Kitoi cultures were biological descendants of Mesolithic, or possibly, Paleolithic inhabitants of the Cis-Baikal region and have elevated frequencies of haplogroups D, F, and 5Ua (Mooder et al., 2006, 2010). These haplogroups help distinguish the Early Neolithic Kitoi from the Late Neolithic Isakovo samples (see below) as well as modern indigenous inhabitants of the region. The sublineage of haplogroup F found in the Kitoi cultures is observed at high levels in modern Kets indicating the possibility of affinity between these two groups (Schurr et al., 2010).

The Late Neolithic mortuary traditions are known as Isakovo, and date between 6000 and 5200 BP (Weber et al., 2010). Evidence for an approximately 800-year discontinuity in the use of formal cemeteries during the Middle Neolithic period separating the Early Neolithic Kitoi and Late Neolithic Isakovo mortuary traditions is supported by multiple sources of data. First, radiocarbon dates show a clear period of abandonment of cemeteries in all Cis-Baikal micro-regions (Angara, Lena, Little Sea, and Southwest Cis-Baikal) between 6800 and 6000 BP (Weber et al., 2006). In addition, a more intensive reliance on freshwater fish is found in the Early Neolithic Kitoi, while Late Neolithic Isakovo people appear to have focused on lagoon/offshore fish, terrestrial mammals, and seal (Weber et al., 1993, 1998; Katzenberg et al., 2010). Genetic discontinuity is also found between the two groups, with the Late Neolithic Isakovo sample having a different sublineage of haplogroup F than the Early Neolithic groups, and possessing the U5a haplogroup suggesting close relationships with Uralic and indigenous people from the Altai region (Mooder et al., 2006, 2010; Schurr et al., 2010). Of further importance is the noted lack of haplogroups H-K, T, V, and X indicating little relatedness to the Western Eurasian populations associated with the Early Neolithic Kitoi people.

Frequencies of individuals with enamel hypoplasia are significantly higher among the Early Neolithic Kitoi compared to Late Neolithic Isakovo cultures, though no relationship between enamel hypoplasia presence and age-at-death is reported (Lieverse et al., 2007; Lieverse, 2010). This may be due to the fact that the presence of enamel hypoplasia represents events of different chronology, duration, and periodicity, and thus, a greater prevalence of individuals with defects may not necessarily produce differential impacts on age-at-death patterns. Studies of postcranial morphology found significantly greater adult femoral length and body mass among the Late Neolithic Isakovo compared to Early Neolithic Kitoi people (Stock et al., 2010). It is possible that differences in adult size between the Early Neolithic Kitoi and Late Neolithic Isakovo may be related to differences in systemic stress, though these factors have not been explored using skeletal growth data.

On this basis, two hypotheses are tested. First, evidence for stunting in longitudinal growth and wasting in

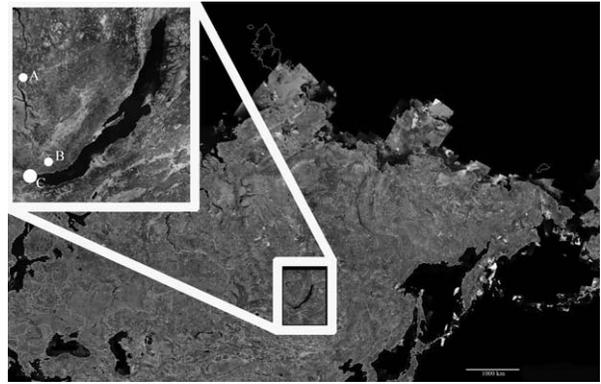


Fig. 1. Locations of the sites yielding human skeletal remains included in this study. A. Ust'Ida I, B. Lokomotiv, C. Shamanka II.

body mass and cortical bone growth will be found in the Early Neolithic Kitoi compared to Late Neolithic Isakovo sample. The Early Neolithic Kitoi will have shorter long bone lengths, smaller body mass, reduced stature, thinner cortical bone, and wider medullary cavities relative to dental age when compared to the Late Neolithic Isakovo. This hypothesis is based on studies documenting evidence for greater systemic stress in the Early Neolithic Kitoi compared to Late Neolithic Isakovo. Second, differences in skeletal growth between the two samples will emerge during infancy and childhood. This hypothesis is based on research indicating that growth disruptions reflecting systemic stress tend to occur at these stages of development.

MATERIALS

The skeletal growth samples used in this study were derived from three archaeological sites. The Early Neolithic Kitoi sample was recovered from two cemeteries, Lokomotiv and Shamanka II, located along the banks of the Angara River in the city of Irkutsk and the southwestern tip of Lake Baikal, respectively (Fig. 1). Radiocarbon dating of human skeletal remains from these sites has been completed for 59 skeletons from the Lokomotiv site and 36 skeletons from the Shamanka II site (Weber et al., 2010). Once calibrated, these cemeteries date between 7800 and 6900 BP. The Late Neolithic sample was recovered from one cemetery, Ust'Ida I, located along the Angara River approximately 150 km north of Irkutsk (Fig. 1). Sixty radiocarbon dates were obtained for 64 individuals from the Ust'Ida I site (Weber et al., 2010). The Late Neolithic component of the cemetery dates between 6000 and 5200 BP.

METHODS

Age-specific sample sizes are listed in Table 1. Age-at-death was estimated using tooth formation and emergence. Tooth formation stages were used to estimate age-at-death in the majority of individuals due to the limited impact of environment on this process and repeated independent confirmation of accuracy between studies (Smith, 1991; AlQhatani et al., 2010). Radiographs for the mandibles and maxillae were obtained using the NOMAD Pro Hand-Held X-ray System (Aribex, Provo, Utah) and Dr. Suni Plus Intraoral Digital Light Sensor (SUNI Medical Imaging Inc., San Jose,

TABLE 1. Sample sizes for the immature Early Neolithic (EN) and Late Neolithic (LN) groups listed by growth parameter

Age	Body mass		Cortical growth ^a		Femoral length		Tibial length		Stature	
	EN	LN	EN	LN	EN	LN	EN	LN	EN	LN
0	2	0	1	1	1	0	1	1	1	2
1	3	0	6	0	4	0	3	0	4	0
2	2	1	2	2	2	2	2	2	3	2
3	2	0	3	2	3	0	3	0	4	1
4	0	0	0	0	1	2	0	0	0	0
5	3	1	1	2	0	2	1	2	1	3
6	1	3	4	4	3	3	3	4	4	3
7	1	0	0	1	0	0	4	1	0	1
8	0	0	2	0	2	0	2	0	4	0
9	0	1	1	2	3	1	1	2	2	2
10	2	2	0	4	1	2	2	3	1	4
11	3	4	3	1	3	3	3	1	3	1
12	0	0	0	1	0	1	0	2	0	1
13	1	0	1	2	1	0	2	1	2	1
14	0	0	0	1	0	0	0	1	0	1
15	0	0	1	1	1	0	1	0	1	0
16	0	0	1	1	1	0	1	1	2	1
Total ^b	20	12	26	25	27	16	29	21	32	23

^aThis sample includes cortical, medullary, and total bone width.

^bAdult sample sizes: body mass (EN Male: 31, EN Female: 19; LN Male: 16, LN Female: 8), femoral length (EN Male: 28, EN Female: 19; LN Male: 17, LN Female: 8), tibial length (EN Male: 21, EN Female: 15; LN Male: 9, LN Female: 2), stature (EN Male: 28, EN Female: 19; LN Male: 17, LN Female: 8).

California). Formation stages were recorded according to standard protocols for the deciduous and permanent dentition, and ages were assigned to each tooth based on reference standards (Liversidge and Molleson, 2004; AlQhatani et al., 2010). The average age obtained for all teeth was used as a final estimate of age-at-death in each individual. Averaging estimates from multiple teeth produces the most accurate results on samples of known age (Smith, 1991).

Where tooth formation was not possible to observe, tooth emergence was used to estimate age. Here, emergence stages were recorded as not emerged, emerged past the alveolus, and emerged into occlusion. Stages of tooth emergence were then compared to a mandibular tooth emergence profile for the Cis-Baikal sample ($n = 53$) based on ages estimated using tooth formation.

It is not possible to accurately determine sex in pre-adolescent skeletal remains, though hormonal differences between male and female infants suggests that growth differences may be found at early stages of development, and certainly into adolescence (Saunders, 2008). This introduces an unknown magnitude of error to skeletal growth studies that cannot be corrected. Averages for adult male and female body mass, femoral length, tibial length, and stature are, however, included to help offset this problem by providing some understanding of how variation in body size manifested between the sexes in these samples.

Longitudinal growth was assessed by comparing linear measurements of the femur and tibia relative to dental age. These bones were chosen because variation in relative sitting height attributable to environmental effects is often reflected in leg length (Tanner et al., 1982; Bogin et al., 2002). Maximum diaphyseal lengths of the femur and tibia were collected using a sliding osteometric board and recorded to the nearest millimeter, following standard osteological protocols (Buikstra and Ubelaker, 1994). Each measurement was collected three times with modal value listed as correct. Maximum

measurements were recorded as correct when modal values were not observed. Adult maximum femoral and tibial lengths were taken from the published literature (Stock et al., 2010) and converted to maximum diaphyseal lengths using equations provided by Ruff (2007). Average adult values for male and female femoral and tibial diaphyseal lengths are included beyond the immature data points in Figure 2.

Single bones are, however, subject to variation in proportional growth and the relative contribution of each limb to stature (Ruff, 2007; Ruff et al., 2013). As a result, femoral and tibial diaphyseal length may not necessarily be perfectly associated with the influence of systemic stress on cumulative stature. Though the adult samples from Cis-Baikal have similar limb proportions (Stock et al., 2010), it remains important to ensure that differences in the growth of stature are similar to the trends observed in femoral and tibial diaphyseal length. Stature was estimated using age-specific equations produced by Ruff (2007). These equations were tested for accuracy on a different sample and were found to perform accurately (Sciulli and Blatt, 2008). In order to maximize sample sizes, the following bones, in order of use and accuracy, were utilized to estimate stature in the Cis-Baikal samples: 1) femur + tibia ($n = 44$), 2) femur ($n = 5$), 3) tibia ($n = 4$), 4) humerus + radius ($n = 1$). After 12 years of age, equations generated by Ruff (2007) include maximum bone lengths. Maximum bone lengths were not measured in the Cis-Baikal sample because both epiphyses (distal and proximal) were infrequently preserved. Maximum diaphyseal lengths were converted to maximum lengths for individuals aged greater than 12 years using ratio conversions reported by Ruff (2007). Limb proportions in the adults from the Cis-Baikal region are similar to high-latitude, cold-adapted samples from the New World (Stock et al., 2010). Adult stature was, therefore, estimated using equations derived for skeletal samples from high latitude, cold environments (Auerbach and Ruff, 2010), and

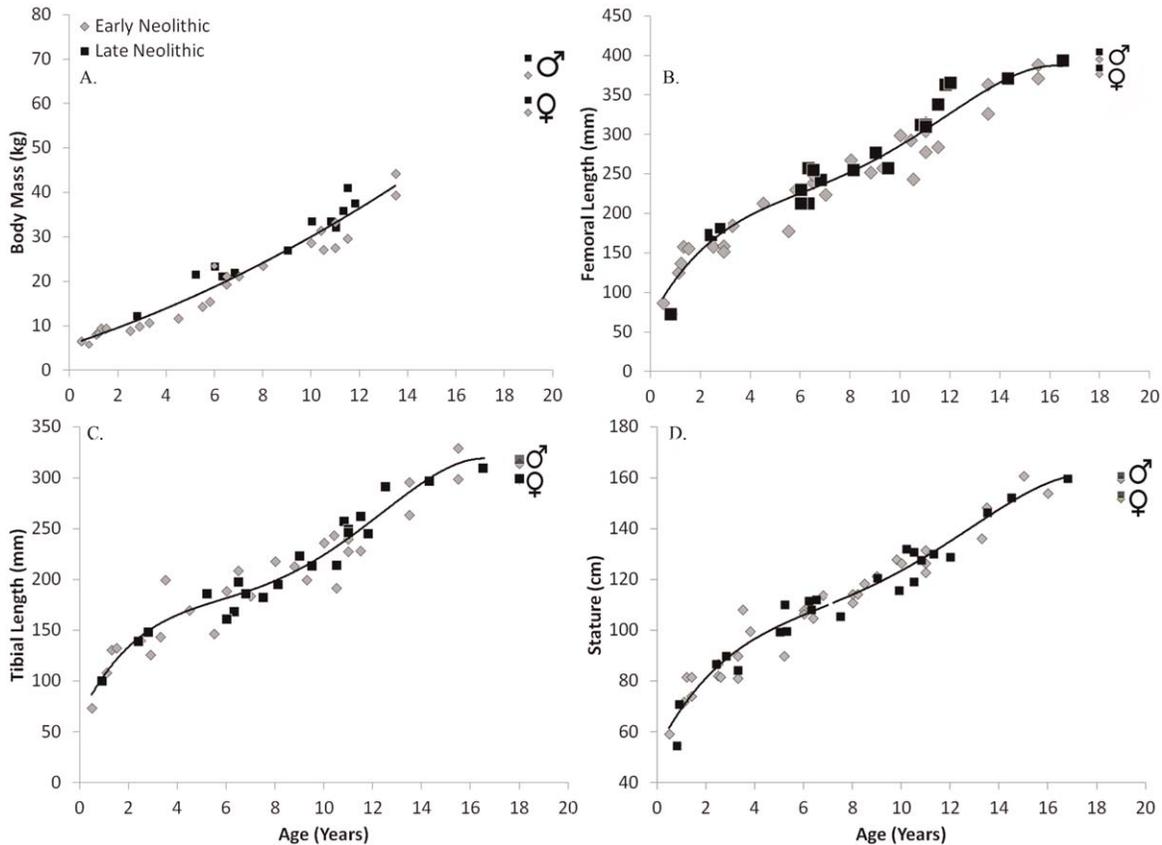


Fig. 2. Skeletal growth trends in (a) body mass, (b) femoral length, (c) tibial length, and (d) stature. Polynomial lines were fit to the data using forward selection. Average adult male and female values are indicated beyond the immature data points.

based on measurements of adult femoral bicondylar length (Stock et al., 2010). Average adult values for male and female stature are included beyond the immature sample in Figure 2.

Growth in body mass was estimated by first measuring the maximum intermetaphyseal breadth of the distal femoral metaphysis or superior–inferior width of the femoral head using standard protocols (Buikstra and Ubelaker, 1994; Ruff, 2007). Body mass was then estimated using a series of age-specific equations that perform well on skeletal growth samples of European and African American ancestry (Ruff, 2007; Sciulli and Blatt, 2008). This study utilized superior–inferior width of the femoral head as the primary indicator of body mass in individuals aged >6.9 years, while maximum intermetaphyseal width of the distal femur was used to estimate body mass in individuals <7.0 years. The maximum age used to compare body mass in this study was 13.5 years due to underlying problems with estimating body mass between 15.0 and 16.0 years (Ruff, 2007). Adult body mass was estimated using measurements of femoral head breadth (Stock et al., 2010). Average adult values for male and female body mass are included beyond the immature data points in Figure 2.

Growth in cortical bone thickness was analyzed by comparing cortical, total bone, and medullary width relative to age between the two foraging samples. Anterior–posterior radiographs of each femur were captured using the above mentioned equipment (NOMAD Pro X-ray device and Dr. Suni digital light sensor). Total bone (T)

and medullary (M) width were measured in accordance with previously established standards (Ives and Brickley, 2004). Cortical thickness was calculated as $T - M$. Measurements were collected using the Professor Suni radiographic software package (Suni Medical Imaging Inc., San Jose, California). T and M were measured at 45% of maximum diaphyseal length (from the distal end) due to the unequal contribution of femoral epiphyses to diaphyseal length (Ruff, 2003). Measurements of adult cortical thickness were not available for either sample, and thus, were omitted from the study.

Line fitting methods that describe the relationship between growth and age were estimated using forward selection. Forward selection fits regression lines of successively higher order terms to find a line that best describes the relationship between two variables (Zar, 2010, p 461–463). The method utilizes a t test to evaluate whether or not the new terms are more successful than the previous terms at describing this relationship. Expressions are added to the equation until the t value is insignificant indicating that the previous choice is best fit to the data. There are multiple precedents in skeletal growth studies for this approach, along with the caveat that these lines do not reflect true growth curves, and are instead used as a tool to evaluate trends in stunting/wasting in comparative perspective (Pinhasi et al., 2005, 2006; Mays et al., 2009). Here, forward selection was used to fit lines to the relevant growth parameter relative to dental age for the pooled Early Neolithic Kitoi and Late Neolithic Isakovo samples.

TABLE 2. Results of the forward selection analysis listing the appropriate model and accompanying equation for each growth parameter

Variable	Model Fit	Equation
Femoral length (mm)	Quartic	$y = -0.0154x^4 + 0.5412x^3 - 6.4006x^2 + 45.513x + 85.031$
Stature (cm)	Quartic	$y = -0.006x^4 + 0.2339x^3 - 3.0675x^2 + 20.483x + 51.286$
Tibial length (mm)	Quartic	$y = -0.0171x^4 + 0.6241x^3 - 7.374x^2 + 43.391x + 74.027$
Medullary width (mm)	Quadratic	$y = -0.0312x^2 + 0.9477x + 5.007$
Body mass (kg)	Quadratic	$y = -0.0351x^2 + 1.6885x + 7.783$
Total bone width (mm)	Quadratic	$y = -0.0328x^2 + 1.6984x + 7.4875$
Cortical width (mm)	Linear	$y = -0.0351x^2 + 1.6885x + 7.783$

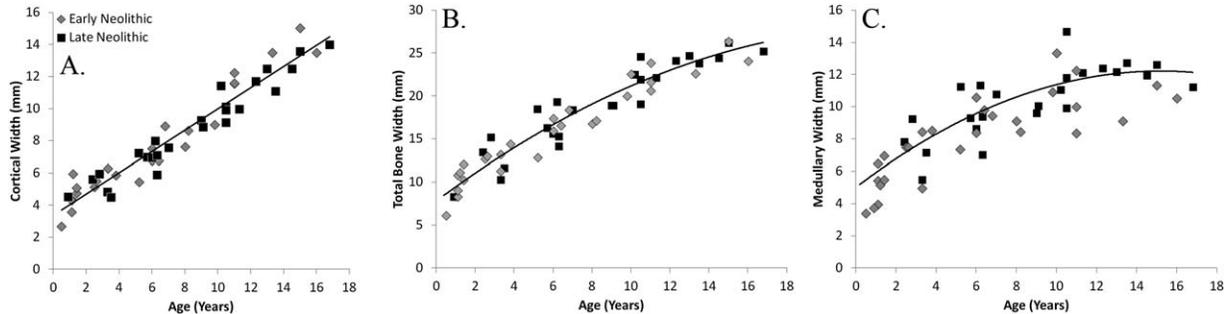


Fig. 3. Skeletal growth trends in (a) cortical thickness, (b) total bone thickness, (c) medullary width. Polynomial lines were fit to the data using forward selection.

Residuals were calculated around the lines fit to the pooled samples, and standardized residuals were calculated by dividing the residuals for each individual by the pooled standard deviation of each growth parameter. Normality in the distribution of standardized residuals was assessed using a Shapiro–Wilk test and homogeneity of variances was evaluated using a folded F -statistic. The choice of statistical test to evaluate differences in the standardized residuals between groups was based on the results of the Shapiro–Wilk and folded F tests. All calculations were performed on SAS 9.1, while all figures were produced using Microsoft Excel 2007 or PASW 19.

The second hypothesis addresses the issue of environmental versus genetic contributions to skeletal growth in the Cis-Baikal samples. Here, it is necessary to estimate the ages at which differences in growth trajectories occur. The age-specific sample sizes used by this study remain too small to carry out statistically meaningful tests between narrow age-groups, but differences in growth can be estimated through careful evaluation of standardized residuals, where significant differences between overall standardized residuals (see above) are found. A similar approach was employed by Ruff et al. (2013) in attempting to reveal the developmental stages where growth differences appeared between Arikara, Çatalhöyük, and Denver samples.

RESULTS

Table 2 presents the results of the forward selection analysis and includes the accompanying equation for each growth parameter. Scatterplots from these analyses are shown in Figures 2 and 3. Results of the Shapiro–Wilk test found that the alpha-levels for the standardized residuals of each growth parameter were >0.05 in each sample indicating a normal distribution. $Q-Q$ plots of these data were visually evaluated, and all data points fell within the 90% confidence intervals of the

lines describing the relationships between observed and expected values for the standardized residuals. Variance homogeneity was also found for each comparison. Standardized residuals for each growth parameter were, therefore, compared between the Early Neolithic Kitoi and Late Neolithic Isakovo using a pooled t -test.

Box plots of the standardized residuals for the growth parameters compared between the two samples are shown in Figures 4 and 5. Significantly greater standardized residuals of body mass ($t = 4.11$, $P < 0.0003$) and femoral length ($t = 2.50$, $P < 0.0198$) were found in the Late Neolithic Isakovo compared to Early Neolithic Kitoi samples (Fig. 4). These differences appear between late infancy and early adolescence (Fig. 2a,b). Differences in cortical thickness ($t = 1.59$, $P < 0.1173$) and medullary width ($t = 1.80$, $P < 0.0786$) were marginally insignificant between the two samples. The Early Neolithic Kitoi had slightly larger cortical thickness and smaller medullary width than the Late Neolithic Isakovo sample (Fig. 5). No significant differences were observed between the two samples for the standardized residuals of total bone width ($t = 0.38$, $P < 0.7027$), tibial length ($t = 0.51$, $P < 0.6171$), or stature ($t = 0.63$, $P < 0.4613$) (Figs. 4 and 5).

DISCUSSION

The first hypothesis of this study predicted that skeletal evidence for stunting and wasting would be observed in the Early Neolithic Kitoi compared to Late Neolithic Isakovo sample and that these differences would be concentrated between infancy and childhood. This hypothesis is mostly supported when skeletal growth parameters associated with body size are compared. The Early Neolithic Kitoi had significantly lower standardized residuals of body mass compared to the Late Neolithic Isakovo sample. Experimental studies point towards relationships between caloric restriction, body mass, and cortical thickness (Hamrick et al., 2009). Body mass is, however, also

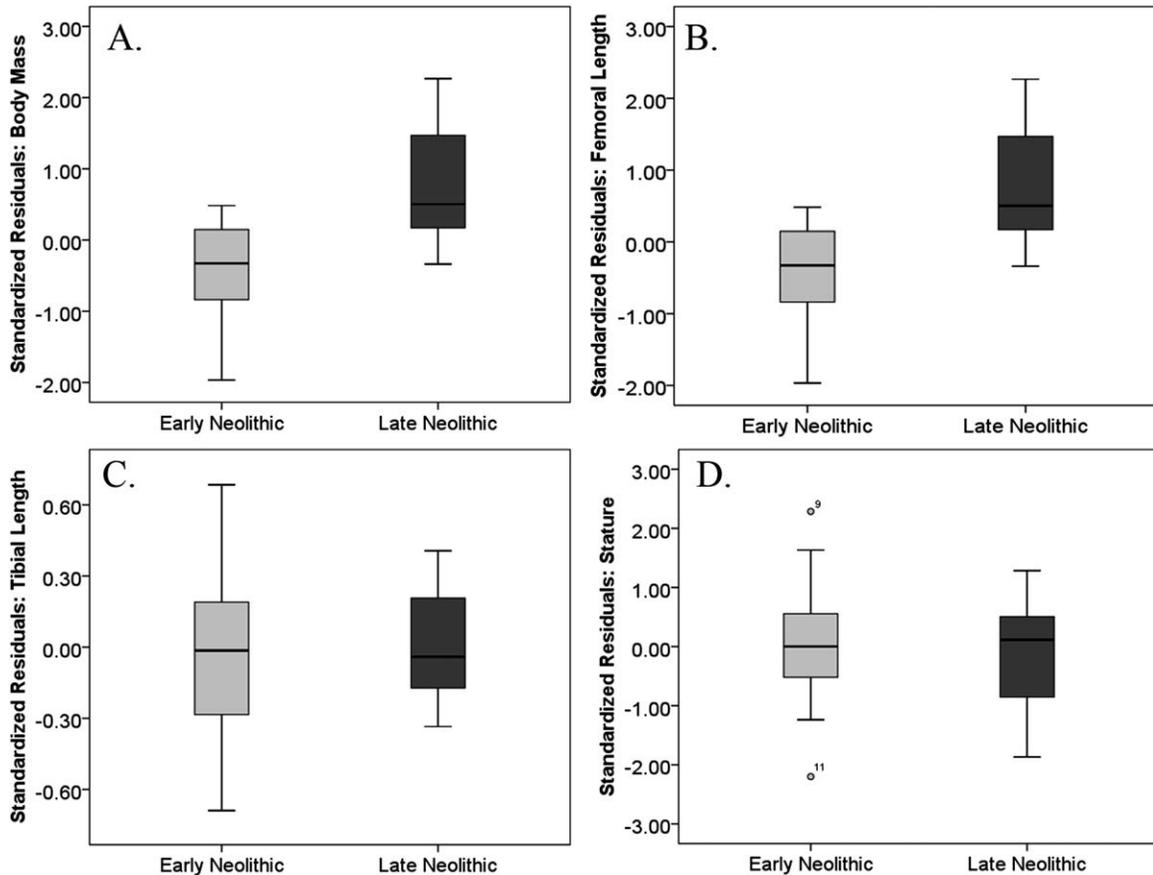


Fig. 4. Standardized residuals of skeletal growth for the Early Neolithic Kitoi and Late Neolithic Isakovo samples: (a) body mass, (b) femoral length, (c) tibial length, and (d) stature.

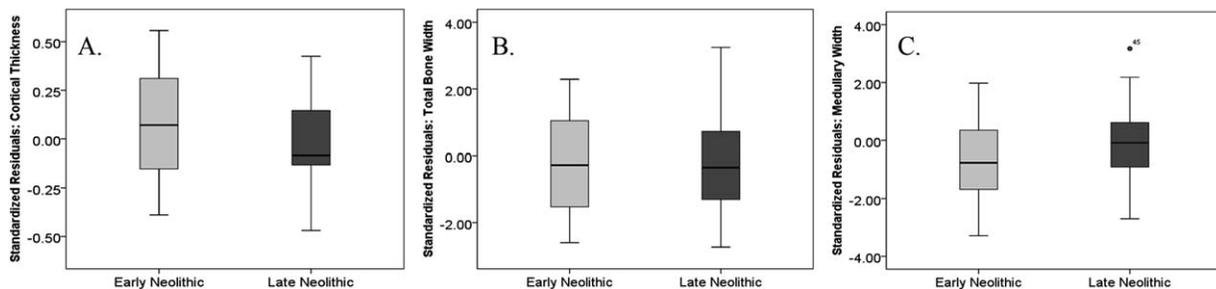


Fig. 5. Standardized residuals of skeletal growth for the Early Neolithic Kitoi and Late Neolithic Isakovo samples: (a) cortical thickness, (b) total bone thickness, and (c) medullary width.

correlated with lean muscle mass and fat mass, both of which reduce when caloric restrictions are applied (Hamrick et al., 2009). Data derived from living humans suggest no significant differences between energetically limited and Western samples in fat-free mass, but significantly greater adiposity in Western compared to energetically limited populations (Campbell et al., 2005; Sherry and Marlowe, 2007; Hruschka et al., 2013). It is not possible to test for variation in adiposity between these two samples, but it is important to note that this difference accounts for variation in body mass between populations where the physiological cost of maintenance varies.

Significant differences in femoral length, but not tibial length and stature were also detected. The residuals for femoral length relative to dental age were significantly larger in the Late Neolithic Isakovo compared to Early Neolithic Kitoi. Previous studies point out that growth in long bone length and stature is sensitive to systemic stress (Mensforth, 1985; Lovejoy et al., 1990; Okazaki, 2004; Pinhasi et al., 2005; Schillaci et al., 2011; Ruff et al., 2013, and others), though the relative sensitivity of each skeletal element remains an open question. The findings of this study may be associated with the timing of variation in the rate of growth between distal and

proximal limb segments. Following birth, the rate of growth is greatest in distal compared to proximal limb segments (Moss et al., 1955). This trend shifts at approximately 3.0 years, when the rates of growth in proximal limb segments overtake the distal elements (Smith and Buschang, 2004). In early adolescence, the rate of growth in distal segments then increases relative to that observed in the proximal segments for a narrow window of time (Smith and Buschang, 2005). Similar trends are reported by studies that track the ontogeny of intralimb indices (Davenport, 1933; Ruff et al., 1993; Ruff et al., 2002; Temple et al., 2011). Because femoral growth stunting in the Early Neolithic Kitoi sample appears between late infancy and early adolescence, it is possible that the distal elements were less affected by this process, and that cumulative stature also remained unaffected.

Differences in body mass and femoral length between the Early Neolithic Kitoi and Late Neolithic Isakovo begin during late infancy and persist through early adolescence. This result suggests that variation in adult body mass and femoral length between the two samples is associated with growth stunting and wasting due to environmental factors and is consistent with the second hypothesis of this study. Growth stunting during this period may be due to the nutritional consequences of weaning (Pinhasi et al., 2005). Weaning is the process where breast milk is gradually removed from infant diets beginning with the introduction of complementary foods and terminating with the cessation of breast feeding (Sellen, 2007). Nutritional consequences of weaning include elevated risk of exposure to resource shortages or reliance on complementary foods of low nutritional quality as the infant no longer relies on breast milk as a primary source of nutrition (Rousham and Humphrey, 2002). In addition, the infant no longer receives passive immunity from breast milk, which increases the risk of respiratory and diarrheal diseases (McDade, 2003). All of these environmental hazards are associated with growth stunting in cross-sectional studies of living humans: these conditions increase energetic investments in maintenance and decrease investments in growth during the transition to complementary foods and period of breast feeding cessation (Becker et al., 1991; Leonard et al., 1995; Adair and Guilkey, 1997; Arpadi et al., 2009). It is, however, important that interpretations tying weaning stressors to growth stunting or wasting in bioarchaeological context are supported by stable isotope evidence for infant feeding behavior (Humphrey, 2008).

Isotopic studies have explored the introduction of complementary foods and age-at-breast-feeding cessation in the Early Neolithic Kitoi compared to Late Neolithic Isakovo of Cis-Baikal (Waters-Rist et al., 2011). Early Neolithic Kitoi populations reduced breast-milk consumption at approximately 2.0 years of age and ceased breast milk consumption between 3.5 and 4.0 years, while the Late Neolithic Isakovo reduced breast milk consumption around 1.0 years and ceased breast milk consumption earlier than 3.0 years. Differences in femoral length and body mass in the current study appear at or around the time of breast feeding cessation.

This suggests that environmental perturbations associated with the cessation of breast feeding may have acted as a catalyst for growth differences between the Early Neolithic Kitoi and Late Neolithic Isakovo samples.

Growth stunting in later childhood and early adolescence often reflects nutritional intake due to diminished

resource availability or dietary quality (Leonard, 1989; Cameron et al., 1998; Berti et al., 2000; Foster et al., 2005). Foragers with narrow dietary spectrums from highly seasonal environments experience greater stress episode durations than those with wider dietary spectrums from less seasonal environments (Guatelli-Steinberg et al., 2004; Temple et al., 2013). Among indigenous, fishing-intensive populations at high latitudes, winter foods are amassed from summer migrations of fish, which vary in intensity and scale, and the availability of these resources is subject to fluctuation based on environmental productivity (Donald and Mitchell, 1975; Shnirelman, 1994).

In the Cis-Baikal region, the Early Neolithic Kitoi were intensively focused on freshwater fish and lived in a cold, dry environment that was highly seasonal in nature (White and Bush, 2010; Katzenberg et al., 2010). In contrast, the Late Neolithic Isakovo had a wider dietary breadth, focusing on freshwater fish, seal, and terrestrial mammals, while living in a less seasonal environment (Weber et al., 1993, 1998; White and Bush, 2010; Katzenberg et al., 2010). There is also evidence suggesting that the Early compared to Late Neolithic environment was less productive due to differences in precipitation and nutritional input into freshwater reserves (White and Bush, 2010). This variation diet and climate is associated with a greater frequency of individuals with linear enamel hypoplasia in the Early Neolithic Kitoi compared to Late Neolithic Isakovo (Lieverse et al., 2007; Lieverse, 2010). Evidence for either emergency breast feeding or nitrogen catabolism in infants/children may also correspond to periods of resource scarcity among the Early Neolithic Kitoi sample (Waters-Rist et al., 2011). This study reports evidence for growth faltering among the Early Neolithic Kitoi compared to Late Neolithic Isakovo, and these trends may also be associated with dietary breadth and resource availability. This interpretation does not seek to diminish the role of infectious disease in producing growth faltering during these years of development (Allen, 1994). However, the available archaeological evidence in the Cis-Baikal region points towards variation in resource availability and dietary breadth as being a primary mover of the growth differences documented by this study.

This study also predicted wasting in cortical bone growth among the Early Neolithic Kitoi compared to Late Neolithic Isakovo due to purportedly varying levels of systemic stress between the two samples and the influence of systemic stress on cortical bone growth. Differences in cortical thickness and medullary width were marginally insignificant, while no differences in total bone width were found. The Early Neolithic Kitoi had slightly greater standardized residuals for cortical thickness and slightly smaller standardized residuals for medullary thickness than the Late Neolithic Kitoi. This portion of the first hypothesis is, therefore, rejected. Previous studies suggest that similarity in periosteal expansion and differences in medullary resorption are tied to nutritional environments (Hummert, 1983; Van Gerven et al., 1985; Mays et al., 2009; Cowgill, 2010). However, endosteal resorption is also inhibited by diaphyseal strain in the preadolescent phase of development, while endosteal deposition is associated with diaphyseal strain during adolescence (Jones et al., 1977; Ruff et al., 1994; Lieberman and Pearson, 2001; Bass et al., 2002). Estrogen inhibits the differentiation of osteoblasts in the periosteal membrane, which increases endosteal deposition

and reduces periosteal expansion in response to strain during this period of development (Ruff et al., 1994; Ogita et al., 2008; Devlin, 2011). Overall then, a variety of environmental and systemic factors act to promote and/or inhibit endosteal bone deposition at different phases of development, and the study of cortical bone growth in mechanically active bones such as the femur may be complicated by these factors (Agarwal, 2008; Agarwal and Beauchesne, 2011).

Among the samples from Cis-Baikal, the majority of Early Neolithic Kitoi individuals have larger residuals for cortical thickness and smaller residuals for medullary width than the Late Neolithic Isakovo after 10 years of age (Fig. 3a,c). The sample of individuals in this age group is small, but these findings indicate that the unexpectedly thicker cortical bone and thinner medullary cavities among the Early Neolithic Kitoi compared to Late Neolithic Isakovo may have been prompted by the combined influence of mechanical activity and systemic factors. Overall, these findings suggest that elevated diaphyseal strain during this window of development may have counteracted the influence of systemic stress on cortical bone growth in the Early Neolithic Kitoi. Indirect support for this interpretation is found in studies of external bone dimensions among the adults from these samples. Significantly greater femoral midshaft diameter and anterior–posterior relative to medio-lateral diameter ratios are reported in the Early Neolithic Kitoi compared to Late Neolithic Isakovo (Stock et al., 2010). Though periosteal expansion is mostly associated with pre-adolescent diaphyseal strain (Jones et al., 1977; Ruff et al., 1994; Lieberman and Pearson, 2001; Bass et al., 2002), the results are consistent with a greater level of strain/mobility in the Early Neolithic Kitoi.

CONCLUSIONS

Significantly smaller standardized residuals for femoral length and body mass were found in the Early Neolithic Kitoi compared to Late Neolithic Isakovo. Stunting in femoral length and wasting body mass begins around the time of breast feeding cessation in both samples and continues through early adolescence. Stunting in femoral length and wasting in body mass may, therefore, reflect variation in the environmental risks associated with the cessation of breast feeding between the two groups. Differences in childhood and early adolescent growth between the two samples may be associated with dietary breadth and resource availability. No differences in the standardized residuals of stature or tibial length were found between the Early Neolithic Kitoi and Late Neolithic Isakovo. This is likely associated with differences in ages for growth acceleration in distal/proximal limb segments, and the fact that the disruption of femoral growth did not impact overall height.

Differences in the standardized residuals of cortical thickness and medullary width were marginally insignificant between the Early Neolithic Kitoi and Late Neolithic Isakovo, while no differences in total bone width were found. The Early Neolithic Kitoi had slightly greater cortical thickness and smaller medullary cavities than the Late Neolithic Isakovo. This trend appears after 10 years of age, and may be associated with a greater level of activity in the Early Neolithic Kitoi compared to Late Neolithic Isakovo during adolescence. If true, these results indicate that mechanical environment

and systemic factors may mask the influence of the physiological cost of maintenance on cortical bone growth.

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