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Chronological and regional variation in developmental stress and behavior of Early and Late Neolithic Cis-Baikal hunter-gatherer juveniles: Insights from diaphyseal cross-sectional geometry



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ABSTRACT

This study explores growth (increase in size) and development (change in structure and function) in Middle Holocene Cis-Baikal hunter-gatherer populations to evaluate chronological and regional variation in developmental health and juvenile behavior using post-cranial Cross-Sectional Geometry (CSG). It also evaluates whether sexual differences in size and habitual behavior were evident by the end of adolescence. Age and body size standardized femur, tibia, and humerus midshaft CSG are used to test for differences between Early Neolithic (EN) and Late Neolithic (LN) juveniles from different micro-regions. Regression of these measures on radiocarbon date tests for differences within archaeological periods.

EN individuals younger than 16 years, particularly those from the Angara River Valley, exhibit lower measures of cross-sectional size/ rigidity than LN juveniles. EN individuals older than 6 years, especially those from the Southwest Baikal had less circular lower limbs and higher humerus percent cortical area than LN individuals. Age standardized cross sectional size/ rigidity decline throughout both the EN and the LN, suggesting decrease in body size during both archaeological periods, whereas changes in femur shape are consistent with increases in juvenile mobility throughout the EN. By the end of adolescence, sexual dimorphism is emerging but not fully established in lower and upper limb robusticity and shape.

The lower cross-sectional area and bending rigidity support higher levels of developmental stress in the EN compared to the LN period, whereas less circular lower limb indices suggest higher terrestrial mobility in the EN. These differences may reflect a higher risk of resource scarcity in the EN, which resulted in higher mobility and greater involvement of juveniles in harvesting aquatic resources. Declines in body size within both archaeological periods emphasize the cyclical nature of developmental stress, perhaps due to declines in resource abundance. The presence of incipient sexual dimorphism by the end of adolescence is consistent with individuals beginning to assume adult roles.

1. Introduction

1.1. Environmental and archaeological background

This paper examines growth and development of postcranial robusticity in Middle Holocene Cis-Baikal hunter-gatherer juveniles to characterize chronological and regional variation in developmental stress levels, the economic roles of children, and social organization in these populations. Growth specifically refers to increases in body size

and development refers to changes in function during growth.

Lake Baikal is located in southeast Siberia, and the term Cis-Baikal refers to the area immediately North and West of the lake (Fig. 1). The populations examined here come specifically from the western portion of the Cis-Baikal, which has been traditionally divided into two micro-regions: the Angara River Valley (Angara) and Southwest Baikal (SW Baikal) (Weber and Bettinger, 2010). The environment consisted predominantly of boreal forest interspersed with patches of more open steppe. Fish were abundant in Cis-Baikal though geographically

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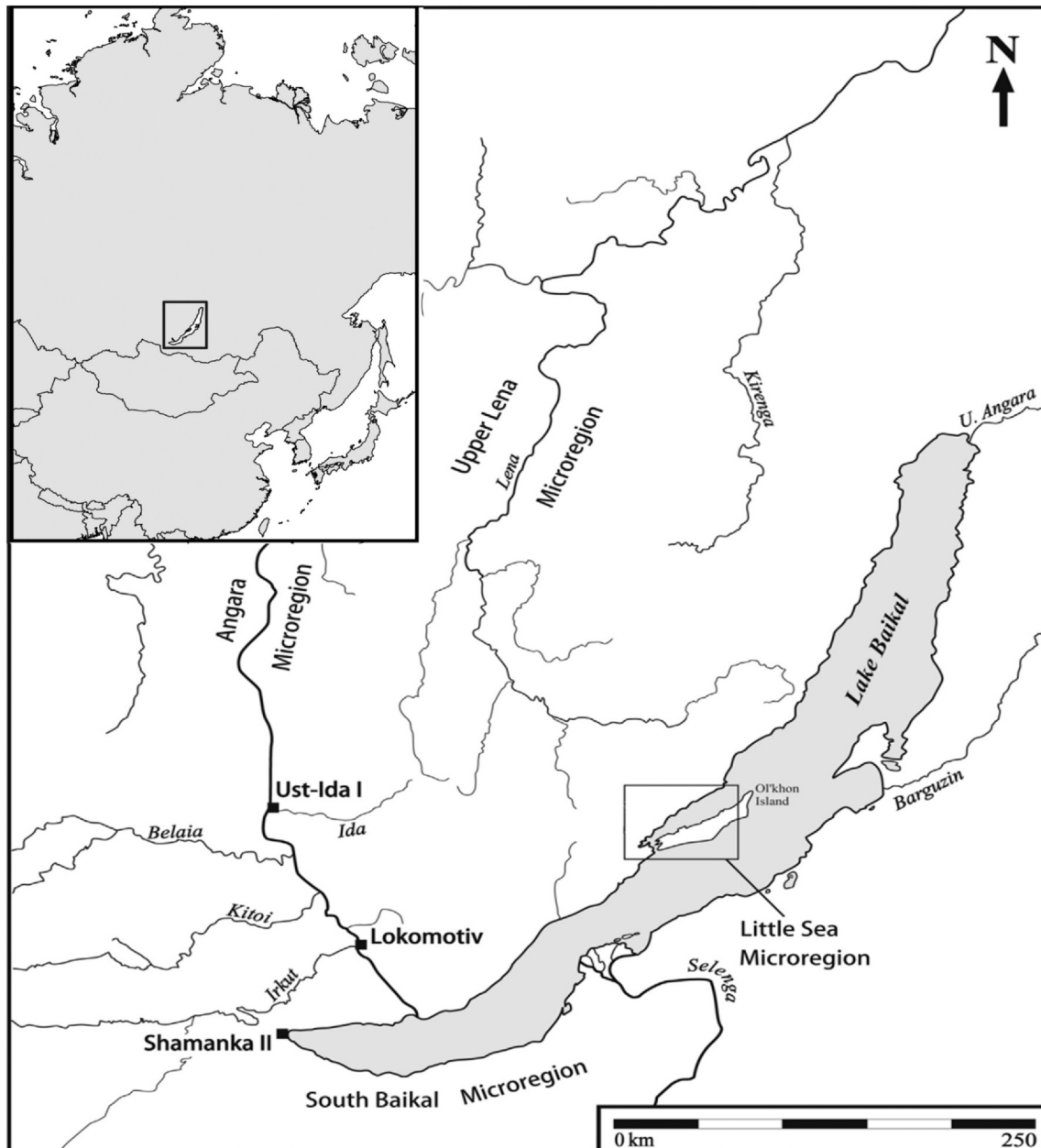


Fig. 1. Map of the Cis-Baikal Region in Asian Context with Micro-regions and Cemeteries used in the Analysis marked.

Table 1
Chronology of Cis-Baikal archaeological periods corrected for the freshwater reservoir effect (Weber et al., 2016a).

Archaeological Period	Years (mean HPD cal BP)	Mortuary Tradition
Late Mesolithic (LM)	8277 +/- 176 to 7503 +/- 14	Khin'
Early Neolithic (EN)	7503 +/- 14 to 7027 +/- 33	Kitoi
Middle Neolithic (MN)	7027 +/- 33 to 5571 +/- 88	None
Late Neolithic (LN)	5571 +/- 88 to 4597 +/- 76	Isakovo/ Serovo
Early Bronze Age (EBA)	4597 +/- 76 to 3726 +/- 34	Glazkovo

variable, and this variability may be related to variation in human subsistence behavior (Losey et al., 2012; Losey and Nomokonova, 2018.; Weber and Bettinger, 2010; Weber et al., 2002). Based on archaeological and modern data, Losey et al. (2012) postulate that lake-shore fisheries provided a stable source of resources year-round. However, as fish were accessible year-round, there was no need for

special labor organization to exploit this fishery. By contrast, the Angara River Valley may have supported some of the richest fisheries in Cis-Baikal. While fish would have been available year-round, seasonal movements would have provided temporally and regionally delimited opportunities for mass harvest, a situation that may have favored significant organization of labor and negotiation of access to productive fishing locations. Archaeological and ethnographic evidence suggests fishing gear included harpoons, nets, and fishing lines. Ungulates (red deer, roe deer, and elk/moose), the main terrestrial game, were hunted with spears and bows (Weber and Bettinger, 2010).

The Middle Holocene period has been divided into several archaeological periods, primarily based on differences in mortuary traditions (Weber and Bettinger, 2010; Weber et al., 2016a). A list of archaeological periods in years calBP is provided in Table 1. A discontinuity in burials during the Middle Neolithic (MN) separates Early Neolithic (EN) populations (7503–7027 calBP) associated with the Kitoi mortuary tradition from the Late Neolithic (LN) Isakovo group (5571–4597 calBP) (Weber et al., 2016a). The Kitoi tradition is distinguished by

copious use of red ochre on bodies, frequent presence of composite fishhooks and bifacial arrowheads, and relatively greater numbers of multiple burials. In the Angara River Valley and Southwest Baikal, the LN burials belong to the Isakovo mortuary tradition. Isakovo burials are oriented with the heads facing upstream (south), and the graves include surface structures. In addition, single burials and pottery are more common than at Kitoi cemeteries whereas fishing gear is relatively rare. For further details about mortuary cultures see [Weber et al. \(2016a and references therein\)](#). Substantial changes in mtDNA haplotypes indicate substantial inflow of new populations at least from the start of the LN, though cranial and dental non-metric traits provide strong evidence for a degree of biological continuity between Angara EN and LN populations ([Movsesian et al., 2014](#); [Waters-Rist et al., 2016](#)). The Early Bronze Age (EBA) was temporally contiguous with the LN, though burial ritual allows for the reliable distinction between EBA and LN graves ([Weber et al., 2016a](#)).

Past research has documented important chronological and geographic variation in behavior and developmental stress. Most studies of adults have pooled LN and EBA individuals due to temporal continuity between these periods, in order to increase sample size. However, due to poor preservation and small sample size, few EBA juveniles are available for analysis. Therefore, we compare only EN and LN juveniles, and this review of past work explicitly notes whether studies compared EN to LN or a pooled LN-EBA sample. Past comparisons of adults found that levels of linear enamel hypoplasia were higher in the EN than the LN-EBA, and EN individuals also had lower statures and body mass compared to LN-EBA adults, suggesting that EN populations experienced higher levels of developmental stress ([Lieverse et al., 2007](#); [Stock et al., 2010](#)). Consistent with this, study of longitudinal growth using juvenile remains demonstrated slower accrual of stature and body mass in EN than LN juveniles ([Temple et al., 2014](#)). Also, isotopic analysis of infant and juvenile remains suggests EN infants began weaning later and finished weaning over a shorter period than LN individuals ([Waters-Rist et al., 2011](#)). Waters-Rist et al. interpreted prolonged breastfeeding as potentially representing an attempt to buffer EN infants from resource scarcity, which is consistent with higher levels of developmental stress in this period.

Behavior also shows considerable chronological and temporal variability. On the basis of cemetery number and distribution, it has been proposed that EN groups were more densely concentrated than LN groups, particularly in the Angara micro-region ([Weber and Bettinger, 2010](#)). Furthermore, isotopic examination of diet indicates that fish constituted a greater proportion of the diet in the EN than the LN ([Weber et al., 2002](#); [Weber and Bettinger, 2010](#); [Weber et al., 2011, 2016a, 2016b](#)). Changes in adult bone rigidity, femoral shape, osteoarthritis, and muscle markers are consistent with higher workloads and terrestrial mobility in the EN than the LN-EBA ([Lieverse et al., 2013, 2016](#); [Stock and Macintosh, 2016](#); [Lieverse et al., 2011](#); [Stock et al., 2010](#)). Greater dependence on aquatic resources, higher loading, and higher terrestrial mobility during the EN may relate to depletion of local terrestrial game. This adaptive strategy may have also increased the frequency or severity of seasonal resource shortfalls, thereby increasing developmental stress ([Lieverse et al., 2007](#); [Waters-Rist et al., 2011](#)). Based on differences in lower limb shape and rigidity, male workloads and mobility appear to have been higher than that of females throughout the Middle Holocene, though sexual dimorphism may have increased in the LN ([Stock and Macintosh, 2016](#)).

While prior studies have predominantly focused on differences between archaeological periods, recent work has shown evidence of behavioral change within archaeological periods. Notably, correction of radiocarbon dates for the freshwater reservoir effect identified growing reliance on aquatic foods across the EN period in the Angara and some groups in the SW Baikal micro-region ([Weber et al., 2016a, 2016b](#)). While analysis of intra-period variation has only just begun, the results tentatively suggest that variation in stress and behavior might exist within archaeological periods, potentially due to diachronic change in

resource abundance and foraging strategies. Individuals from different micro-regions also exhibit distinct ranges of dietary stable isotope values, suggesting distinct foraging ranges ([Weber et al., 2016a, 2016b, 2011](#)). These may translate into differences in habitual behavior. For instance, EN Angara individuals exhibit greater joint degeneration and muscle marker formation than contemporaneous individuals from the Southwest Baikal ([Lieverse et al., 2013, 2016](#)). While the relationship between osteoarthritis and behavior is not straightforward, this is a potential indicator of higher workloads in the former group. Isotope values of individuals from the same cemetery also vary considerably, suggesting that groups using the same cemetery also had distinct foraging ranges.

Taken together, prior work suggests substantial chronological and geographic variability in health and adult behavior. Workloads, terrestrial mobility, physiological stress, and dependence on aquatic resources appear to have been higher in the EN than the LN. Within archaeological periods, geographic and chronological differences in resource distribution constitute additional axes for variability in behavior and physiological stress. A fine-grained exploration of developmental health throughout childhood would significantly expand knowledge of Middle Holocene life history. Also, the economic role of children has not been examined, and this could allow new insights into the foraging strategies of family units and group mobility. This study will therefore use Cross-Sectional Geometric properties (CSG) of limb bones to explore chronological and regional differences in developmental stress and juvenile behavior.

1.2. Skeletal biomechanics

Diaphyseal bone strength and rigidity refer to a bone's ability to resist failure or deformation under applied loads. This is quantified using diaphyseal CSG, the amount and distribution of cortical bone perpendicular to the diaphysis' long axis. While factors such as genetics and hormones also contribute to CSG, the amount and distribution of cortical bone predominantly reflect functional adaptation to the magnitude and orientation of strain engendered by habitual loading ([Pearson and Lieberman, 2004](#); [Ruff et al., 2006a](#)).

Bioarchaeological studies of adults have widely employed CSG to reconstruct behavior in past populations. These studies investigated a diverse range of topics including ecogeographic and chronological variation in hunter-gatherer behavior ([Holt, 2003](#); [Shackelford, 2007, 2014](#); [Sparacello et al., 2016](#); [Stock and Pfeiffer, 2004](#)), behavioral changes across subsistence transitions ([Bridges, 1989](#); [Macintosh et al., 2014a, 2014b, 2017](#); [Marchi et al., 2006](#); [May and Ruff, 2016](#); [Ogilvie and Hilton, 2011](#); [Sládek et al., 2016](#)), and the locomotion of past hominin species ([Ruff, 2009](#); [Shaw and Stock, 2013](#)). Lower limb shape and strength identify differences in levels of terrestrial mobility, because bipedal locomotion creates greater loads in the anteroposterior than the mediolateral plane ([Holt, 2003](#); [Lieverse et al., 2011](#); [Marchi et al., 2006](#); [Shaw and Stock, 2009, 2013](#); [Sparacello and Marchi, 2008](#); [Stock and Pfeiffer, 2004](#)). Variation in upper limb shape and strength has also been linked to the practice of different subsistence modes and the employment of different technology ([Cameron et al., 2018](#); [Macintosh et al., 2014a](#); [Shackelford, 2014](#); [Stock and Pfeiffer, 2004](#)).

Research on the growth and development of CSG constitutes a smaller but growing focus of investigation, which allows new insights into activity and health ([Cowgill, 2014, 2010](#), p. 20; [Cowgill and Hager, 2007](#); [Osipov et al., 2016](#); [Ruff et al., 2013](#)). Adult CSG primarily reflects functional adaptation during development, because the juvenile skeleton exhibits markedly greater mechanosensitivity ([Duncan and Turner, 1995](#); [Kish et al., 2015](#); [Lieberman et al., 2001](#); [Pearson and Lieberman, 2004](#); [Ruff et al., 2006a, 1994](#); [Steinberg and Trueta, 1981](#)). Thus, adult levels of diaphyseal CSG are primarily achieved during growth, and clinical studies demonstrate that differences in bone strength developed during childhood are maintained into adulthood ([Bass et al., 2002](#); [Bradney et al., 1998](#); [Burrows, 2007](#); [Kontulainen](#)

et al., 2002; Nordström et al., 1996).

Two sources of mechanical load drive functional adaptation during ontogeny: activity and body mass (Lieberman et al., 2001). From the perspective of activity, studying juvenile robusticity development provides insight into the ages at which behavioral patterns began to differ between populations. Also, a growing body of literature has emphasized the utility of CSG for reconstructing differences in body mass, particularly in juveniles (Cowgill, 2018, 2010; Osipov et al., 2016; Pomeroy et al., 2018; Ruff et al., 1991). Methods for estimating body mass from juvenile joint dimensions or stature have limited accuracy due to a lack of ontogenetic samples of known body mass. An additional advantage of CSG for body mass estimation is that growth in diaphyseal cross-sectional size and strength tracks body mass more closely than growth in joint dimensions or diaphyseal length (Cowgill, 2018, 2010; Ruff, 2007, 2003; Ruff et al., 1994). Indeed, comparisons of juvenile CSG values from different populations standardized by body mass estimates from joint dimensions still shows patterning reflective of differences in body size (Cowgill, 2010; Osipov et al., 2016). This strongly suggests that CSG properties are more sensitive to differences in body mass than other skeletal dimensions. Therefore, analysis of CSG can potentially provide new insights into levels of developmental stress as well as activity during growth.

1.3. Research questions

This study examines the following research questions to shed light on chronological and regional variation in juvenile behavior and health in Middle Holocene Cis-Baikal hunter-gatherer groups.

1. Were there differences between populations from different archaeological periods and micro- regions in the accrual of bone robusticity and changes in shape with age?
2. If differences exist, are they driven by differences in developmental stress levels or behavior?
3. Do sexual differences in bone robusticity characteristic of a sexual division of labor emerge by the end of adolescence?

2. Materials and methods

2.1. Sample description

In total, 105 Cis-Baikal individuals were included in this analysis. They ranged in age from perinates to young adults, individuals in which dental development was complete, but the skeleton still showed some sign of skeletal immaturity. Sample sizes for each cemetery are given in Table 2. Twenty- nine EN individuals come from the Angara River Valley Lokomotiv cemetery, 41 from the EN Southwest Baikal Shamanka II site, and 35 from LN Ust-Ida in the Angara River Valley. Two EBA individuals younger than 16.0 years of age were used for the purposes of generating regressions for dental age based on long bone length, and 4 EBA young adults were used to create an equation for predicting body mass from the femoral head (see below). However, these individuals were not compared to EN and LN individuals due to small sample size.

Table 2
Sample composition by archaeological period, microregion, and age cohort.

Micro-region/ Time Period	Indeterminate Sex Juveniles < 16.0 Years Old	Adolescent/ Young Adult Females	Adolescent/ Young Adult Males
Early Neolithic Angara River Valley	17	8	4
Late Neolithic Angara River Valley	30	1	4
Early Neolithic South Baikal	27	5	9
Total	74	14	17

2.2. Age cohorts and statistical comparisons between archaeological periods and micro-regions

The sample was divided into two cohorts:

Cohort 1: Individuals younger than c.a. 16 years of age of indeterminate sex.

Cohort 2: Adolescent/ Young Adults females and males older than 14 years of age.

The upper bound of c.a. 16 years was chosen for Cohort 1 for several reasons. First, endosteal contours are available in this age range. Diaphyses of individuals older than this did not fit on the x-ray sensor used for capturing internal dimensions, so CSG were calculated using only periosteal dimensions (see below). Second, sex could be consistently estimated for individuals older than this, which allows females and males to be analyzed separately. Inclusion of young adults is justified on the grounds that the heightened skeletal response to loading seen in juveniles persists after the end of longitudinal growth, gradually diminishing to levels characteristic of older adults throughout young adulthood (Ruff et al., 2006a). To be considered a young adult, individuals had to exhibit fused epiphyses indicative of completed longitudinal growth, a lack of degeneration on joint surfaces (e.g. pubic symphysis) and a lack of fusion in epiphyses that close between 20 and 25 years (e.g. medial clavicle, sacral segments). A lack of wear on the first molar was also considered diagnostic of young adulthood, because dental attrition rates in Cis-Baikal populations are extremely high, such that first molars will exhibit dentine exposure by the end of young adulthood (Lieverse et al., 2007b).

Two females and two males with skeletal age between 14 and 16 years old were also included in the second cohort to increase sample size for sex-difference analysis. This grouping further ensures that we capture sexual differences over the entirety of the period during which this can be tracked. Removing these individuals did not change the results.

In Cohort 1, EN and LN individuals of indeterminate sex were compared to each other. EN individuals from different micro-regions were also compared to each other and to the LN Angara group. While previous studies have sometimes employed statistical testing in sub-cohorts with narrower age-ranges to assess when significant differences emerge, this reduces sample size, and uneven age distributions between groups can produce statistical artifacts (Cowgill, 2010; Osipov et al., 2016). Following Cowgill (2014), statistical comparisons were carried out for the entire cohort. We then employed a scatterplot of values against age to assess the age at which significant differences emerged. The second cohort of adolescents and young adults was divided into four subgroups for comparisons: EN Females, EN Males, LN Females, and LN Males. All statistical comparisons were made using Mann-Whitney's *U* test. As small sample sizes reduce statistical power, we set an alpha level of $p < 0.1$ for statistical significance, and exact *p*-values are reported for each comparison. Statistical analysis was carried out using the R Statistical Package (R Core Team, 2019).

2.3. Age estimation

When possible, age was estimated from dental development using the Queen Mary University of London Atlas (AlQahtani et al., 2010). For teeth embedded in the mandible and maxilla, crown and root

Table 3

Equations for age estimation from diaphyseal lengths and femoral metaphyseal/ epiphyseal dimensions from other variables.

Predicted Measure	Measurement	N	R ²	SEE	Equation
Dental Age from Diaphyseal Length	Early Neolithic				
	Tibia Diaphysis	23	0.95	1.19	Dental Age = 0.074(x)-7.109
	Femur Diaphysis	24	0.96	1.00	Dental age = 0.060(x)-6.927
	Ulna Diaphysis	19	0.95	1.28	Dental Age = 0.106(x)-8.046
	Humerus Diaphysis	23	0.95	1.26	Dental Age = 0.091(x)-8.392
	Clavicle Diaphysis	20	0.94	1.34	Dental Age = 0.197(x)-9.787
	Late Neolithic/ Early Bronze Age				
	Tibia Diaphysis	22	0.94	0.92	Dental Age = 0.070(x)-6.841
	Femur Diaphysis	21	0.89	1.46	Dental Age = 0.061(x)-7.878
	Ulna Diaphysis	8	0.94	1.11	Dental Age = 0.124(x)-11.381
Body Mass in 14.5–16.5 year old cohort	Humerus Diaphysis	21	0.93	1.19	Dental Age = 0.092(x)-9.565
	Clavicle Diaphysis	21	0.89	1.43	Dental Age = 0.219(x)-12.027
	Femur Head	23	0.927	1.997	Body Mass = 2.236(x)-39.921
	Femur Distal Breadth	29	0.918	2.94	Femur Distal Metaphysis ML Breadth = 1.062(x) + 4.222

development were assessed using dental radiographs collected 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, California). In total 75 individuals had dentition for which maturation could be assessed.

For individuals lacking observable dentition, Ordinary Least Squares (OLS) regression of diaphyseal length on dental age was used to create equations for age-estimation. As a previous study showed differences in bone length for age in EN and LN individuals, separate regression equations were created for each time period (Temple et al., 2014). These equations are given in Table 3. For the youngest individuals, regression equations produced negative age estimates, because these individuals fell below the size range of individuals with preserved dentition. In these cases, skeletal fusion was used to assign the individuals to the nearest half year interval (0.5, 1.0, 1.5 years of age). Young adults were identified as described above in Section 2.2.

2.4. Sex estimation

Prior to puberty, no method of sex estimation performs reliably. Beginning in adolescence, increases in sex hormone concentrations lead to more marked sexual differences in skeletal morphology (Humphrey, 1998). Six individuals older than 14.0 years had been molecularly sexed using DNA analysis in prior studies. For the remainder of the adolescent/ young adult sample, Dr. A. Lieverse provided sex estimations based on pelvic and cranial morphology (Lieverse, personal comm.).

2.5. Osteometrics and cross-sectional geometry

The femur distal metaphysis and proximal epiphysis were measured with digital calipers. Diaphyseal lengths were taken using an osteometric board. The best-preserved femur and tibia for each individual were selected for modeling CSG. Given bilateral asymmetry due to handedness, left and right humeri were analyzed separately and also averaged to increase sample size. If only one side was available, this was used in place of the average value.

CSG was evaluated at midshaft (50% fused length) of the femur, tibia, and humerus. In the femur, this corresponds to 45.5% of diaphyseal length from the distal end, because the distal epiphysis contributes more to fused length than the proximal one (Ruff, 2003). For individuals younger than 16 years of age, models of cross-sections CSG were created using a method similar to the “latex cast method,” which utilizes a periosteal contour and biplanar radiographs to approximate the endosteal contour (O'Neill and Ruff, 2004). The majority of periosteal contours were acquired using a Konica-Minolta Virtuoso 3D scanner. Due to time constraints, periosteal contours for several additional individuals were acquired using silicone Cuttersill molding putty. Physical molds were digitized on a desktop scanner, and periosteal

contours were extracted from 3D scans in Geomagic Design X. Biplanar radiographs were collected using the same radiographic equipment used for dental x-rays. Anterior, posterior, medial, and lateral, cortical thickness were then measured and plotted in the digitized periosteal contour in Image J, approximating the endosteal contour as an ellipse. CSG were calculated from digitized models using the MomentMacroJ v1.4. plugin for ImageJ (Ruff 2006). Periosteal contours were not available for several individuals, because the bones were too poorly preserved to place physical molding material and discoloration prevented accurate laser scanning. In these cases, CSG was calculated from biplanar radiographs alone using the ellipse model method equations (O'Neill and Ruff, 2004).

Biplanar radiographs were not available for individuals older than 16.0 years due to size limitations of the radiographic sensor. CSG for individuals older than 16.0 years were calculated directly from periosteal contours (Davies et al., 2012). The technique shows high correlations and small mean errors compared to CSG calculated using methods that incorporate both periosteal and endosteal contours (Macintosh et al., 2013).

CSG analysis calculated areal measurements and Second Moments of Area (SMAs). Total Area (TA) measures the entire subperiosteal area, and Cortical Area (CA) measures the amount of cortical bone. While both area measures have been employed as measures of resistance to compression, TA also shows strong correlations with J, the measure of overall diaphyseal rigidity, because average bending strength correlates strongly with the distance between the section centroid to the most distant fiber (Pearson and Lieberman, 2004; Ruff, 2008; Sparacello and Pearson, 2010). Percent cortical area (%CA) reflects the percentage of cross-section occupied by cortical bone, and it is calculated as: %CA = (CA/TA)*100. While this measure does not directly measure bone strength, it can help to identify differences in the relative rates of periosteal deposition and endosteal resorption. Lower %CA has been associated with higher physiological stress, due to increased endosteal resorption (May and Ruff, 2016). Conversely, higher %CA has also been associated with higher activity levels (Ruff et al., 1994). This is predominantly due to higher periosteal bone deposition, so one would also expect to see higher levels of CA. However, higher activity may also decrease endosteal resorption (Pearson and Lieberman, 2004). As a ratio, %CA is size-free, and it is thus capable of reflecting differences in stress independently of measures related to body size such as TA, CA, and bending moments.

SMAs quantify resistance to bending or rigidity about any plane (I). Conventionally, anteroposterior (I_x), mediolateral (I_y), maximum (I_{max}), and minimum (I_{min}) bending rigidity are calculated. The Second Polar Moment of Area (J) is proportional to twice the average bending rigidity about any two planes, making it a suitable proxy for overall bone rigidity (Ruff, 2008a, 2008b). This was calculated as the sum of I_{max} and I_{min} or I_x and I_y if the ellipse model method was used. The SMA

ratios I_x/I_y and I_{max}/I_{min} serve as a measure of cross-sectional shape, because they capture relative reinforcement of the diaphysis about perpendicular planes.

2.6. Body mass estimation

2.6.1. Individuals less than 17.5 years old

Following prior studies, body mass was estimated using equations for the juvenile distal femoral metaphysis and femur head epiphysis for individuals younger than 17.5 years (Ruff, 2007). Following prior studies, the distal metaphysis measurement was used for individuals 6.5 years of age or younger and the femoral head was used for individuals older than 6.5 years (Cowgill, 2010; Osipov et al., 2016; Temple et al., 2014). The Ruff (2007) equations could not be employed for 35 cases. Six individuals between the age of 14.5–16.5 years of age were in an age cohort that Ruff (2007) could not generate significant equations for. Modifying a technique employed in Harrington (2010) and developed with the assistance of C.B. Ruff (Person Comm, 2010), an OLS regression equation was created to predict body mass from proximal femur epiphysis diameter using individuals in the 13.5–14.5 year old cohort and individuals ranging in age from 17.5 to young adult. This technique has the advantage of using interpolation from the same sample to generate body mass estimates. To increase sample size, 4 EBA young adults were included in the regression equation. The equation and measures of accuracy reported for the reference sample are provided in Table 3. A further 4 individuals with an estimated age of less than 6.5 years did not have a preserved distal femoral metaphysis. For these individuals, this measurement was predicted using an OLS regression of distal femur metaphysis breadth on proximal tibia metaphysis breadth following (Cowgill, 2010).

2.6.2. Individuals older than 17.5 years

Body mass for older adolescents and young adults was estimated using the Ruff et al. (2012) standards for the adult femoral head. If the femoral head was not available, the Squyers and Ruff (2015) equations for the distal femur and proximal tibia epiphysis were used. One potential shortcoming of the body mass estimation approach used here is that Cohort 2 includes both adolescents older than 16 years, in which body mass is estimated using the Ruff (2007) juvenile equations, and young adults, for whom body mass is estimated using equations for adults. Furthermore, body mass for individuals between 14.5 and 16.5 years was interpolated from individuals in which body mass was calculated using either juvenile or adult body mass equations. However, Ruff (2007) notes that the difference in body mass calculations derived with juvenile and adult standards decreases throughout adolescence and is insignificant by 17 years. Thus, the use of different methods is unlikely to introduce a significant bias in older adolescents.

2.7. Standardization for age and body size

To discern differences in robusticity related to behavior requires controlling for differences in skeletal robusticity attributable to body size. Similarly, growth studies must account for size differences due to age. To allow comparisons between individuals throughout development, biomechanical properties were corrected for variation due to age or body size in the following ways. First, TA, CA, J, shape ratios, and %CA were regressed on age by fitting polynomial curves to the data for individuals younger than 16.0 years (see rationale for age cohort above). The curve of best fit was assessed using the Bayesian Information Criterion, because it penalizes the addition of extra terms, thereby reducing the risk of overfitting (Pomeroy et al., 2018). Second, CSG properties were standardized to control for body size. Following prior studies, the natural log of area measures (TA and CA) were regressed on the natural log of body mass and the natural log of SMAs on the natural log of body mass*bone length² (Cowgill, 2010; Osipov et al., 2016). For all curve-fitting procedures standardized residuals were

generated to assess either the relationship to age or body size. To standardize for body size in females and male adolescents and young adults, area measures were divided by body mass and SMAs by (body mass × bone length)² (Ruff, 2008b; Ruff, 2000). No regressions of variables against age were carried out for adolescents and young adults, because the age of young adults cannot be reliably estimated.

2.8. Analysis of intra-period variation in body size and diaphyseal robusticity/shape

Because equations that corrected radiocarbon dates for the Freshwater Reservoir Effect utilized $\delta^{15}\text{N}$ values, they could not be applied to individuals whose $\delta^{15}\text{N}$ was potentially affected by nursing (Weber et al., 2016a). Therefore, corrected radiocarbon dates were not available for children younger than 5 years. For the remainder of the sample younger than 16 years, age or body mass standardized residuals (generated as described above) were regressed on the mean calibrated corrected radiocarbon date for each individual using OLS. Separate regressions were carried out for the EN and LN periods. As this analysis was restricted to individuals between the ages of 5–16 years with a radiocarbon date, there is a reduction in sample size compared to previously described analyses of CSG. As a result, regressions for individual cemeteries may not produce reliable results. Therefore, regressions were only carried out for the pooled EN sample, but not cemetery specific samples. However, individuals from different cemeteries are marked in plots to demonstrate how they conform to whole period trends.

3. Results

3.1. Individuals < 16 years old

Plots of standardized residuals for TA, CA, and J generated by regressing CSG on age and body size estimates are respectively presented in Figs. 2 and 3 grouped by archaeological period and micro-region. Sample sizes and descriptive statistics are provided in Table 4, and results of statistical comparisons are given in Table 5. For both age and body size- standardized residuals of femur and tibia midshaft TA, CA, and J, there is substantial overlap between groups. However, LN Angara individuals exhibit a higher range than EN individuals, especially at the femur midshaft (Figs. 2, 3). EN-LN comparisons differ significantly for femur areas and J. As shown in Table 5, comparison of both age- and body size- standardized residuals by micro-region also detect some significant differences between the LN Angara group and both EN groups (Table 5). EN S Baikal and EN Angara groups only show a difference in age-standardized residuals for tibia midshaft J. Humerus TA, CA, and J do not differ significantly between archaeological periods or micro-regions.

Boxplots of standardized residuals for limb shape ratios regressed on age in Fig. 4 also illustrate considerable overlap between groups. However, for the lower limb, a substantial number of individuals in the LN Angara group fall in the lower end of the total sample distribution, suggesting that in general EN juveniles have less circular lower limbs. Furthermore, the EN SW Baikal produces the highest range of residuals. Comparisons by micro-region and archaeological period indicate significant differences between the combined EN-LN groups and the EN SW Baikal and LN Angara, but not between the EN Angara and LN Angara groups (Table 5). In contrast, there are no statistically significant differences in upper limb shape.

Plots of standardized residuals from regression of %CA are given in Fig. 5. There are no significant differences in femur or tibia midshaft %CA. Conversely, EN humerus %CA is significantly higher than the LN group (Table 5). When the EN sample is divided by microregion, this difference remains statistically significant for the EN SW Baikal- LN Angara comparisons, and for the EN Angara - LN Angara comparison of average values (Table 5). EN SW Baikal right humerus %CA is also

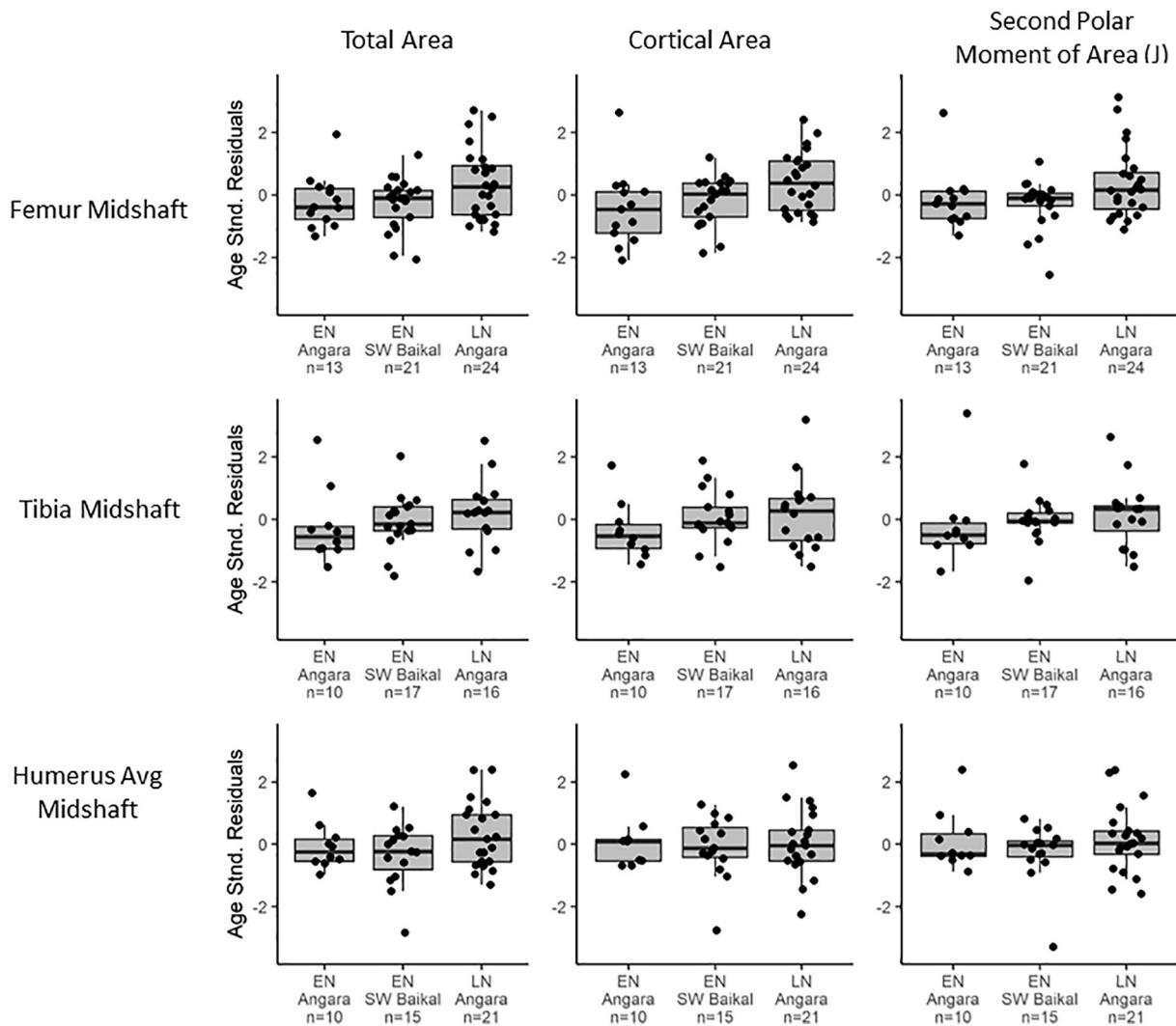


Fig. 2. Boxplots of Age-Standardized Area and Polar Second Moment of Area (J) with Overlaid Raw Data: Individuals Younger than 16.0 Years. (EN: Early Neolithic; LN: Late Neolithic; Angara: Angara River Valley micro-region; S Baikal: South Baikal micro-region).

significantly higher compared to the EN Angara group. As age standardized TA and CA of the humerus did not differ significantly between groups, the reason for differences in %CA is unclear. To investigate this question, humerus TA and CA were plotted against age with OLS lines fit to the data. As shown in Fig. 6, LN individuals exhibit a higher y-intercept for a regression of humerus TA against age than EN individuals, whereas CA shows less differentiation between archaeological periods. Thus, relatively greater TA in the LN group explains differences in %CA between groups.

To investigate the age at which CSG differences emerge, variables showing statistically significant differences were plotted against age. As an example, plots of standardized residuals for age standardized and body size standardized femur CA, femur I_x/I_y , and average humerus %CA are given in Fig. 7. LN individuals exhibit a tendency towards greater age standardized residuals for femur CA from around 2.0 years, whereas differences in body size standardized residuals become evident after approximately 6.0 years. EN individuals exhibit a higher range of age standardized residuals for femur I_x/I_y and humerus %CA after approximately 6.0 years.

3.1.1. Intra-archaeological period change in diaphyseal robusticity and shape: individuals less than 16.0 years

To assess change in diaphyseal robusticity and shape within archaeological periods, standardized residuals from regressions of

variables on either age or body size were regressed on radiocarbon dates separately for EN and LN samples. R^2 values for correlations are provided in Table 6, and examples of statistically significant regressions are provided in Fig. 8 and Fig. 9. As regression require both bio-mechanical variables and a calibrated radiocarbon date, sample size is reduced compared to prior comparisons. Therefore, analysis is restricted to the combined EN sample and the LN sample.

On all plots, only significant regression lines are shown. As illustrated in Fig. 8a, age standardized residuals for total area, cortical area, and J show a negative relationship to radiocarbon date in both the EN and LN, though not every variable exhibits a statistically significant correlation (Table 6). In other words, individuals born later in the EN or LN generally have lower bone rigidity for their age. For body size standardized measures, only the EN sample exhibits a significant relationship between right humerus variables and radiocarbon date (Fig. 8b; Table 6). Contrasting results for age and body size-standardized residuals raise the possibility that trends in age standardized area and SMA measures reflect change in body size. To further evaluate if body size changed within archaeological periods, standardized residuals of body mass estimates and diaphyseal length generated from regressions against age were regressed on radiocarbon date. As demonstrated in Fig. 8c and d, both body mass and diaphyseal length decrease significantly throughout the LN, but the regressions for the EN sample are not statistically significant (Table 6).

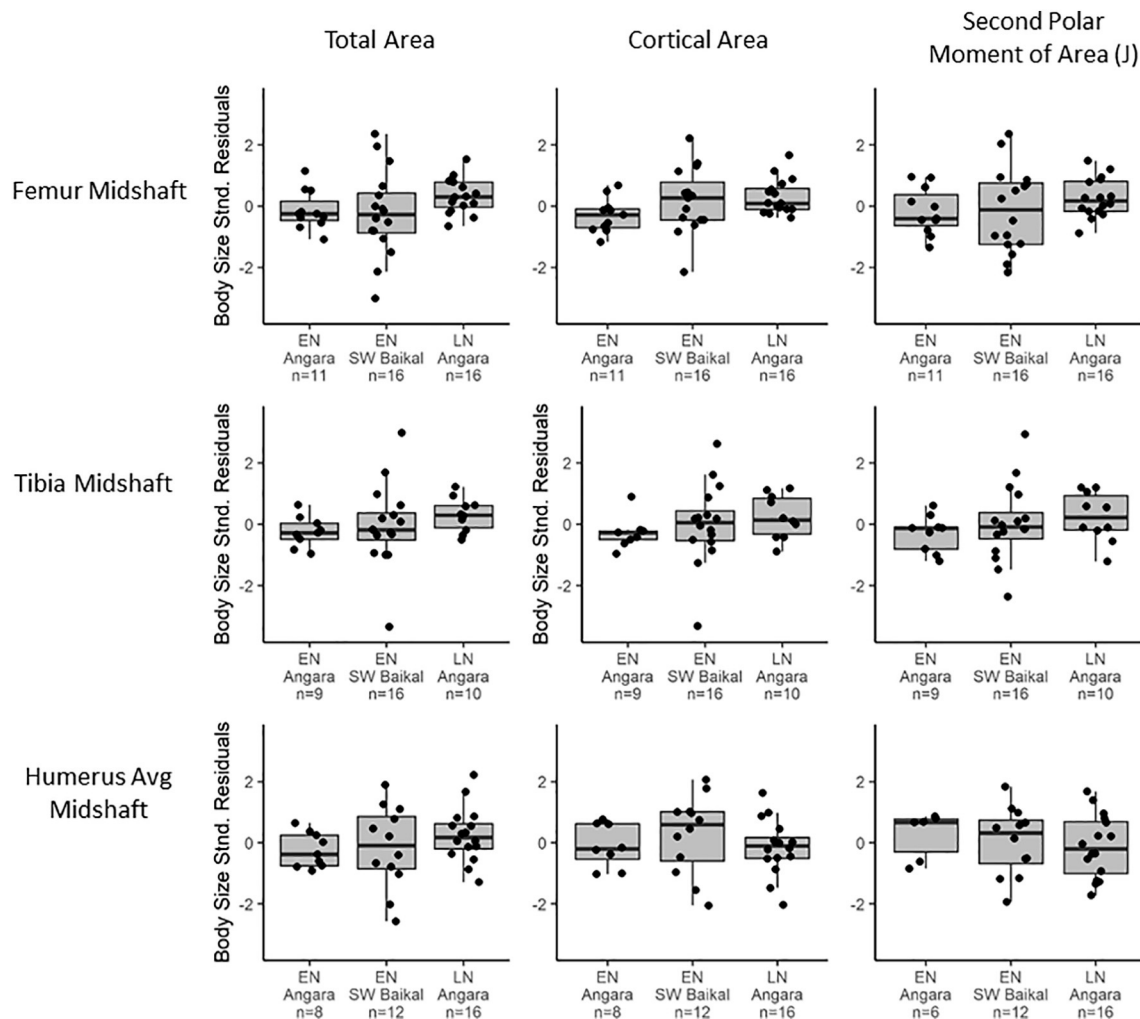


Fig. 3. Boxplots of Body Size-Standardized Area and Polar Second Moment of Area (J) with Overlaid Raw Data: Individuals Younger than 16.0 Years. (EN: Early Neolithic; LN: Late Neolithic; Angara: Angara River Valley micro-region; S Baikal: South Baikal micro-region).

As shown in Fig. 9a, age-standardized residuals for femur midshaft I_x/I_y show a significant positive correlation with radiocarbon date in the EN (Table 6). Paradoxically, as seen in Fig. 9b, tibia midshaft shape becomes more circular in individuals born later in the EN sample, though the correlation coefficient is markedly lower than for I_x/I_y . LN individuals do not exhibit a significant correlation between radiocarbon date and lower limb shape. However, as shown in Fig. 9c, humerus I_x/I_y decreases significantly during the LN, indicating that the humerus becomes more circular throughout this period.

3.2. Sexual dimorphism in adolescents/ young adults

Analysis of sexual dimorphism utilized adolescents and young adults for which sex estimation was possible. Descriptive statistics are shown in Table 7. Boxplots of TA and J for the femur, tibia, and average humerus midshaft are given in Fig. 10 for EN and LN females and males. Plots tentatively indicate greater male size-standardized tibia robusticity compared to females in both the EN and LN (Fig. 10). The sole LN female also produces lower values for the humerus than LN males. Boxplots of shape ratios in Fig. 11 show that males also have higher tibia SMA ratios in both archaeological periods and the humerus midshaft of females is less circular (Fig. 11). As only one LN female is available, statistical testing compared only EN males and EN females. Results reported in Table 8 demonstrate significant sexual differences in tibia midshaft J, tibia I_{max}/I_{min} , and humerus shape. Thus, by young

adulthood, some differentiation is evident between females and males in the EN sample, but significant overlap in bone rigidity and shape remains. The LN sample may also exhibit sexual dimorphism, but low sample size makes this unclear.

4. Discussion

4.1. Summary of results

Comparison of TA, CA, and J regressed on either age or body-size indicates that LN individuals have significantly greater lower limb diaphyseal rigidity than EN individuals (Figs. 2 and 3; Table 5). The EN Angara juveniles exhibit the lowest range of either age- or body size-standardized lower limb TA, CA, and J, though they are not significantly different from EN SW Baikal juveniles. EN juveniles, particularly those from the SW Baikal, also have less circular lower limbs and higher humerus percent cortical area than LN juveniles (Figs. 4 and 5; Table 5). Differences in TA, CA, and J regressed on age emerge around 2 years, whereas differences in body size standardized variables, lower limb shape, and humerus percent cortical area emerge after 6 years (Fig. 7). Analysis of chronological variation in CSG finds that age-standardized TA, CA, and J decrease throughout both the EN and the LN (Fig. 8; Table 6). Lower limbs may also become less circular throughout the EN (Fig. 9). Adolescent and young adults exhibit sexual dimorphism in tibia robusticity as well as lower and upper limb shape,

Table 4
Descriptive statistics: individuals younger than 16.0 years of age.

Variable	EN combined			EN Angara			EN SW Baikal			LN Angara		
	N	Mean	IQR	N	Mean	IQR	N	Mean	IQR	N	Mean	IQR
Age Standardized Residuals												
Femur Midshaft												
TA	34	-0.13	0.95	13	-0.39	0.98	21	-0.11	0.87	24	0.25	1.57
CA	34	-0.07	1.26	13	-0.47	1.32	21	0.02	1.07	24	0.37	1.58
%CA	34	0.07	1.68	13	-0.51	1.55	21	0.19	1.39	24	0.06	0.99
J	34	-0.13	0.76	13	-0.29	0.88	21	-0.11	0.41	24	0.15	1.17
Ix/Iy	34	0.13	1.24	13	0.18	0.92	21	0.09	0.77	24	-0.39	1.28
I _{max} /I _{min}	32	0.12	0.96	13	-0.16	0.57	19	0.17	0.92	23	-0.5	1.52
Tibia Midshaft												
TA	27	-0.25	1.03	10	-0.56	0.7	17	-0.15	0.77	16	0.22	0.93
CA	27	-0.19	0.99	10	-0.53	0.76	17	-0.11	0.67	16	0.27	1.34
%CA	27	-0.25	1.49	10	-0.42	0.86	17	0.31	1.92	16	0.01	1.16
J	27	-0.1	0.57	10	-0.49	0.64	17	-0.05	0.31	16	0.33	0.79
Ix/Iy	27	0.26	1.03	10	0.03	0.8	17	0.33	1.24	16	-0.41	1.33
I _{max} /I _{min}	26	0.04	1.54	10	-0.51	1.22	16	0.41	1.6	16	-0.29	1.34
R Humerus Midshaft												
TA	19	-0.01	1.28	7	0.04	1.36	12	-0.16	1.15	17	0.35	1.34
CA	18	-0.15	1.27	6	-0.62	1.38	12	0.1	1.09	17	-0.08	1.22
%CA	18	0.29	1.6	6	-0.07	0.4	12	0.68	1.5	17	-0.6	0.81
J	19	-0.28	0.84	7	-0.44	1.19	12	-0.17	0.66	17	0.04	0.73
Ix/Iy	19	1.03	0.22	7	1.06	0.18	12	1.1	0.22	17	1.1	0.22
I _{max} /I _{min}	17	1.67	0.29	7	1.61	0.19	10	1.81	0.29	16	1.58	0.36
L Humerus Midshaft												
TA	20	-0.01	0.93	8	-0.18	0.65	12	0.18	1.09	14	0.03	1.24
CA	20	0.11	0.98	8	-0.03	0.54	12	0.18	1.25	14	-0.15	0.77
%CA	20	0.41	1.19	8	0.07	1	12	0.51	1.68	14	-0.19	1.38
J	20	-0.14	0.41	8	-0.16	0.35	12	-0.09	0.49	14	-0.05	0.63
Ix/Iy	20	1.04	0.2	8	1.03	0.08	12	1.04	0.33	14	1.16	0.12
I _{max} /I _{min}	17	1.58	0.17	8	1.6	0.29	9	1.58	0.19	14	1.56	0.62
Avg Humerus Midshaft												
TA	25	-0.23	0.84	10	-0.25	0.7	15	-0.23	1.08	21	0.16	1.51
CA	24	-0.02	0.98	9	0.08	0.69	15	-0.12	0.95	21	-0.04	0.99
%CA	24	0.41	1.37	9	0.04	0.96	15	0.61	1.63	21	-0.3	1.14
J	25	-0.14	0.74	10	-0.32	0.71	15	-0.04	0.51	21	0.02	0.74
Ix/Iy	25	1.03	0.22	10	1.03	0.16	15	1.09	0.31	21	1.13	0.18
I _{max} /I _{min}	21	1.65	0.26	10	1.6	0.2	11	1.66	0.27	21	1.55	0.25
Body Size Standardized												
Femur Midshaft												
TA	27	-0.25	1.18	11	-0.25	0.62	16	-0.28	1.3	16	0.3	0.82
CA	27	-0.15	1.07	11	-0.29	0.62	16	0.09	1.11	16	0.09	0.68
J	27	-0.41	1.67	11	-0.41	1.01	16	-0.12	2	16	0.17	0.97
Tibia Midshaft												
TA	25	-0.19	0.7	9	-0.28	0.52	16	-0.18	0.88	10	0.3	0.72
CA	25	-0.22	0.72	9	-0.27	0.28	16	0.06	0.97	10	0.15	1.16
J	25	-0.13	0.99	9	-0.13	0.71	16	-0.09	0.85	10	0.22	1.12
R Humerus Midshaft												
TA	16	-0.01	1.23	6	-0.22	0.97	10	0.06	1.55	14	0.01	1.09
CA	15	0.41	1.63	5	0.34	1.35	10	0.54	1.49	14	-0.19	0.72
J	16	0.48	1.6	6	0.39	1.22	10	0.48	1.54	14	-0.1	1.46
L Humerus Midshaft												
TA	17	-0.44	1.06	7	-0.51	0.77	10	-0.27	1.96	10	0.15	0.73
CA	17	0.52	1.46	7	-0.12	1.02	10	0.69	1.85	10	-0.18	1.12
J	14	0.15	1.22	4	0.2	0.81	10	0.15	1.69	10	-0.14	1.92
Average Humerus Midshaft												
TA	21	-0.38	1.25	9	-0.38	0.99	12	-0.1	1.7	16	0.17	0.81
CA	20	0.32	1.41	8	-0.2	1.14	12	0.59	1.6	16	-0.1	0.67
J	18	0.53	1.36	6	0.67	1.07	12	0.31	1.42	16	-0.2	1.69

though significant overlap remains between females and males by young adulthood (Figs. 10 and 11; Tables 7,8).

4.2. Distinguishing body size and habitual loading signals in juvenile CSG

On the whole, it is likely that the CSG differences between EN and LN juveniles younger than 16.0 years reflect differences in both body mass and activity levels. Untangling the effects of body mass and activity requires critical analysis of patterning in the data. Initially, lower limb CSG and shape ratios appear contradictory. LN individuals exhibit higher measures of both age standardized and body size standardized

area and J, which would be consistent with greater terrestrial mobility (Figs. 2 and 3; Table 5). However, the less circular lower limbs of EN juveniles are consistent with higher terrestrial mobility in this archaeological period (Fig. 4; Table 5). It is possible that differences in lower limb shape could reflect differences in movement directionality or terrain traversed. However, as discussed in Section 4.3, these are less likely explanations for differences between groups than distance traveled during foraging rounds.

Body size standardization may not fully control for body size differences, because standards for juvenile body mass estimation have only been derived from a single modern urban sample. Also, TA, CA,

Table 5
Results of Mann-Whitney statistical comparisons: individuals younger than 16.0 years of age.

Comparison	Age standardized						Size standardized		
	TA	CA	J	% CA	I _x /I _y	I _{max} /I _{min}	TA	CA	J
Femur Midshaft									
EN-LN	0.06**	0.01**	0.04**	0.82	0.03**	0.21	0.03**	0.05**	0.14
EN Angara- EN SW Baikal	0.80	0.19	0.57	0.22	0.53	0.62	0.87	0.34	0.87
EN Angara-LN Angara	0.15	0.02**	0.08**	0.34	0.24	0.30	0.04**	0.01**	0.13
EN S Baikal- LN Angara	0.10	0.06**	0.10	0.73	0.03**	0.29	0.08**	0.38	0.29
Tibia Midshaft									
EN-LN	0.25	0.56	0.21	0.63	0.06**	0.14	0.14	0.27	0.32
EN Angara- EN SW Baikal	0.22	0.13	0.08**	0.41	0.41	0.31	0.60	0.30	0.60
EN Angara-LN Angara	0.20	0.24	0.17	0.74	0.29	0.70	0.08**	0.08**	0.18
EN S Baikal- LN Angara	0.44	0.99	0.40	0.35	0.06**	0.07**	0.34	0.66	0.59
R Humerus Midshaft									
EN-LN	0.27	0.83	0.62	0.01**	0.82	0.23	0.47	0.33	0.31
EN Angara- EN SW Baikal	0.65	0.75	0.97	0.07**	0.97	0.27	0.71	0.31	0.79
EN Angara-LN Angara	0.66	0.66	1.00	0.32	0.80	0.72	0.44	0.82	0.35
EN S Baikal- LN Angara	0.23	1.00	0.50	< 0.01**	0.91	0.15	0.60	0.26	0.47
L Humerus Midshaft									
EN-LN	0.48	0.96	0.36	0.04**	0.06**	0.80	0.19	0.31	0.75
EN Angara- EN SW Baikal	0.97	0.91	0.97	0.52	0.91	0.24	0.81	0.42	0.95
EN Angara-LN Angara	0.48	0.87	0.44	0.15	0.13	0.48	0.16	0.60	0.64
EN S Baikal- LN Angara	0.63	0.82	0.46	0.05**	0.12	0.83	0.39	0.28	0.91
Avg Humerus Midshaft									
EN-LN	0.22	0.97	0.41	0.01**	0.30	0.27	0.22	0.44	0.44
EN Angara- EN SW Baikal	0.81	0.77	0.98	0.35	0.94	0.17	0.81	0.34	0.62
EN Angara-LN Angara	0.49	0.97	0.66	0.09**	0.33	0.79	0.15	0.98	0.41
EN S Baikal- LN Angara	0.21	1.00	0.39	0.01**	0.46	0.14	0.51	0.24	0.63

EN: Early Neolithic; LN: Late Neolithic; Angara: Angara River Valley micro-region; SW Baikal: Southwest Baikal micro-region.

** $p < 0.01$.

and J track growth in body mass more closely than joint dimensions or bone length, and body mass is the “main determinant of bone strength in the growing lower limb” (Cowgill, 2018, p. 2; Ruff, 2007). In adults, body mass also accounts for 80% of the variation in cross-sectional geometric properties (Pomeroy et al., 2018). This creates problems for interpreting cross-sectional properties, precisely because they are standardized by formula for joint dimensions, which are less sensitive to the effects of body mass. Experimental studies show that articular surfaces, on which body mass estimates are based show lower sensitivity to mechanical loading (Lieberman et al., 2001). While this means they are less likely to be affected by differences in activity, it is also possible that TA, CA, and J may be sensitive to changes in body mass that do not cause changes in joint dimensions (Cowgill, 2018; Osipov et al., 2016; Cowgill, 2010). Therefore, because joint dimensions may be less sensitive to differences in body mass than cross-sectional properties, we evaluate patterning in both age and body size standardized properties critically, assuming that regressing properties on body size estimated from joint dimensions may not fully control for body size differences.

Consistent with this, prior bioarchaeological studies confirm that juvenile body size standardized measures show patterning between populations that recapitulate expected differences in body mass (Cowgill, 2018, 2010; Osipov et al., 2016). As ratios, I_x/I_y and I_{max}/I_{min}, measure the relative magnitude of loads about different axes, they inherently control for body mass. Therefore, it may be the case that greater lower limb TA, CA, and J values in LN juveniles reflect greater body mass, whereas the less circular lower limbs of EN juveniles reflects functional adaptation to greater terrestrial mobility. Consistent with this, it has previously been shown that EN juveniles have lower body mass for age than LN juveniles younger than 16 years old (Temple et al., 2014). Furthermore, differences in lower limb shape emerge around 6 years (Fig. 7). Older children have greater locomotor ability and become too heavy to carry, making it likely that a difference in femur shape after 6 years reflects functional adaptation to greater mobility in the EN.

While femur and tibia midshaft TA, CA, and J in the EN group may

reflect reduced body mass, EN and LN groups show equivalent ranges of TA, CA, and J at the humerus midshaft (Figs. 3 and 4). Upper and lower limb CSG show similar correlations to body size proxies, so the non-weight-bearing role of the humerus is unlikely to totally account for this difference (Ruff, 2003). Thus, if body size related loads were the only factor driving patterns in the upper limb, one would expect to see greater age and body size standardized residuals in the LN group, as was observed in the lower limb. Instead, higher behavior induced loading may make up for lower body mass induced load in EN individuals.

Interestingly, a lack of differences in lower limb %CA do not support differences in physiological stress between EN and LN groups. %CA has no direct mechanical relevance, but it reflects differences in the relative rates of periosteal deposition versus endosteal resorption during development. Previous studies have identified lower %CA as an indicator of nutritional stress, because malnutrition and illness increase endosteal bone resorption (Garn et al., 1969; Larsen et al., 1995; May and Ruff, 2016; Van Gerven et al., 1985). Thus, a priori, one would expect lower %CA in the EN sample, especially given other lines of evidence for higher developmental stress in this population (Lieverse et al., 2007; Temple et al., 2014). However, it is unclear if cross-sectional geometry and %CA respond to stress in the same way. Prior work on the Medieval Nubian site of Kulubnarti is informative. Juvenile remains at this site had a high prevalence of cribra orbitalia indicating significant malnutrition or illness, and the group has both higher tibia %CA and low body-size standardized CSG compared to other juvenile samples (Van Gerven et al., 1985; Cowgill, 2010). This suggests that severe systemic stress can increase endosteal resorption and reduce bone strength due to reduced body mass. The EN Cis-Baikal groups exhibit only reduced lower limb TA, CA, and J compared to LN individuals, but no differences in lower limb %CA. A possible explanation for the EN group not showing lower %CA but reductions in CSG is that stress may have been less severe in these groups than in Kulubnarti. Therefore, body mass may have been lower for age, but stress was potentially not severe enough in the EN to accelerate endosteal resorption. Proving this hypothesis would require further study using animal models or

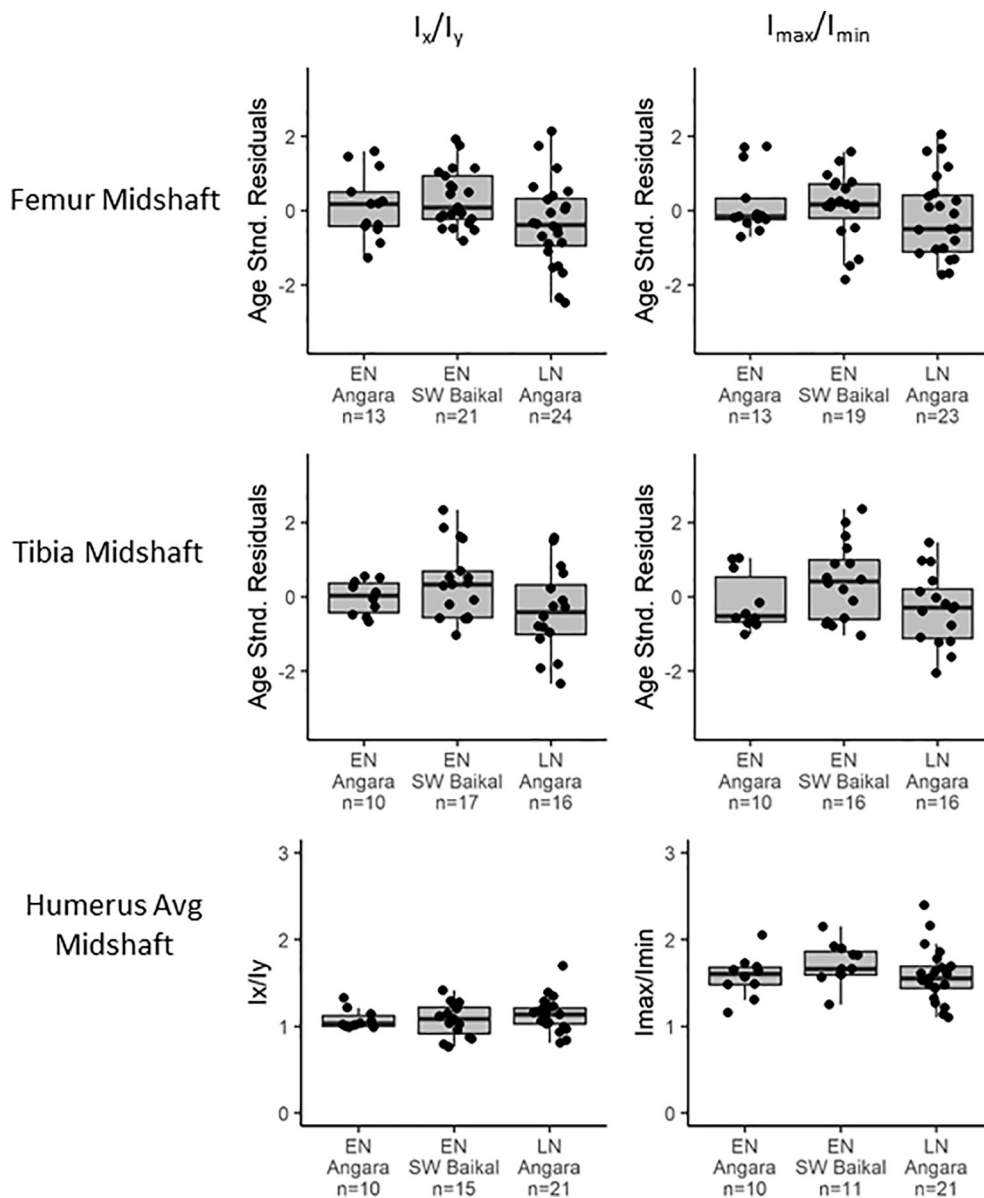


Fig. 4. Boxplots of Age Standardized Second Moment of Area Ratios (I_x/I_y and I_{max}/I_{min}) with Overlaid Raw Data: Individuals Younger than 16.0 Years. (Humerus values do not show a significant relationship to age, so raw values used). (EN: Early Neolithic; LN: Late Neolithic; Angara: Angara River Valley micro-region; S Baikal: South Baikal micro-region).

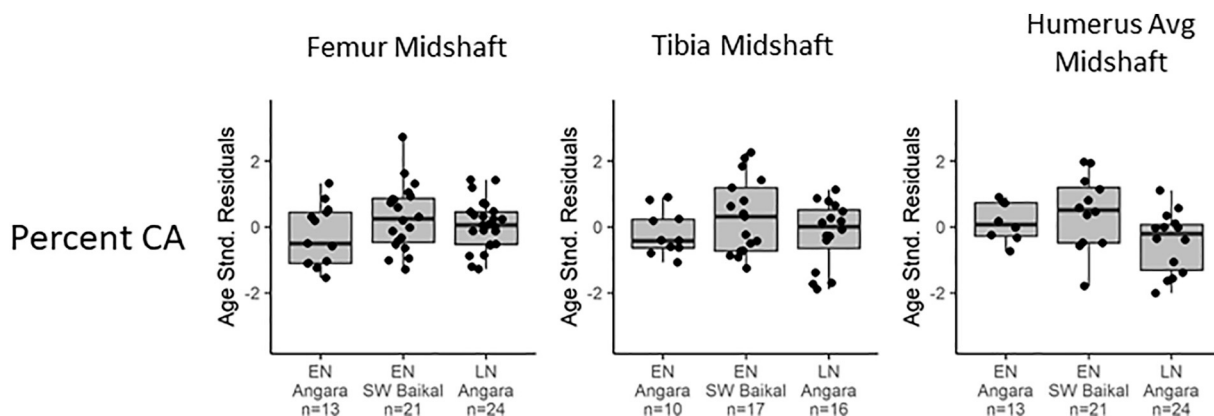


Fig. 5. Boxplots of Percent Cortical Area with Overlaid Raw Data: Individuals Younger than 16.0 Years. (EN: Early Neolithic; LN: Late Neolithic; Angara: Angara River Valley micro-region; S Baikal: South Baikal micro-region).

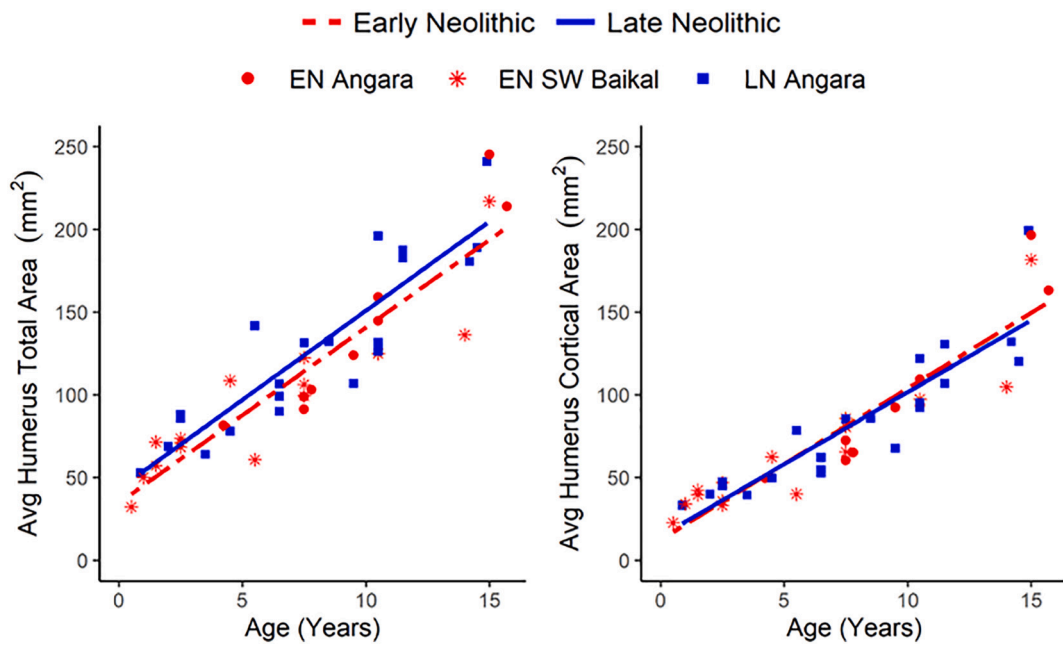


Fig. 6. Scatterplots of Average Humerus Total Area and Cortical Area against Age: Individuals Younger than 16.0 Years. (Angara: Angara River Valley micro-region; S Baikal: South Baikal micro-region).

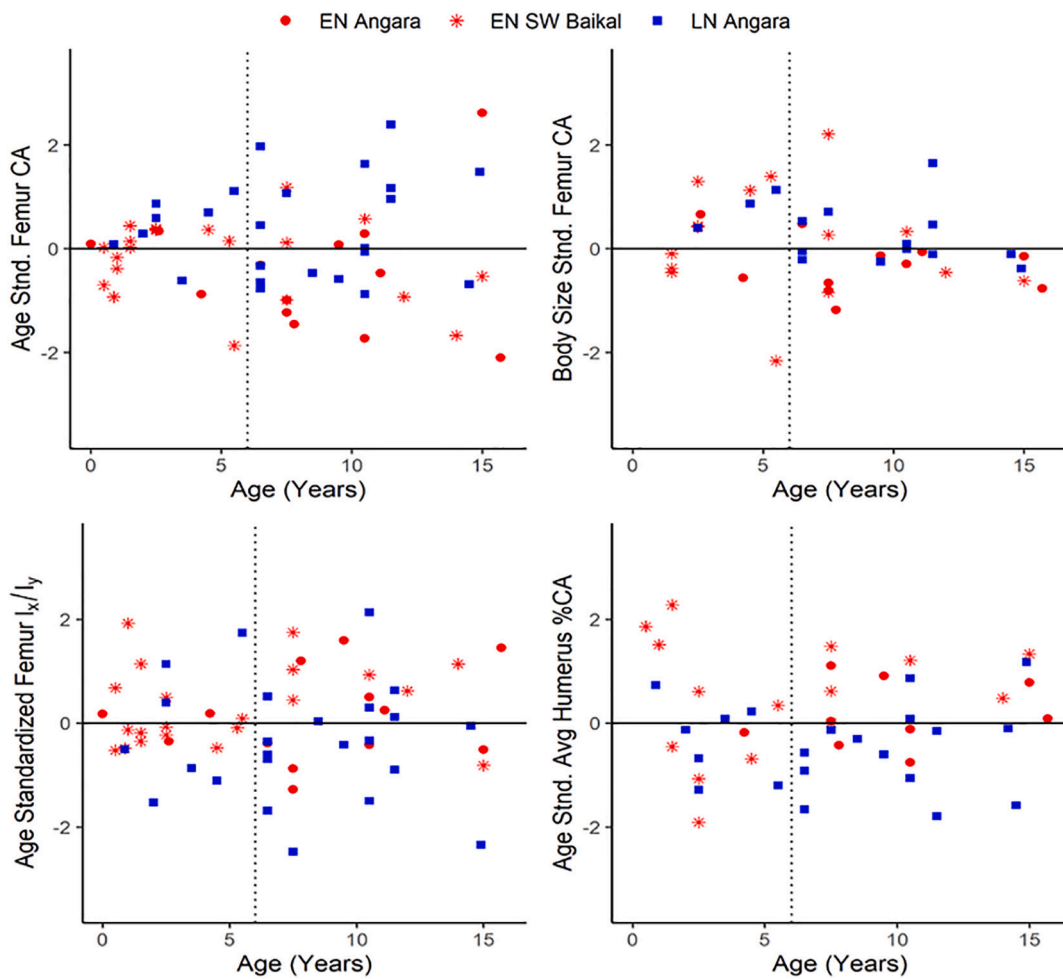


Fig. 7. Scatterplots of Age and Body Size Standardized Residuals Against Age: Individuals Younger than 16.0 Years. (Angara: Angara River Valley micro-region; S Baikal: South Baikal micro-region).

Table 6

R² values for regressions of cross-sectional geometry, body mass, and diaphyseal length on calibrated radiocarbon date: individuals younger than 16.0 years of age.

Variable	Age standardized		Body size standardized	
	EN combined	LN	EN combined	LN
Femur Midshaft				
TA	0.07	0.13**	0.08	0.09
CA	0.30**	0.13**	0.03	0.04
J	0.08	0.14**	0.06	0.07
%CA	0.18**	0.07		
Ix/Iy	0.3**A	0.06		
Imax/Imin	0.05	0.07		
Tibia Midshaft				
TA	0.26**	0.06	0.02	0.06
CA	0.37**	0.05	0.01	0.07
J	0.27**	0.08	0.04	0.13
%CA	0.07	0.04		
Ix/Iy	0.04	0.08		
Imax/Imin	0.19**	0.12		
Left Humerus Midshaft				
TA	0.05	0.52**	0.1	0.07
CA	0.06	0.22	0.14	0.05
J	0.08	0.37**	0.15	0.09
%CA	0.1	0.13		
Ix/Iy	0.11	0.84**		
Imax/Imin	0.03	0.07		
Right Humerus Midshaft				
TA	0.33**	0.14	0.31**	0.09
CA	0.37**	0.14	0.23	0.09
J	0.29**	0.02	0.34**	0.09
%CA	0	0.28**		
Ix/Iy	0.04	0.31**		
Imax/Imin	0.1	0.11		
Avg Humerus Midshaft				
TA	0.20**	0.13	0.13	0.09
CA	0.22**	0.20**	0.16	0.03
J	0.15**	0.12	0.17	0.02
%CA	0	0.04		
Ix/Iy	0.04	0.50**		
Imax/Imin	0.1	0.07		
Body Mass and Diaphyseal Lengths				
Body Mass	0.07	0.49**		
Femur	-0.02	0.12**		
Tibia	0.05	0.13**		
Avg Humerus	0.02	0.5**		

A: values positively correlated with radiocarbon date. All other variables show negative correlations. EN: Early Neolithic; LN: Late Neolithic.

** $p < 0.1$.

comparisons of populations in which more is known about differences in developmental stress.

Paradoxically, % CA is significantly higher in the humerus midshaft of EN juveniles than LN juveniles (Fig. 5; Table 5). As systemic stress should affect the whole body, it is unlikely that differences in one limb reflect variation in physiological stress. Instead it may potentially reflect increased upper limb loading in the EN. While %CA itself does not have mechanical relevance, it does measure rates of periosteal bone deposition and endosteal resorption. Most noticeably, increased loading increases the rate of periosteal deposition, but it may also reduce the rate of endosteal resorption (Pearson and Lieberman, 2004; Ruff et al., 1994). For instance, juvenile ball players exhibit reduced endosteal area compared to non-throwing controls, suggesting decreased resorption during growth (Weatherholt and Warden, 2018). In later adolescence, the endosteal surface transitions from bone resorption to bone deposition (Frisancho et al., 1970; Garn, 1970; Neu et al., 2001; Wang et al., 2005). Thus, LN humeri may adapt to increased loading through periosteal expansion, whereas EN juveniles also experienced decreased endosteal resorption and possibly increased endosteal deposition in adolescence, potentially because loading was more intense. Behavioral interpretations of this patterning are considered in Section 4.4 below.

4.3. Differences in developmental stress between archaeological periods

Interpretation of lower TA, CA, and J values in the EN as indicative of reduced body size compared to LN juveniles agrees with prior research suggesting higher developmental stress in the EN. EN adults and juveniles exhibit higher frequencies of enamel hypoplasia as well as reduced adult and juvenile stature and body mass (Lieverse et al., 2007; Stock et al., 2010; Temple et al., 2014). Concordant with Temple et al.'s study, our data suggest that difference in body size between EN and LN groups emerged early in childhood between 2 and 6 years of age (Fig. 7). Thus EN children may have experienced more physiological stress in the weaning period than LN children, perhaps due to illness or to seasonal food shortages (Temple et al., 2014; Waters-Rist, 2011; Waters-Rist et al., 2011).

On the basis of grave numbers and cemetery distributions, it has been proposed that EN populations were more densely concentrated than LN groups, especially in the Angara micro-region (Lieverse et al., 2016, 2013; Weber and Bettinger, 2010). Furthermore, EN groups greater reliance on fish may have tethered them to productive fishing locations for longer periods of the year than was the case in the LN (Lieverse et al., 2013). Either factor or both could have depleted local terrestrial game, thereby increasing vulnerability to seasonal food shortages (Lieverse et al., 2007; Weber and Bettinger, 2010). In addition, climate modeling tentatively suggests that increased aridity may have increased terrestrial game populations and concentrated them in particular localities during the LN (Weber and Bettinger, 2010; White and Bush, 2010). Therefore, terrestrial ungulates may have been more abundant and less dispersed during the LN, reducing risk of resource shortfall.

4.4. Inter-archaeological period variation in juvenile behavior

The differences detected between EN and LN juveniles have implications for interpreting individual mobility, parental foraging behavior, and the economic role of children. While no modern ethnographic example is a reliable model for the behavior of past populations, general patterns in child behavior derived from multiple case studies can prove informative of how and why hunter-gatherer children may have moved around the landscape and foraged (Lew-Levy et al., 2017). Differences in lower limb robusticity and shape are primarily indicative of differences in terrestrial mobility, defined as the total distance traveled by walking or running during an individual's lifetime (Stock, 2006; Ruff and Larsen, 2014). Ethnographic examples indicate that, prior to adolescence, children generally travel from camp when either the entire group moves or the care-giving adult, usually the mother, takes the child foraging (Hawkes, 1995; Henry et al., 2005; MacDonald, 2007).

Therefore, the less circular lower limbs of EN juveniles may reflect either more frequent local foraging or travel over longer distances, presumably in the company of care-giving adults (Fig. 4; Table 5). This is also the same pattern seen in adults. EN females have less circular lower limbs than LN-EBA females, suggesting greater terrestrial mobility (Stock and Macintosh, 2016). It is important to note that biomechanical data is most relevant to the characterization of individual rather than group mobility. Bone morphology is influenced by accumulated mechanical loading bouts. Comparing individual mobility signatures cannot directly provide evidence of differences in how movement was organized, e.g. number of residential moves, daily foraging distance, number of individuals travelling together. Based on archaeological and environmental evidence, Weber (Weber, n.d) argues that residential (group) mobility was generally lower in the EN than the LN, due to crowding of populations and tethering to productive fishing locations in the Angara and southwest Baikal regions. Therefore, the less circular femora of EN individuals may reflect that local depletion of resources around the group residence required individual foragers to travel more frequently or over longer distances to acquire resources

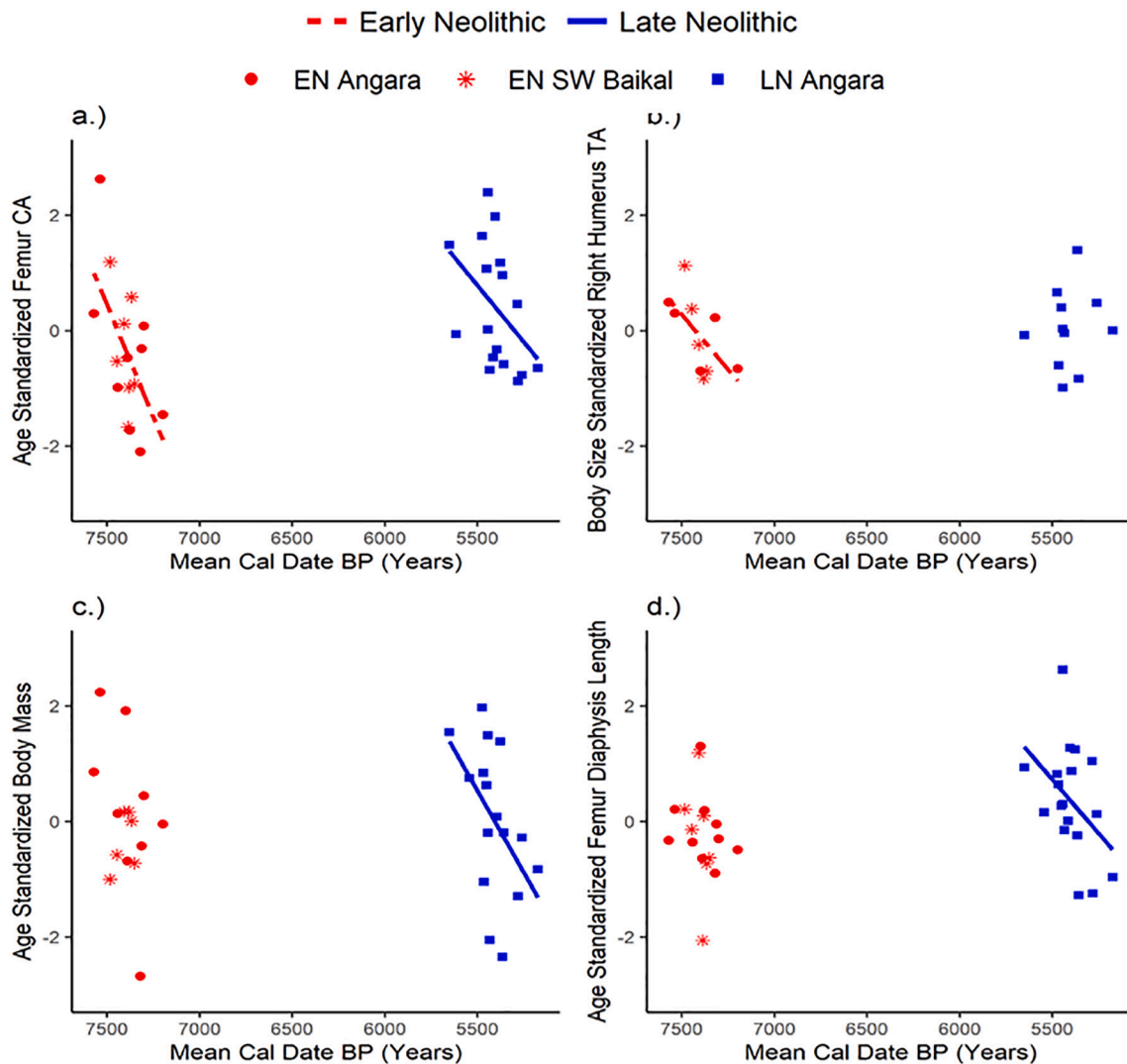


Fig. 8. Scatterplots of Area Measures, Body Mass Estimates, and Diaphyseal Length Regressed on Calibrated Radiocarbon Date: Individuals Younger than 16.0 Years. Only Significant Regression Lines Shown. (Angara: Angara River Valley micro-region; S Baikal: South Baikal micro-region).

(Lieverse et al., 2013). One also cannot exclude the possibility that, although EN groups moved residences less frequently, they may have done so over longer distances due to the reduced abundance of local terrestrial game. In contrast, due to reduced population pressure or the more favorable distribution of game due to environmental changes, LN foragers may have not had to travel as far during individual foraging rounds (Weber and Bettinger, 2010; White and Bush, 2010; Weber, n.d).

It is also possible that differences in terrain traversed and activity types contribute to differences in lower limb shape, but this seems unlikely to explain all the variation observed. Differences in activities engaged in may alter limb shape, because they alter strain distribution in the lower limb. Notably, Shaw and Stock (2009) found that field hockey players had more circular diaphyses than runners. This was attributed to field hockey requiring multidirectional movement and directional changes, which results in a more symmetric strain distribution than running. Terrain relief may also affect lower limb shape. Theoretically, sloped terrain should increase anteroposterior strains due to changes in posture, but rugged terrain may increase mediolateral strain, due to variation in ground reaction forces and multidirectional movement (Ruff et al., 2006b; Higgins, 2014).

However, neither differences in activity type or terrain relief provide convincing explanations for the differences observed between

groups in the Cis-Baikal. All groups would have foraged in similar terrain- boreal forest, lakeshore, riverbanks- for the same types of resources, and using the same tools. Terrain in the SW Baikal and lower Angara River Valley is “occupied by extensive stretches of rolling hills” which reach heights of 1000–1100 m (Weber, 2003). Around the cemetery where the LN sample was excavated, the landscape becomes slightly flatter (hills 400–600 m high). While this difference may contribute to the patterning detected, it remains unclear if it is large enough to account for all the differences observed. Indeed, past studies that interpreted variation in lower limb shape as indicative of differences in terrain traversed mostly compared pastoralists traversing mountain ranges to individuals from non-mountainous regions (Marchi et al., 2006). In these cases, differences in terrain are larger than in the Cis-Baikal. Therefore, it is reasonable to assume that a significant portion of the differences in lower limb shape relates to differences in habitual distance traveled.

Increased humeral %CA and equivalence in age and body size standardized humerus area and J are consistent with greater juvenile upper limb loading in the EN than the LN, which is the same pattern seen in adults (Figs. 2, 3, 5; Table 5) (Stock et al., 2010). Greater involvement by EN children in fishing could explain this patterning. Fish constituted a greater proportion of the diet in the EN than the LN, and dependence on aquatic resources increased throughout the EN period

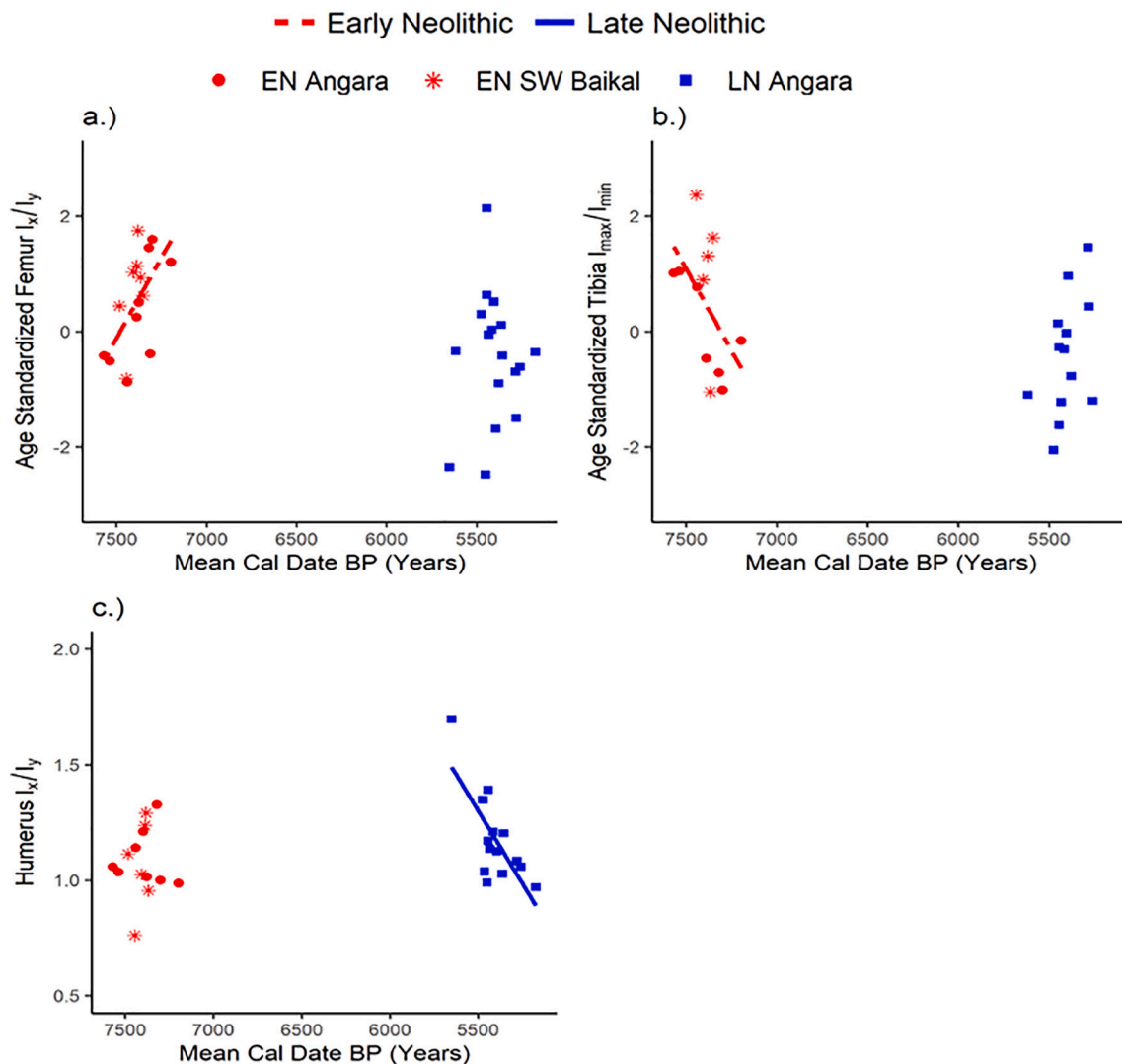


Fig. 9. Scatterplots of Diaphyseal Shape Ratios Regressed on Calibrated Radiocarbon Date: Individuals Younger than 16.0 Years. Only Significant Regression Lines Shown. (Angara: Angara River Valley micro-region; S Baikal: South Baikal micro-region).

(Weber et al., 2016a, 2016b, 2011). The use of fishing gear, watercraft use, and subsequent processing of the catch would place considerable strains on the upper limb, and hunter-gatherer children become proficient at fishing from an early age, deriving substantial yields in this activity (Bird and Bird, 2002; Gurven and Kaplan, 2006; Lancy, 2015). Substantial involvement by children in fishing has also been observed in hunter-gatherers from broadly comparable environmental contexts to that of Lake Baikal such as the Ainu of Hokkaido and the Siberian Evenki (Watanbe, 1972; Turov, 2010). In addition, it is possible that EN juveniles may have been more involved in domestic tasks such as carrying loads and processing food, which would increase adult foraging productivity (Hawkes, 1995; Henry et al., 2005).

The preceding discussion has emphasized the potential role of children as economic actors. However, it should be noted that hunter-gatherer childhood behavior is not extremely structured, with substantial portions of the day spent in undirected play (Lew-Levy et al., 2017). Indeed, the amount of time devoted to subsistence appears to increase progressively throughout childhood and intense instruction in foraging begins in adolescence. This inherent heterogeneity complicates straightforward reconstruction of behavioral differences from skeletal remains. However, it should not obscure the fact that cross-cultural studies show that children are proficient food collectors by middle childhood, implying that considerable time is devoted to foraging,

whether as “play” or under adult direction. Thus, a considerable portion of the variation detected in biomechanical properties likely reflects differences in subsistence behavior or group movement.

4.5. Geographic differences in behavior and health

Health and behavior may also exhibit geographic variation. The EN Angara group produces the lowest range of values for TA, CA, and J, and more comparisons of EN Angara-LN Angara groups are significant than for EN SW Baikal-LN Angara (Figs. 2 and 3; Table 5). This may reflect particularly low body mass in the EN Angara group due to particularly high developmental stress. As discussed above, several large EN cemeteries are known from the Angara River Valley but only one has been excavated in the SW Baikal micro-region. This may be a tentative indication that higher population density increased developmental stress in this micro-region (Lieverse et al., 2016, 2013; Weber and Bettinger, 2010).

The EN SW Baikal group also produces the highest values for lower limb shape ratios and humerus %CA (Figs. 4, 5; Table 5). Evidence of greater terrestrial mobility and upper limb loading may reflect ecogeographic differences in foraging behaviors. Both Angara groups foraged in a riverine environment, whereas SW Baikal individuals buried at Shamanka II, the sole cemetery known in this micro-region, show

Table 7
Descriptive statistics: females and male adolescents older than 16.0 years and young adults.

Variable	EN Female			EN Male			LNEBA Female			LNEBA Male		
	N	Median	IQR	N	Median	IQR	N	Median	IQR	N	Median	IQR
Femur Midshaft												
TA	6	8.2	1.42	6	8.24	1.4	1	8.05		4	7.81	0.68
J	4	0.0035	0.0013	4	0.0038	0.0005	1	0.004		3	0.0036	0
Ix/Iy	6	1.26	0.23	6	1.4	0.2	1	1.15		4	1.16	0.71
I _{max} /I _{min}	6	1.31	0.21	6	1.53	0.2	1	1.46		4	1.46	0.21
Tibia Midshaft												
TA	9	6.1	0.82	8	6.82	1.97	1	5.12		6	6.76	0.64
J	8	0.0034	0.001	8	0.0045	0.0017	1	0.0022		5	0.0045	0.0006
Ix/Iy	9	1.5	0.2	8	1.42	0.43	1	1.06		6	1.77	0.43
I _{max} /I _{min}	9	2.25	0.42	8	2.89	0.34	1	1.97		6	2.61	0.23
R Humerus Midshaft												
TA	9	4.55	0.63	10	4.84	1.56	1	3.74		6	4.7	0.51
J	9	0.002	0.0012	8	0.0023	0.0014	1	0.0014		6	0.0024	0.0005
Ix/Iy	9	1.2	0.08	11	1.04	0.17	1	1.23		6	0.86	0.33
I _{max} /I _{min}	9	1.81	0.15	10	1.61	0.49	1	1.99		6	2.07	0.17
L Humerus Midshaft												
TA	9	4.12	1.18	10	4.5	1.39	1	3.44		5	4.16	0.47
J	9	0.0017	0.001	8	0.0019	0.001	1	0.0012		5	0.0019	0.00016
Ix/Iy	9	1.12	0.26	11	0.9	0.16	1	1.25		5	0.84	0.05
I _{max} /I _{min}	9	1.82	0.14	10	1.6	0.18	1	1.90		5	1.66	0.28
Avg Humerus Midshaft												
TA	11	4.3	0.96	10	4.62	1.44	1	3.60		6	4.53	0.64
J	11	0.0018	0.0011	8	0.002	0.0012	1	0.0014		6	0.0022	0.00047
Ix/Iy	11	1.18	0.19	11	0.99	0.18	1	1.24		6	0.85	0.2
I _{max} /I _{min}	11	1.82	0.16	10	1.56	0.31	1	1.95		6	1.86	0.2

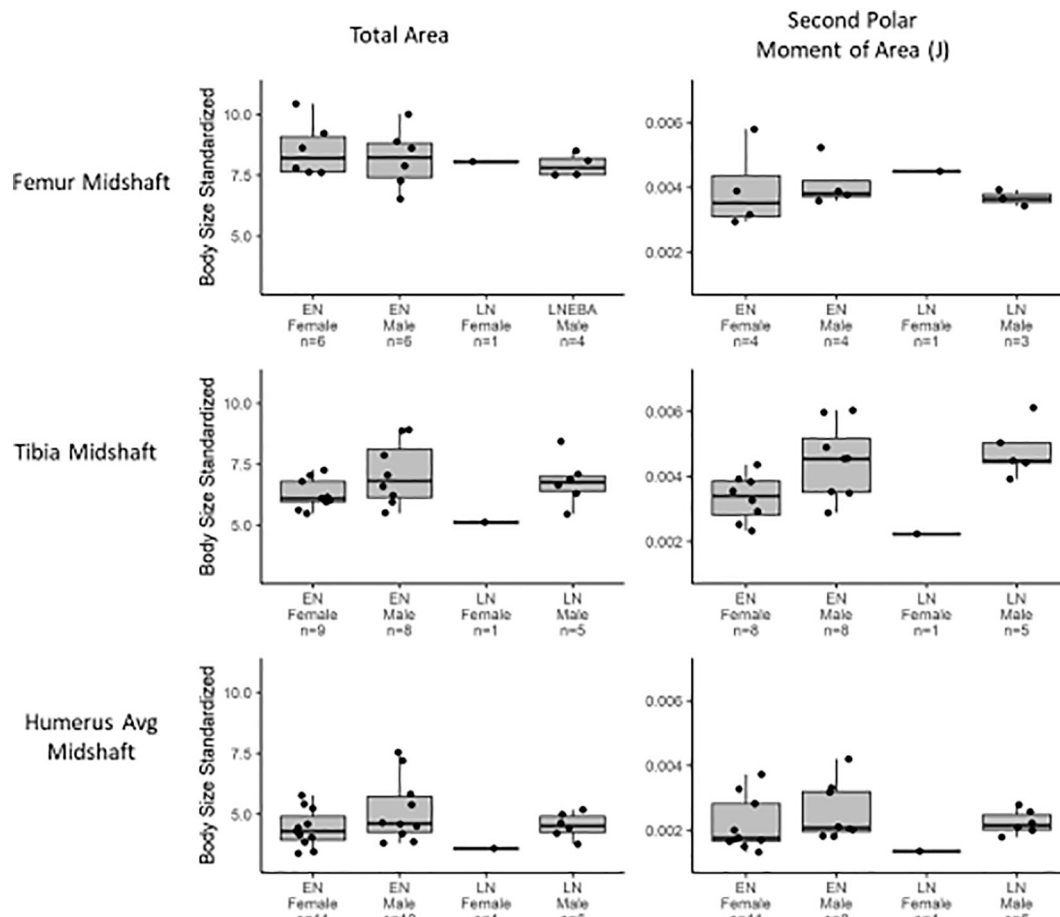


Fig. 10. Boxplots of Body Size Standardized Area and Second Polar Moment of Area (J): Adolescent and Young Adult Females and Males. (EN: Early Neolithic; LN: Late Neolithic).

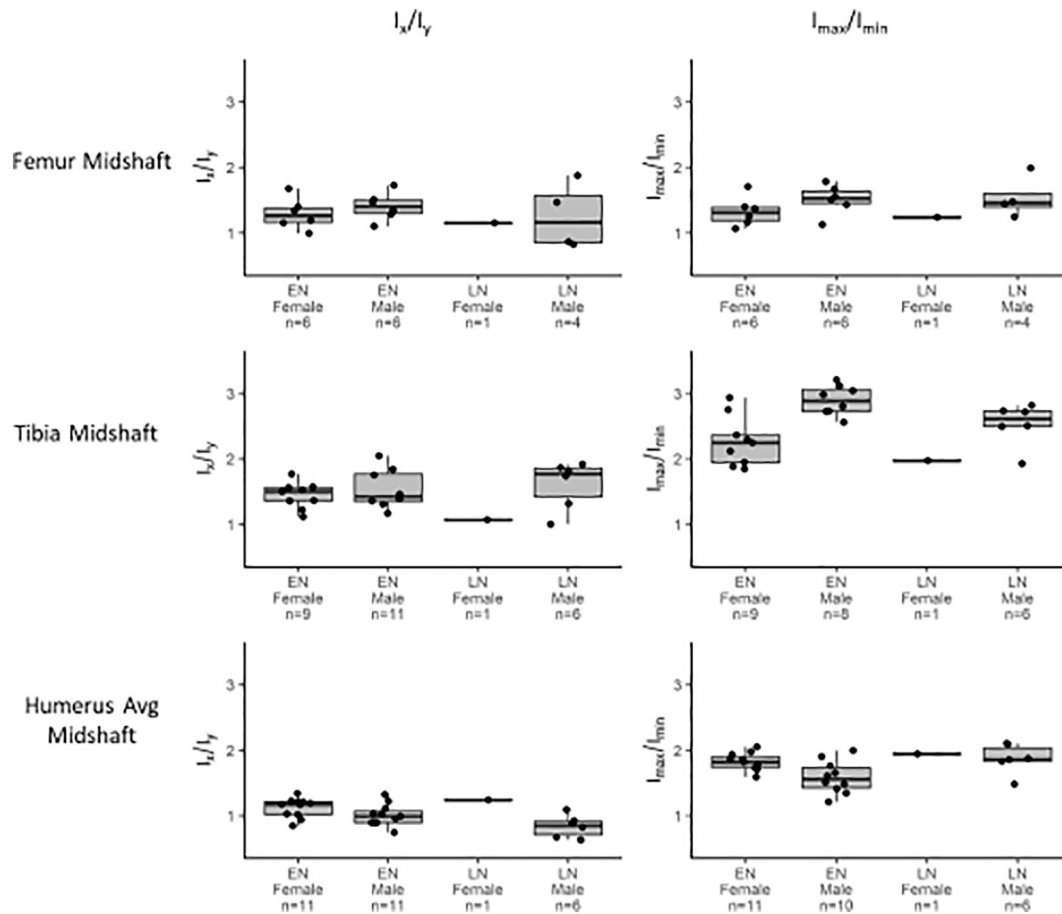


Fig. 11. Boxplots of Shape Ratios: Adolescent and Young Adult Females and Males. (EN: Early Neolithic; LN: Late Neolithic).

Table 8
Results of non-parametric comparisons of early neolithic adolescent/ young adult females.

Variable	p-value
Femur Midshaft	
TA	0.70
J	0.89
I_x/I_y	0.39
I_{max}/I_{min}	0.18
Tibia Midshaft	
TA	0.2
J	0.06**
I_x/I_y	0.74
I_{max}/I_{min}	< 0.001**
R Humerus Midshaft	
TA	0.16
J	0.14
I_x/I_y	0.09**
I_{max}/I_{min}	0.08**
L Humerus Midshaft	
TA	0.55
J	0.42
I_x/I_y	0.2
I_{max}/I_{min}	0.03**
Avg Humerus Midshaft	
TA	0.2
J	0.13
I_x/I_y	0.13
I_{max}/I_{min}	0.03**

** $p < 0.1$.

considerable dietary diversity (Weber et al., 2016b). Some groups using this cemetery subsisted on Lake Baikal fish, while others appear to have acquired their fish elsewhere. Isotopic data from the Fofanovo cemetery in the Selenga River Delta are quite different, making this location unlikely (White et al., this volume). The Irkut River valley remains another possibility, though no human isotopic data is available from this region. Consequently, the distinctive biomechanical signatures of SW Baikal juveniles may reflect the greater diversity of foraging strategies practiced by groups buried in this micro-region, though this requires further study.

4.6. Intra-archaeological period changes in developmental stress and behavior

Given the close relationship between body size and CSG, the trends for reductions in age-standardized TA, CA, and J in individuals with more recent radiocarbon dates suggest that body size decreased throughout both the EN and LN (Fig. 8; Table 6). Thus, developmental stress may have fluctuated cyclically throughout the Middle Holocene. If, as discussed above, depletion of terrestrial game occurred throughout the EN, the decline in body size in this period may again reflect increasingly frequent seasonal resource shortfalls. As the LN shows similar patterning, it is reasonable to speculate that scarcity of terrestrial game was also a growing problem throughout this period (Fig. 8; Table 6). Supporting this, isotopic evidence suggests increasing reliance on aquatic resources throughout the LN in this region, just as in the EN (Weber, submitted). Whether this reflects resource depletion due to population pressure or natural fluctuations in abundance, which can be considerable in boreal forests, remains unclear (Kelly, 1995). Regressions of body size standardized TA, CA, and J on radiocarbon are

not statistically significant for most variables. As size-standardization should at least partly control for body mass, this supports the hypothesis that negative trends in age standardized TA, CA, and J reflect intra-archaeological period changes in body size. It is unclear why EN individuals still show a significant negative trend in body size standardized humerus variable. It may be an artifact of reduced sample size, or it represents a real decrease in upper limb loading.

Trends in femoral shape suggest potential changes in juveniles' mobility throughout the EN. The increase in femur midshaft I_x/I_y throughout the EN is consistent with increased terrestrial mobility (Fig. 8a; Table 5). Paradoxically, tibia midshaft I_{max}/I_{min} shows the opposite pattern, but the R^2 is much lower, meaning the trend is weaker (Fig. 8b). Furthermore, prior studies have demonstrated a closer link between femoral midshaft shape and terrestrial mobility than tibia midshaft shape (Holt, 2003; Stock, 2006). Interestingly, the patterning in EN femoral shape would conform to expectations that depletion of local resources lead to greater distance traveled during residential moves or foraging trips throughout the EN. Lastly, humerus I_x/I_y shows a negative relationship with radiocarbon date in the LN sample, implying the diaphysis becomes more circular with age (Fig. 8c). The mechanical complexity and wide range of manual activities make interpreting this trend difficult. However, it does suggest a behavioral change in the types of upper limb loading engaged in by LN juveniles. Also, as discussed below, it may reflect a higher prevalence of male juveniles in later LN burials.

4.7. Sex differences: adolescent/ young adult females and males

Small sample size complicates evaluation of sex differences in adolescents and young adults. Still, visual inspection of plots tentatively indicates that, by young adulthood, males have stronger and less circular lower limbs and more circular upper limbs than females (Figs. 10, 11; Table 6). However, these differences are incipient; substantial overlap remains between the sexes. This contrasts with prior work on adults of all ages, which showed clearer sexual dimorphism. Adult males from all time periods have stronger upper and lower limbs than females, and males also have less circular lower limbs (Stock et al., 2010; Lieveise et al., 2011; Stock and Macintosh, 2016). Thus, patterns of sexual differences in bone strength characteristic of adults may not have been fully established by the end of young adulthood.

Emerging greater male robusticity may partly reflect hormonal differences, as testosterone appears to heighten the periosteum's sensitivity to loading, and it upregulates both body and muscle size (Orwoll, 2003; Ruff, 2003). Behaviorally driven differentiation is also likely. Meta-analyses of ethnography indicate that, by late adolescence, many hunter-gatherer males may begin devoting substantial time and effort to big game hunting (Koster et al., 2019; Lew-Levy et al., 2017; MacDonald, 2007). Prior work on Cis-Baikal adults suggest that logistic hunting forays contributed to greater body-size-standardized CSG and the less circular diaphyses of males, because they required long distance travel and carrying heavy loads to and from camp (Lieveise et al., 2011; Stock and Macintosh, 2016). Upper limb shape has not been previously analyzed in Cis-Baikal adults. However, the same sexual dimorphic pattern in humerus shape has been noted in other hunter-gatherer populations (Cameron et al., 2018; Stock and Pfeiffer, 2004). These studies interpreted less circular upper limbs in females as indicative of greater involvement in tasks such as hide processing and butchery, which involve uneven distribution of strains within the diaphysis. The fact that upper limb shape shows sexual dimorphism also has implications for interpreting the negative correlation between humerus I_x/I_y and radiocarbon date in the LN juveniles younger than 16.0 years. Rather than reflecting a change in juvenile behavior, this trend may potentially reflect the presence of more male juveniles in later LN burials.

Significantly, few sexual differences are statistically significant, and visual comparison shows considerable overlap (Figs. 10, 11; Tables 7,

8). While this may reflect small sample size, it may also indicate that sexual differences have not been fully established. Ethnographic studies suggest that adolescents/ young adults do not allocate their foraging time in the same way as older adults (Lew-Levy et al., 2017; Sugiyama and Chacon, 2005). Although hunting time increases, young males, in particular, still devote more time to other foraging behaviors (e.g. fishing, gathering) than older adults, because achieving high proficiency in hunting takes many years (Koster et al., 2019). For this reason, the heavy overlap between female and male adolescents/ young adults may partly reflect that sexual differences in behavior have not been fully established.

5. Conclusion

Overall, this study of growth and development in CSG suggests complex chronological and regional variation in developmental stress and juvenile behavior among Middle Holocene Cis-Baikal hunter-gatherers. Evidence from CSG supports a decline in developmental stress from the EN to the LN, which is consistent with prior studies. However, developmental stress also appears to have increased within both archaeological periods. Furthermore, skeletal evidence of adaptation to higher habitual loading and terrestrial mobility among EN populations emerges after the sixth year of life, and this is consistent with prior studies indicating greater skeletal robusticity and higher terrestrial mobility in EN adults. Changes in developmental stress and behavior between archaeological periods may reflect that depletion of terrestrial game stocks increased the risk of seasonal resource shortfalls among EN groups. Thus, entire EN groups or caregiving adults may have had to travel farther to access resources. As past studies suggest that EN groups appear to have depended more on aquatic resources, patterning in upper limb robusticity is consistent with greater involvement in fishing by EN juveniles. Intra-archaeological period trends may reflect changes in developmental stress and foraging behavior due to reductions in resource abundance during both the EN and the LN. Within the EN, the Angara micro-region sample may have had the lowest body size for age, and EN Southwest Baikal juveniles exhibit signs of greater terrestrial mobility. This tentatively suggests geographic variation in health and foraging strategies within the EN, potentially due to differences in population size and environment. By the end of adolescence, differences in limb robusticity and shape may indicate incipient sexual dimorphism in mobility, workloads, and upper limb use, though small sample size makes these interpretations tentative. Future studies can evaluate intra-archaeological period trends in adult robusticity as has been done here with juveniles, and they can also expand the analysis to adults from the EBA and other micro-regions. Future work can also compare the Middle Holocene patterning to that seen in juvenile hunter-gatherers from other ecogeographic contexts.

Declarations of Competing Interest

The authors declare that they have no conflicts of interest.

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CRediT authorship contribution statement

B. Osipov: Conceptualization, Methodology. **L. Harrington:** Supervision, Conceptualization. **D. Temple:** Conceptualization. **A.W. Weber:** Conceptualization.

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