#### The Ontogeny of Postcranial Robusticity and Shape in Middle Holocene Cis-Baikal Hunter-Gatherer Populations

by

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#### Abstract

This dissertation investigates changes in bone robusticity and shape from birth to young adulthood in Middle Holocene (~7,500- 3,700 years cal BP) Cis-Baikal hunter-gatherer populations. First, how biomechanical properties change with age throughout the upper and lower limb is evaluated. Second, the study uses bone robusticity and shape to examine chronological and inter-cemetery variation in the genetics, health, and behavior of Cis-Baikal juveniles.

Robusticity and shape are quantified throughout the appendicular skeleton using crosssectional geometry. Inter-limb robusticity ratios, and asymmetry in upper limb robusticity and shape are also analyzed. Ontogenetic patterning is evaluated using visual analysis, curve-fitting, and statistical comparisons. Statistical tests and visual analysis are used to detect differences between individuals from different archaeological periods and cemeteries, as well as the age at which these differences emerged.

Analysis of general developmental patterns highlights the interacting influences of body mass, activity levels, and hormones on age-related change in external and internal bone dimensions as well as robusticity. Lower limb shape and interlimb robusticity ratios track adaptation of the lower limb to changes in body shape, bipedal locomotion, and weight bearing. Upper limb shape development is consistent with adaptation to multi-axial bending and torsion, but there are regional differences. These likely reflect heterogeneity in range of motion and the localized influence of specific muscles and ligaments. Analysis of asymmetry development shows that right dominance emerges earlier in the humerus than the clavicle or ulna, indicating that this element is most sensitive to side differences in mechanical loading. Comparisons of individuals from different archaeological periods and cemeteries find little evidence for differentiation attributable to genetic variation prior to the age of 16 years. Differences in size-unstandardized robusticity, body mass estimates, and interlimb robusticity ratios indicate Late Neolithic individuals had higher body masses than Early Neolithic juveniles from shortly after birth, suggesting the former group experienced less developmental stress. The study also indicates geographic variation in developmental stress during the Early Neolithic. Juveniles buried at Lokomotiv appear to have had lower body masses for age than contemporaneous Shamanka juveniles.

Although body mass differences complicate behavioral comparisons, Early Neolithic juveniles appear to have been more mobile and placed higher loads on their upper limb than Late Neolithic juveniles after the age of six years. Higher Early Neolithic juvenile mobility may reflect the depletion of terrestrial resources by more densely concentrated populations. Alternatively, mobility may have declined in the Late Neolithic due to a greater abundance or more homogeneous distribution of terrestrial game. The development of stronger upper limbs in the Early Neolithic is consistent with juveniles being more involved in fishing or other forms of specialized labor. The former appears especially likely given strong evidence for greater dependence on aquatic resources during this period. The greater differentiation of Early Neolithic Shamanka than Lokomotiv from Late Neolithic Ust-Ida reflects either small Lokomotiv sample size or the unique foraging strategies of Shamanka groups.

Sexual dimorphism in bone robusticity and limb shape appears to have been established in all archaeological periods by the end of adolescence. Strength differences may partly result from the effect of sex hormones on bone accrual. However, differences in workloads and mobility levels are also consistent with the sexual division of labor. Lastly, chronological change in behavior appears more pronounced among females than males. This is consistent with the results of prior studies, which hypothesize that female subsistence behavior changed more throughout the Middle Holocene. Overall, analysis of Cis-Baikal juveniles demonstrates that bone robusticity and shape undergo significant changes during development that reflect variation in mechanical environment throughout the body. Changes in robusticity and shape between archaeological period are consistent with variation in juvenile health, mobility levels, and economic roles.

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#### **Chapter 1: Introduction**

The goal of this project is to analyze the ontogeny of long bone robusticity in Middle Holocene Cis-Baikal hunter-gatherer populations. This will provide an important new line of evidence for quantifying and understanding variation in behavior, developmental stress, and genetic variation in these hunter-gatherer groups. To introduce the topic this section briefly introduces the concept of long bone robusticity and the importance of studying how this aspect of skeletal biology develops. It then outlines why considering this property of skeletal elements can improve understanding of Middle-Holocene Cis-Baikal prehistory. I conclude by laying out the questions that will guide my research.

Studies of bone robusticity can provide a wealth of information about behavior, body size, and genetic differences in past populations (Pearson and Lieberman, 2004; Ruff et al., 2006; Ruff et al., 2008). In biological anthropology, the term robusticity refers to the strengthening of a skeletal element through the addition of bony tissue perpendicular to the long axis of the element (Ruff and Hayes, 1983a; Ruff, 1994; Stock, 2006). Throughout life, long bones alter their shape and size in response to mechanical stimuli produced as the body interacts with its external environment. Importantly, mechanical stimulation generates a localized reaction, meaning that different habitual activities, behaviors repeated throughout life, can produce different patterns of bone robusticity. Thus, it has been well established that a relationship exists between long bone strength and the intensity and types of mechanical loading experienced during an individual's lifetime (Ruff and Hayes, 1983a; Ruff et al., 2006; Stock, 2006). Consequently, many biomechanical studies of past populations have utilized bone robusticity and shape as an indicator of habitual behavior patterns and activity levels.

While most studies have utilized robusticity and shape to reconstruct behavior, other studies have emphasized that robusticity and shape have a multi-factorial etiology. For this reason, analysis of diaphyseal morphology also offers a window into the diet, disease load, and genetic history of past populations (Ruff et al., 1999; Ruff et al., 2006a; Agarwal, 2008; Cowgill, 2010; Wallace et al., 2010; Duren et al., 2013). Diet and diseases load control rates of bone deposition and resorption throughout life (Garn et al., 1970; Ruff et al., 1999; Kodama et al.,

2000; Agarwal, 2008). As one of the skeleton's primary functions is to support the weight of the body, health related changes in body mass may have a particularly marked effect on bone robusticity development (Cowgill, 2010). Additionally, genetic selection for either robust or gracile skeletal elements could have occurred over many generations, either by chance or as adaptation to differences in activity levels (Churchill, 1999; Wallace et al., 2010; Roseman and Auerbach, 2015). Genetic selection for different body shapes in response to climate also affect bone shape and size (Ruff, 1994; Holliday, 1997; Ruff et al., 2006b; Roseman and Auerbach, 2015). Indeed, variation in CSG has been shown to display eco-geographic patterning in both modern and prehistoric populations indicative of adaptation to both climate and activity levels (Pearson, 2000; Stock, 2006).

Bone robusticity can convey a wealth of information about how past populations interacted with their environment. This project focuses on how bone robusticity develops from birth to young adulthood, because the extent to which bone alters in response to external stimuli varies throughout life. Most studies have measured the robusticity of adult bones, but patterns of bone strength develop primarily during the juvenile period. While bone responds to genetic signals and changes in its mechanical environment and individual health throughout life, adulthood can be characterized as a period of homeostasis followed by senescence (Pearson and Lieberman, 2004; Ruff et al., 2006). Bone cells primarily act to maintain the existing form of skeletal elements, and, with increasing age, reductions in bone replacement lead to pronounced bone loss (Ruff and Hayes, 1983b). Bones change shape and increase in size most dramatically prior to skeletal maturity. During this period, the rate of bone deposition responds readily to mechanical loading (Ruff et al., 1994; Pearson and Lieberman, 2004). Furthermore, insufficiencies in diet, the experience of illness, and genetic differences can alter the rate and manner of bone accrual (Garn et al., 1970; Cowgill, 2010; Wallace et al., 2010). Genetic variation may also influence bone forming cells to track towards different adult endpoints for shape and size.

This project will focus on bone robusticity ontogeny in Middle Holocene Cis-Baikal hunter-gatherers. Burials date to 8277 +/- 176 to 3726 +/- 34 calibrated years before present (Weber et al., 2015). It has been well established that these populations exploited both aquatic and terrestrial animals, and that subsistence behavior varied regionally as well as over time

(Weber et al., 2011; Weber and Bettinger, 2010). Mortuary traditions also show variation that indicates cultural change throughout the Middle Holocene (Weber et al., 2002; Weber and Bettinger, 2010). Little is known, however, about how children contributed to subsistence in these populations or at what age they began to practice adult foraging behaviors. Both factors would have had an important effect on social structure and how behavior was transmitted across generations (Hewlett and Lamb, 2005; Ruff, 2008). Previous skeletal studies by the Baikal-Hokkaido Archaeology Project have demonstrated the existence of chronological change as well as geographic differences in genetics, behavior, and health (Weber and Bettinger, 2010). Given the relationship between robusticity, behavior, and health, considering growth from a biomechanical perspective can improve understanding of how these differences manifested with age. Studying the ontogeny of long bone robusticity, how skeletal elements achieved their adult form, may produce insights into how children behaved in these populations. It may also add a unique perspective on child health. This would complement previous studies based on other lines of data, including skeletal stress markers, variations in longitudinal growth, and dietary evidence gleaned from analysis of faunal remains and stable isotope signatures. This project will also interpret temporal and regional variation in Cis-Baikal juvenile CSG with reference to ethnographic studies of child foraging. These consider how age-specific physical and mental constraints shape juvenile behavior in specific environmental contexts (e.g. Jones et al., 1994; Hawkes et al., 1995; Bliege Bird and Bird, 2002a,b; Hewlett and Lamb, 2005 and references therein; Guerven and Kaplan, 2006).

This dissertation project also has wider relevance, because biomechanical analyses of juveniles constitute a still relatively small but growing subfield in biological anthropology and bioarchaeology. Increased ethnographic awareness of how varied child contributions to subsistence are in modern hunter-gatherer groups highlights the importance of considering behavioral diversity in the past (Hewlett and Lamb, 2005). Preliminary comparisons of bone strength development between populations suggest that population differences in health, genetics, and behavior interact to produce distinct ontogenetic patterns (Cowgill, 2010). This conclusion is based on limited research, and additional analytical methods can be brought to bear on this question. Thus, this research has the potential to generate findings relevant to the archaeology of the Middle Holocene Cis-Baikal. It also sets the stage for contributions to the larger research question of how and why skeletal robusticity varies prior to adulthood.

The above outlined project will consider the following research questions:

1. What is the pattern of age-related variation in bone strength among Cis-Baikal populations?

2. Do the patterns detected correlate with evidence for chronological or regional variation in the genetic makeup, subsistence behavior, diet, and health among populations in this region?

#### **1.1 Structure of Dissertation**

Chapter 2 explores previous research into skeletal biomechanics and the importance of studying bone strength ontogeny in past populations. Chapter 3 describes prior archaeological research pertaining to the Middle Holocene period of the Cis-Baikal region. This involves summarizing the chronology of human settlement during this period, what is known about the environment, and past studies of behavioral change and variation in developmental health during the Middle Holocene. Chapter 4 describes the methods I will employ to gather and analyze my data. Results are presented in three chapters sorted by variable type: Body size standardized and size-unstandardized measures of bone size and strength (Chapter 5), bone shape (Chapter 6), and interlimb robusticity ratios (Chapter 7). Subsequently, the discussion is divided into two chapters. Chapter 8 considers general ontogenetic trends and the extent to which behavior, body size, genetics, and hormones affect the growth process. Chapter 9 presents bioarchaeological interpretations of the data, considering both chronological and regional variation in behavior, developmental stress, and genetics. Chapter 10 summarizes the main findings and explores potentials for future research.

# **Chapter 2: Biomechanical Analyses of Bone: Basic Principles and Ontogenetic Perspectives**

#### **2.1 Bone Functional Adaptation**

The need to withstand the forces generated during the performance of everyday tasks is an important but not the only determinant of skeletal robusticity. Adaptation to mechanical loading occurs throughout an individual's lifetime, but the skeleton exhibits the greatest sensitivity to mechanical loading during ontogeny, the period during which an organism establishes its adult form (Ruff et al., 1994; Pearson and Lieberman, 2004; Ruff et al., 2006a). This chapter investigates the determinants of bone robusticity accrual during ontogeny. First, the dominant models for how bone responds to mechanical stimulus are described, emphasizing the multiplicity of factors that modulate bone's response to loading during the juvenile period. Genetics and health influence the development of skeletal form, making it necessary to explore how these factors can modulate the accrual of bone robusticity in response to loading. To conclude, the chapter undertakes a general overview of how current understanding of skeletal biomechanics has been applied to bioarchaeological studies of past populations, especially regarding immature individuals.

The skeletal response to mechanical loading has been a long-running focus of biological and anthropological research. Originally formulated in the late 1800s, "Wolff's law" proposed that bone responded to mechanical stimuli in a mathematically predictable fashion (Frost, 2003; Ruff, 2006a). Subsequent studies supported the existence of a functional response to mechanical stimulation, but they failed to detect a strict mathematical relationship between loading and bone accrual and resorption (Bertram and Schwartz, 1991; Frost, 1987; Frost, 1994; Frost, 1996; Frost, 2003; Pearson and Lieberman, 2004; Ruff et al., 2006a). Research beginning in the latter half of the 20<sup>th</sup> century has fostered a greater appreciation of the role nutrition, disease, hormone concentrations, and genetics in modulating the processes of bone accrual and maintenance throughout life (Garn et al., 1969; Frisancho et al., 1970; Lanyon, 1992; Lovejoy et al., 2003; Pearson and Lieberman, 2004; Ruff et al., 2006a; Agarwal, 2008; Duren et al., 2013). Consequently, while bone clearly adapts to its mechanical environment throughout life, the nature of this adaptation proves predictable only in the general sense, and bone size and shape have a multi-factorial etiology (Ruff et al., 2006a). To reflect the fact that mechanical stimulus is

just one of several determinants of bone morphology, current studies of bone's response to mechanical loading eschew "Wolff's Law" in favor of "bone functional adaptation" (Ruff et al., 2006a).

The following discussion of bone functional adaptation focuses on Cross-Sectional Geometry (CSG). This term specifically describes the amount and distribution of cortical bone within a two-dimensional cross-section perpendicular to a bone's long axis. Thus, it accounts for both cross-section size and shape. Biomechanical theory also recognizes that bone's material structure plays a role in preventing mechanical failure (Pearson and Lieberman, 2004; Ruff, 2008; Gabel et al., 2017). While loading does induce alterations in bone density and other material properties, biologists, paleontologists, and bioarchaeologists focus on cross-sectional geometry for several reasons (Burrows, 2007). Firstly, diagenic processes can degrade bone after death, making material analysis difficult (Ruff, 2008). Secondly, it has been experimentally demonstrated that bone predominantly responds to mechanical stimuli by altering its geometry. Indeed, comparative analysis of a wide range of species indicates that material properties appear to have been highly conserved over the course of vertebrate evolution (Erickson et al., 2002; Ruff, 2008). Most importantly, the deposition of additional bone and changes in shape will have a greater effect on bone's mechanical competence than alteration of the material itself (Trinkaus et al., 1994; Duncan et al., 2001; Robling et al., 2002; Kontulainen et al., 2002; Warden et al., 2005). Consequently, geometric properties are easier to measure and should vary more in response to different levels of mechanical stimulation than material properties.

Mechanical stimuli produce changes in bone robusticity in the following way. Loading of the skeleton by the weight of the body and muscle contractions generates force. The application of force produces deformation of bony tissue known as strain (Biewener, 1992). Excessive strain would result in material failure. To prevent this, bone possesses a genetically encoded feedback mechanism capable of perceiving localized strain and adjusting CSG, its size and shape. This keeps strain well below the yield point, the strain threshold above which permanent deformation occurs (Biewener, 1992; Carter and Beaupre, 2001; Pearson and Lieberman, 2004). Therefore, the skeleton does not habitually operate close to its yield point, because the adaptive response appears to incorporate a "safety factor," overbuilding the diaphysis so that habitually applied strains remain well below the yield point (Biewener, 1992; Pearson and Lieberman, 2004). As a

result, mechanical loading, even during intense physical activity, engenders elastic strain, a temporary deformation that the structure recovers from and resumes its original configuration (Biewener, 1992; Pearson and Lieberman, 2004). Heightened levels of elastic strain result in CSG changes that ensure strain remains safely below the yield point. Thus, the strength of an element does not directly measure the force placed on the skeleton during life. One can only infer that more robust elements habitually experienced relatively greater loads than more gracile ones. The exact mechanisms by which bone measures strain levels remains unclear. Strain perception may involve the physical deformation of processes extending from osteocytes, alterations in intercellular fluid flow, the generation of electrical charge, or the accumulation of micro-cracks through repeated loading (Lanyon, 1992; Pearson and Lieberman, 2004). These mechanisms may act alone or in concert to elicit an osteological response when strain magnitude exceeds a threshold value (Zernicke et al., 2006).

Lanyon (1982) describes a simple feedback model of how mechanical stimuli lead to changes in bone robusticity. A diagram illustrating this model is provided in Figure 2.1.1. As a bone experiences changes in the manner and intensity of use, bone cells respond to keep local strains within an "optimal customary strain level," ensuring strain magnitudes remain well below the yield point at which mechanical failure occurs. More bone will be laid down in response to increased strain. If strain is applied along a specific plane or axis, the diaphysis will predominantly undergo reinforcement along this axis. Greater deposition of bone along axes experiencing higher strains will ultimately induce changes in the transverse shape of the long bone diaphysis or shaft. Conversely, when activity becomes less strenuous, strain falls below the optimal customary level, triggering cortical bone resorption. Osteoblasts, bone forming cells, and osteoclasts, bone resorbing cells, bring about these changes through the processes of modeling and remodeling. Modeling, or deposition of new bone at the periosteal periphery of a bone, occurs primarily in immature skeletal elements (Frost, 1987). Through this process changes in the rate of bone deposition and "modeling drifts," initiated by alterations in strain levels can produce dramatic alterations of cross-sectional size, shape, and cortical thickness (Frost, 1987, 2003). In organisms of any age, bone will also undergo remodeling. This process allows for repair and alterations throughout life, as osteoblasts and osteoclasts work in concert to remove old material and replace it with new bone. During this process, groups of osteoblasts and osteoclasts, referred to as Basic Multicellular Units (BMUs) work in concert to replace bone

(Frost, 1987). Normally this process results in a net loss of bone. However, increased mechanical stimulus can also signal BMUs to increase the activity of osteoblasts relative to osteoclasts (Frost, 1987, 1996). This will reduce the amount of bone lost during remodeling, and it may potentially lead to small amounts of bone accrual (Frost, 1987).



Frost's (1987, 1996, 2003) "mechanostat" model provides a more nuanced understanding of bone functional adaptation, accounting for genetic, hormonal, dietary, and disease related influences on bone's response to mechanical stimulus. A schematic illustrating this model is given in Figure 2.1.2. Like Lanyon's model, the mechanostat postulates the existence of a feedback loop between mechanical stimulus and bone strength that alters bone geometry, size and shape, to keep strain within a certain range. The mechanostat consists of multiple biochemical pathways and signalling mechanisms. These gather and transmit information about the loading environment. When strain levels either exceed or fall below a certain threshold value, the "setpoint," the mechanostat propagates effector signals that either promote or inhibit the activity of cells responsible for cortical bone deposition and resorption (Frost, 1987, 1996, 2003; Rauch and Schoenau, 2001). The mechanostat most notably expands on Lanyon's model by explicitly incorporating non-mechanical factors such as hormone levels, nutrition, disease, and genetics into the feedback loop. These factors act upon the sensitivity of the mechanostat to mechanical stimuli. For example, they can lower or raise the strain thresholds above or below which a response occurs. These non-mechanical factors may further control the process of bone functional adaptation by directly regulating the activity/ number of osteoblasts and osteoclasts. Note that, in the mechanostat model, mechanical loading remains the main driver of increases or

decrease in bone robusticity; other factors merely modulate the extent of the response (Rauch and Schoenau, 2001).



Figure 2.1.2: Mechanostat model of bone functional adaptation (Adapted from Schoenau, 2005)

Both the Lanyon feedback model and Frost's mechanostat model identify strain magnitude as the signal generated by loading responsible for functional adaptation (Lanyon, 1982; Frost, 1987, 1996). However, several other authors have noted that both the duration and rate of strain, as well as alterations in strain distribution during exercise bouts, likely also influence the extent and nature of bone's response to mechanical stimulus (Rubin and Lanyon, 1984; Lanyon, 1992; Duncan and Turner, 1995; Forwood and Turner, 1995; Lanyon and Skerry, 2001; Pearson and Lieberman, 2004; Shaw and Stock, 2009a; Judex and Carlson, 2009). Consequently, high intensity activity does not necessarily have more osteogenic potential than more sustained or mechanically heterogeneous behavior that engenders lower strain magnitudes.

Studies of humans and animals confirm that alterations in mechanical strain produce changes in skeletal robusticity (Rubin and Lanyon, 1984; Lanyon, 1992; Forwood and Turner, 1995; Lieberman et al, 2001; Warden et al, 2005; Shaw and Stock, 2009a, b). Studies of upper limb asymmetry provide the classic example. Humeral asymmetry is dramatically more pronounced among modern human tennis players and Upper Paleolithic *H. sapiens* and Neanderthals than in non-tennis playing modern humans and most archaeological populations (Trinkaus et al., 1994; Haapsalo et al., 1996). Studying paired humeri controls for interindividual differences in diet, genetics, and health. It also accounts for the possibility that changes reflect a generalized response to high activity throughout the skeleton. Therefore, high bilateral asymmetry in Upper Paleolithic humans and tennis players most likely reflects adaptation of the dominant limb to more intense loading.

Comparisons of athletes playing different sports to each other and controls that do not regularly engage in strenuous exercise further demonstrate that differences in activity can be discerned from bone size and shape. Furthermore, the effects of behavioral differences are confined to the regions of the skeleton where mechanical loading differs. Shaw and Stock (2009a) found that cross-country runners and field hockey players exhibited significantly more robust lower limbs than non-athletic controls. In addition, the lower limb bone shape of crosscountry runners differed from that of hockey players. The shape difference reflects that the leg bones of runners are strengthened along the anteroposterior axis, which experiences the heaviest loads during unidirectional movement, *i.e.* running with only occasional changes of direction. Field hockey player lower limb elements appeared more symmetrically reinforced, as would occur when movement is multi-directional. Additional studies of lower limb robusticity also detected differences between different groups of athletes in lower limb strength, and the degree of differentiation between groups correlated with the differences in weight-bearing engendered by the activity (Duncan et al., 2001 Rantalainen et al., 2010; Niinimäki et al., 2016). Similarly, study of the upper limb found differences in strength and shape between controls and athletes placing higher loads on their upper limb (Shaw and Stock, 2009b; Nikander et al., 2006; Warden et al., 2009). Importantly, the above studies specifically demonstrate specifically that broad differences in load magnitude or movement type can be discerned from comparisons of CSG. It remains unclear if reconstructions of mechanical environment from bone robusticity can discern fine gradations in activity levels (Cowgill, 2014a). However, the fact that exercise interventions of significantly lower intensity than characteristic of professional athletes can produce changes in CSG would suggest that they can (Bradney et al., 1998; MacKelvie et al., 2003, 2004; Burrows, 2007).

Decreases in activity levels also conform to the expectations of bone functional adaptation. Animals with paralyzed or immobilized limbs exhibit declines in the bone mass and strength of the affected elements (Bertram and Swartz, 1991; Ruff et al., 2006a). Likewise, clinical literature and paleopathological studies indicate that long periods of bed rest or immobilization result in bone loss (Trinkaus et al., 1994; Frost, 1996). However, all these studies deal with the complete or almost total removal of loads. In many of these cases, changes in hormone levels and nutrition associated with illness could also have influenced results. Whether reduction in strain intensity or frequency of loading can also lead to resorption has not been adequately explored. Cortical thinning does occur naturally in old age, with osteoporosis representing the most extreme manifestation of this natural tendency (Lanyon and Skerry, 2001; Santos et al., 2017). While osteoporosis related thinning primarily results from oxidative stress and reduction in estrogen concentrations, several researchers have noted that increases in activity during old age act to slow or halt this natural tendency (Lanyon and Skerry, 2001; Ruff et al., 2006a; Santos et al., 2017). Indeed, it has been suggested that the greater robusticity of older individuals from past populations compared to modern older adults may partly reflect the continued placement of greater loads on the skeleton due to participation in foraging and other activities (Ruff and Hayes, 1983a,b; Ruff et al., 2006a; Bradney, 2007). This maintains bone robusticity into old age. Reduced activity among the elderly in modern populations may thus magnify the natural tendency for the skeleton to lose bony tissue with age. Thus, while theoretical models of bone functional adaptation predict declines in bone strength due to reduced loading, little is known about how this process would affect healthy individuals prior to the late portion of the life course.

## **2.2** The Ontogeny of Bone Robusticity: Age Related Variation in Bone's Response to Loading

Bone's sensitivity to loading varies throughout life, with adulthood being primarily a time of homeostasis followed by senescence (Pearson and Lieberman, 2004; Ruff, 2006a). While bone responds to mechanical stimulus throughout life, the rate of new bone formation diminishes throughout adulthood, and, during older adulthood, net bone loss occurs (Ruff and Hayes, 1983b; Seeman, 2003; Santos et al., 2017). Bone primarily accrues material and strength during ontogeny, the period in which it develops its adult size and shape. Mechanical stimuli during this period markedly accelerates the rate of bone deposition, and bone accrues in a manner that maximizes its contribution to skeletal strength (Frost, 1987, 2013; Ruff et al., 1994; Carter and Beaupre, 2001; Lieberman et al., 2001; Pearson and Lieberman, 2004; Burrows, 2007). Development in different mechanical environments can therefore greatly alter the rate and manner of bone accrual. Due to physiological and hormonal changes, the ability for mechanical stimulus to produce increases in bone robusticity markedly declines after individuals reach

physical maturity. As a result, differences in adult levels of robusticity largely reflect functional adaptation during the developmental period (Pearson and Lieberman, 2004; Ruff et al., 2006a; Bradney, 2007). The following section examines age-related changes in bone's response to loading, focusing on the reasons that skeletal morphology undergoes the greatest functional adaptation prior to maturity.

The juvenile skeleton manifests a more effective response to loading than the adult skeleton for several reasons. Firstly, juvenile mammals have more osteoblasts, osteoclasts, and the osteoprogenitor cells that produce these cells than adults; these cells also exhibit greater sensitivity to loading (Duncan and Turner, 1995; Pearson and Lieberman, 2004; Kish et al., 2015). As a result, an equivalent level of loading will lead to the deposition of more bone in juveniles than adults. Greater gains in robusticity during the juvenile period also reflect age related changes in where within the diaphysis bone deposition occurs. Multiple studies of bone accrual have demonstrated that, prior to mid-adolescence, bone primarily responds to loading by adding material on the outer, sub-periosteal surface or "periosteal envelope" (Garn et al., 1970; Frisancho et al., 1970; Ruff et al., 1994; Goldman et al., 2009). During this period, the interior surface or "endosteal envelope" of the limb bone cortex exhibits resorption, though increased loading may also reduce the rate of resorption (Ruff et al., 1994; Pearson and Lieberman, 2004). In late adolescence the sensitivity of the sub-periosteal envelope to loading begins to gradually decrease. At the same time, the endosteal envelope gradually transitions from a state of bone resorption to bone deposition (Garn, 1970; Frisancho et al., 1970; Ruff et al., 1994). Consequently, increases in mechanical loading after mid-adolescence will engender deposition predominantly at the internal surface, and this effect becomes more pronounced with age. The amount of bone deposited on the periosteal surface in response to loading will also gradually decrease after mid-adolescence. This is important, because bone cross-sections gain more strength from material deposited farther from the center (Ruff et al., 1994; Pearson and Lieberman, 2004; Ruff, 2008; Sparacello and Pearson, 2010; Davies et al., 2012). This reflects how the contribution of material to cross-sectional strength increases with the square of the distance to the section's center (Sparacello and Pearson, 2010). Thus, once the endosteal envelope becomes the primary site of bone deposition, changes in mechanical repertoire will have a reduced effect on bone robusticity.

As increases in periosteal diameter increase strength more than bone formation on the endosteal surface, it is important to understand that the change with age in the sensitivity of the periosteal and endosteal envelopes largely reflect hormonal influences. In the context of the mechanostat, one can attribute this to several potential interactions between hormones and the signalling pathways controlling bone functional adaptation. Hormones may alter the strain threshold above or below which bone is added or removed. Alternatively, they may attenuate the activity of bone forming and resorbing cells (Frost, 1987). Age related changes in the sensitivity of the periosteum to loading appears to mirror the longitudinal growth of the skeleton, even demonstrating a growth spurt in adolescence (Ruff et al., 1994; Ruff et al., 2003 a,b). This relationship has been used to imply that growth hormone concentrations play a significant role in determining the sensitivity of the periosteal surface to loading (Ruff et al., 1994). The response of the endosteal surface to loading correlates with sex hormone concentrations. Estrogen appears to stimulate endosteal deposition by lowering the threshold above which mechanical strain will stimulate bone deposition at this surface. Fetal development supports this hypothesis. The fetus is exposed to high placental estrogen levels. As a result, bone is deposited on the endosteal surface prior to birth, and the marrow cavity of fetuses and newborns tends to be smaller than that of slightly older children (Rauch and Schoenau, 2001). After birth, when sex hormone concentrations are low, the endosteal surface exhibits resorption. Beginning in mid-adolescence, estrogen levels increase, and this leads to endosteal apposition (Frisancho et al., 1970; Ruff et al., 1994; Goldman, 2009). Testosterone, in contrast, appears to maintain the sensitivity of the periosteal envelope in males for several years longer than in females. Importantly, the importance of hormones in modulating bone's response to loading suggests that older childhood and adolescence constitute an "optimal window" for bone accrual (Carter and Beaupre, 2001; Bass et al., 2002; Pearson and Lieberman, 2004). High levels of both growth hormone and sex hormones, as well as the greater sensitivity of juvenile bone cells to loading, make the skeleton extremely responsive to mechanical stimulus during this period.

Importantly, the "juvenile period" in which bone exhibits a heightened response to loading extends beyond the age range in which growth in bone length occurs. The sensitivity of bone cells and the periosteal surface to mechanical loading declines gradually after midadolescence (Ruff et al., 2006a). Thus, the skeleton will show a heightened response to strain for some time after growth in stature has ceased, at least into the mid-20s (Bertram and Swartz, 1991; Ruff et al., 2006a). The prolongation of juvenile like growth into the third decade has considerable benefits. Body mass and muscle size, the primary generators of mechanical strain, increase considerably during late adolescence and young adulthood as the body "fills out" (Ruff et al., 1994; Ruff, 2003a,b; Ruff et al., 2013). Consequently, late adolescence/young adulthood constitutes an important target for investigations of bone functional adaptation during ontogeny, particularly among males, who grow longer than females and continue to accrue significant amounts of muscle in this period (Ruff, 2003a,b; Ruff et al., 2006a). The exact endpoint of the ontogenetic period for bone robusticity remains unclear, and bone may lose different features of the precocious juvenile response to loading at different ages. For example, the number of osteoprogenitor cells and osteoblasts may begin to decline after ten years, but juvenile-like deposition of new bone on the periosteal surface will continue into adolescence (Nishida et al., 1999; Gabel et al., 2015). Still, by middle adulthood, bone cells respond less to loading, and mechanical loading will primarily lead to bone deposition on the endosteal bone surface.

Figure 2.2.1 demonstrates how different levels of loading during childhood will lead to marked differences in adult levels of robusticity. A high level of loading leads to higher levels of periosteal deposition, and increased strain can also reduce the rate of endosteal resorption (Pearson and Lieberman, 2004). Conversely, a lower level of loading will lead to more gradual accrual of bone at the sub-periosteal surface and higher levels of resorption at the endosteal envelope. This produces a less externally expanded diaphysis than seen in more active juveniles, and the cross-section also contains less bone internally. High levels of loading in adulthood cannot compensate for this, as loading engenders less of a response, and bone will primarily be added internally. This imparts less strength then deposition of new bone further from the center of the section.

Figure 2.2.1: Effects of high and low levels of loading during childhood on adult limb robusticity (modified from Ruff et al., 1994).



Experimental evidence confirms the heightened response of juvenile bone to strain. When subjected to equivalent exercise regimens, juvenile pigs and rats showed increases in crosssection size and strength, but adults did not (Steinberg and Trueta, 1981; Lieberman et al., 2001). Strain magnitudes engendered by activity do not vary between juvenile and adult animals, so this difference reflects age related variation in the response to mechanical environments (Carter and Beaupré, 2001). Many clinical studies have also examined how children's bones respond to changes in mechanical loading. These found that even minor increases in activity levels among children produce gains in bone mineral content, density, and CSG relative to controls (Nordstrom et al., 1996; Bradney et al., 1998; Bass et al., 2002; Burrows, 2007). Adults that experienced high levels of loading in childhood preserve gains in bone strength (Khan et al., 1998). Indeed, individuals that begin exercise regimens earlier in childhood have more robust skeletal elements as adults than those that start later. For example, individuals that started playing racquet sports before puberty exhibited greater asymmetry and stronger playing arms than those that started in late adolescence (Haapsalo et al., 1996; Kountulainen et al., 2002). Thus, individuals who are more active as juveniles will have markedly stronger skeletons as adults.

#### 2.3. Adaptation to Climate and Other Genetic Related Variation

Not all developmental variation in bone strength reflects differences in functional adaptation. At least some aspects of appositional bone growth are genetically canalized. Genetically encoded variation in bone robusticity can stem from either the adaptation of body shape to climate, population level differences in baseline robusticity levels, or genetically modulated differences in bone sensitivity to loading.

Of the genetic factors capable of influencing bone size and shape, climate related variation in morphology has received the most attention in the anthropological literature. Populations in cold climates have undergone genetic selection over many generations for a body type that minimizes heat loss (Ruff, 1994; Holliday, 1997; Roseman and Auerbach, 2015). As a result, these groups exhibit heavier and broader bodies as well as shorter extremities compared to populations that have adapted to warmer climates (Pearson, 2000; Stock, 2006; Davies and Stock, 2014). Greater body size and the higher mediolateral loads generated by a wider body will make cold-adapted populations appear more robust prior to standardization of cross-sectional properties for body size and shape (Pearson, 2000; Stock, 2006; Shaw and Stock, 2011). Higher mediolateral strains may also produce changes in lower limb shape (Weaver, 2003; Ruff, 2006b; Cowgill, 2014b). Most famously, it has been noted that Neanderthals have rounder femoral diaphyses than Pleistocene anatomically modern humans. This has been attributed to their hyperpolar body shape rather than a difference in mobility levels, an interpretation less concordant with other lines of biomechanical and archaeological evidence (Weaver, 2003; Shaw and Stock, 2013 and references therein). Research on skeletal development suggests that climate related differences in limb proportions and body shape first manifest in-utero and persist throughout development (Cowgill et al., 2012). Therefore, biomechanical studies of juveniles must anticipate ecogeographic patterning like that observed in adults.

Other genetically encoded variation may arise from the fact that prehistoric human populations descended from many isolated small founding groups. Indeed, skeletal measurements indicative of differences in body size and shape show correlations with both climate and population structure (Roseman and Auerbach, 2015). It is therefore possible that genetic differences in baseline levels of robusticity or bone mechanosensitivity exist between populations, but the extent of such variation in both modern and prehistoric populations remains unclear (Frost, 2003; Peacock et al., 2005; Ruff, 2006a; Wallace et al., 2010; Duren et al., 2013). Indeed, paleoanthropological studies have postulated a genetic propensity towards greater robusticity irrespective of loading levels as one reason for the greater robusticity of Pliocene and Pleistocene hominins relative to modern *H. sapiens* (*e.g.* Churchill, 1999; Lovejoy et al., 2003).

A similar effect could account for some differentiation between Holocene human populations. Studies of animal models support this possibility. Different strains of mice vary in their baseline robusticity levels and the amount of bone that is laid down in response to equivalent loading regimens (Kodama et al., 2000). Additionally, mouse strains bred from individuals displaying high activity levels are more robust at birth compared to controls (Wallace et al, 2010). This demonstrates that, over many generations, high activity levels can lead to the evolution of greater skeletal robusticity. Whether such selection can occur in a natural population remains an open question.

#### 2.4. Variation Related to Nutrition and Illness

Bioarchaeological analyses must account for the extent that differences in robusticity between groups reflect nutrition and illness. A growing body of literature on CSG has considered the effects of malnutrition and disease on the process of bone deposition and resorption, and these suggest that these factors explain a substantial portion of CSG variation in modern and prehistoric populations (*e.g.* Garn et al., 1969; Agarwal, 2008; Ruff, 2008; Mays, 2009; Cowgill, 2010). Here the discussion specifically deals with the effect of nutritional deficiency, whether this results from poor diet or diseases that lead to nutrient deficits (e.g. diarrhea, parasitic infection). First, the potential for poor health to directly alter bone accrual during growth is discussed. Second, the indirect effect that nutrition and illness have on robusticity due to their effect on body mass is examined.

Several studies indicate that modern and archaeological juveniles experiencing substantial nutritional deficits or chronic illness lose bone during growth (Garn et al., 1969; Himes, 1975; Van Gerven et al., 1985; Mays et al., 2009). Resorption occurs specifically on the endosteal surface, and individuals experiencing severe and prolonged stress may therefore have wider medullary cavities than those that do not (Garn et al., 1969; Agarwal, 2008). Bone resorption benefits an individual experiencing physiological stress by releasing stored minerals into the bloodstream (*e.g.* calcium and phosphate) when, as a result of poor diet or disease, levels of these essential nutrients are low (Agarwal, 2008). As bone further from the center contributes more to bone strength, resorbing bone at the endosteal surface minimizes losses in bone strength (Sparacello and Pearson, 2010). Consequently, biomechanical investigations of nutritionally compromised children and adults show that, even when acute malnutrition or illness lead to endosteal resorption, strength is comparable to that of healthier individuals (Garn et al., 1969; Van Gerven et al., 1985; Ruff, 1999). Indeed, relative to better nourished individuals, their cortices may expand more rapidly to offset the internal loss of cortical tissue (Garn et al., 1969; Van Gerven et al., 1985; Ruff et al., 2013). As material further from the center of a cross-section provides more strength, this allows for a continued increase in robusticity throughout development despite poor nutrition.

It is currently unclear how much of a reduction in calories or nutrient is required to induce endosteal resorption (Lambert et al., 2005). In animal models, reductions on the order of 35% of recommended calorie intake, did not lead to decreases in bone quality, but more severe restriction did (Lambert et al., 2005). Thus, the skeletal gracility of lower body weight individuals and populations may have little to do with alterations in the rate of endosteal resorption, except in extreme cases. Instead diet and disease load may indirectly modulate bone robusticity through the effect that these factors have on body mass. Body mass constitutes the most consistent load applied to the skeleton, and this property will be affected by differences in nutrition, disease load, and genetics (Ruff, 2008; Cowgill, 2010). In an analysis of children radiographed at regular intervals during development, cross-sectional properties show a strong correlation with body mass, explaining at least 80 percent of the variation in juvenile bone strength (Ruff, 2003a). A less massive body experiences lower but proportional strains to those of a larger one under equivalent mechanical loading conditions (Lieberman et al., 2001).

Consequently, if differences in body mass are maintained throughout development, skeletons of less well-nourished individuals would appear more gracile than better nourished ones, because they adapt to support a lower body mass (Cowgill, 2010). Support for this supposition comes from studies of individuals diagnosed as "constitutionally thin," healthy individuals with a genetic predisposition to a low body mass index, and animals on a reduced diet (Lambert et al., 2005; Galusca et al., 2008). These individuals display reduced levels of bone strength compared to well-nourished individuals (Lambert et al., 2005; Galusca et al., 2008). However, this variance disappears once CSG is standardized for differences in body mass. These examples demonstrate the important point that differences in robusticity can, in and of themselves, serve as an indicator of differences in health. Provided activity levels are similar, less well-nourished individuals will appear gracile due to mechanical adaptation to lower body

mass during the ontogenetic period (Cowgill, 2010; Robbins et al., 2010). High levels of physiological stress can also stimulate resorption at the endosteal surface during growth, but exactly how severe or sustained a developmental perturbation must be to bring about such an effect remains unclear.

#### 2.5. Previous Bioarchaeological Studies of Bone Robusticity and Its Ontogeny

Past research on adult skeletal remains has produced important insight into chronological and regional behavioral variation. This section briefly reviews past research in this field, demonstrating the potential for investigations to shed light on the behavior of past populations. Most studies have focused on adults, and these have made significant contributions to understanding variation in the subsistence practices and mobility of past populations. Studies from a developmental perspective have been far more limited, usually comparing populations that practiced different subsistence modes. CSG has seldom been used to explore chronological change in juvenile economic roles or how sexual dimorphism develops during growth. Still, the small number of studies that have been carried out demonstrate that, in addition to offering new behavioral perspectives, analyses of juvenile robusticity can also provide insight into differences in health and genetics.

Bone robusticity has most famously been employed in archaeological studies examining the effects of the adoption of agriculture on behavior and workloads in various regions of the world. In some regions, the transition to agriculture is associated with decreases in both upper and lower limb robusticity, but in others the opposite occurs (Ruff et al., 1984; Bridges, 1989; Bridges et al., 2000; Ruff and Larsen, 2001; Ogilvie, 2005; Ogilvie and Hilton, 2011; Macintosh et al., 2014a; Macintosh et al., 2017). This may reflect how, in some cases, foraging may have been either less or more physically demanding than farming. How adoption of agriculture altered workloads depended on a diverse set of factors including: the type of cultivation practiced, the availability of non-cultivated resources, the technology employed, and changes in demography (Bridges et al., 2000; Ogilvie, 2005; Ogilvie and Hilton, 2011).

While the transition to agriculture engendered regionally heterogeneous changes in workloads, the lower limbs of agricultural populations appear generally more circular than those of preceding forager populations from the same region (Ruff and Larsen, 2014). Such change reflects a general decrease in mobility concurrent with the adoption of agriculture. Bipedal
locomotion places greater anteroposterior loads on the lower limb. As a result, foragers, which habitually traveled greater distances than agriculturalists to forage, had more anteroposteriorly reinforced limbs. Interestingly, levels of sexual dimorphism in lower limb shape also decrease in most regions following the adoption of agriculture (Ogilvie., 2005; Ruff and Larsen, 2014; Macintosh et al., 2014a). This has been attributed to a decrease in male mobility, as the adoption of agriculture required greater male commitment to agricultural labour. As a result, they less frequently undertook long distance hunting expeditions (Ogilvie, 2005; Ruff and Larsen, 2014).

More pertinent to the current examination of bone robusticity in Cis-Baikal huntergatherers are studies of robusticity in past hunter-gatherer populations. These highlight substantial chronological and regional variation in past foraging behavior. For instance, Holt (2003) and Shackelford (2007) demonstrate a chronological reduction in lower limb robusticity as well as changes in shape across the Old World during sequential phases of the Upper Paleolithic. During the same period, upper limb robusticity increases (Churchill et al., 2000). These changes are consistent with reductions in mobility. Increases in upper limb robusticity have been specifically linked to increased focus on processing low yield resources, because increases in population density during the Upper Paleolithic depleted terrestrial game populations.

Compared to Holocene hunter-gatherer populations, Upper Paleolithic foragers generally exhibit elevated levels of bone strength and humeral asymmetry, indicating either a change in foraging strategies or the technology employed following the end of the Last Glacial Maximum (Trinkaus et al., 1994; Holt, 2003; Ruff, 2008; Sladek et al., 2016). However, this represents a general trend, and some Holocene populations appear as robust as Paleolithic humans (Ruff et al., 1993; Trinkaus et al., 1994; Holt, 2003; Marchi et al., 2006). Indeed, the considerable variation in the cross-sectional geometry of Holocene hunter-gatherer upper and lower limbs emphasizes their behavioral diversity (Stock and Pfeiffer, 2001; Stock and Pfeiffer, 2004; Stock, 2006; Shaw and Stock, 2013; Shackleford, 2014). Differences between these populations appear related to variation in terrestrial and aquatic mobility, the resources available, and technology employed (Stock and Pfeiffer, 2001; Weiss, 2003; Stock and Pfeiffer, 2004; Stock, 2006; Lieverse et al., 2011). Within populations, males and females also show varying levels of

dimorphism with regards to cross-sectional properties, which testifies to differences in the sexual division of labor among Holocene hunter-gatherer populations inhabiting different environments.

In contrast to the large literature focused on adult skeletal remains, anthropological study of juvenile bone strength has been limited. Several have confined themselves to the study of general ontogenetic trends. Ruff (2003a, 2003b) and Sumner and Andriacchi (1996) studied the development trajectories of a contemporary and an archaeological human population respectively. They confirmed that the developmental trajectory of robusticity tracked the accrual of body mass and muscle area, the factors primarily responsible for mechanical strain. For instance, changes in the relative velocity with which the cross-sectional properties of the upper and lower limb accrued corresponded to changes in modes of locomotion, *e.g.* crawling versus walking (Ruff, 2003b). Cowgill et al. (2010) used a sample of modern and archaeological populations to study the development of femoral midshaft shape. This study demonstrated that developmental changes in shape across development represent a continual process of functional adaptation to behavior and body shape.

Only a small number of studies have compared the bone strength development of prehistoric and modern populations that practiced diverse lifeways and occupied different environments (Cowgill and Hager, 2007; Cowgill, 2008; Cowgill, 2010; Cowgill, 2014a,b; Osipov et al., 2016). Importantly, the variation detected by these studies cannot be explained entirely by differences in behavior. Body size and genetics are likely also important determinants of variation between populations. A large survey of Holocene ontogenetic samples practicing a diversity of subsistence modes (hunter-gatherer, horticulturalist, pastoralist, agriculturalist, modern urban), showed that significant differences in bone robusticity and shape arise shortly after birth (Cowgill, 2010; 2014b). Cowgill (2010) primarily attributed systemic differentiation in cross-sectional size and strength to nutrition related variation in body mass *in-utero* and throughout growth. This reflects the fact that it proves difficult to control for differences in body size. Metaphyseal measurements have served as a proxy for body mass in analyses of juveniles. However, the development of joint surfaces appears more genetically canalized than the accrual of CSG, which responds more dramatically to fluctuations in body mass (Lieberman et al., 2001). Given this limitation in size-standardization of CSG, Cowgill (2010) hypothesized that

some of the inter-population patterning detected in archaeological samples likely reflected unaccounted differences in body mass. The fact that individuals from the population with strong evidence for chronic malnutrition had more gracile diaphyses than better nourished individuals that likely worked less supports this hypothesis (Cowgill, 2010). In addition to health-related differences, genetically encoded variation in both body size and CSG may explain why many population comparisons show differentiation characteristic of adults from very early in ontogeny. High activity groups may demonstrate some genetic predisposition for increased bone formation, and functional adaptation maintains or perpetuates such differences later in ontogeny (Cowgill, 2010, 2014a,b).

A more recent ontogenetic study restricted to Holocene hunter-gatherer populations also found some systemic differentiation attributable to variation in genetics or body size (Osipov et al., 2016). However, differentiation between samples also increased with age, which one would expect as individuals begin to learn adult subsistence roles. This finding emphasizes the importance of behavior in determining skeletal robusticity and shape. Juveniles from populations for which other lines of evidence suggest high levels of terrestrial mobility, exhibited strong lower limbs relative to upper limbs, and this difference increased with age. Conversely, individuals from populations more dependent on aquatic resources had stronger upper arms, which may relate to boat use as well as involvement of juveniles in fishing and processing of aquatic resources.

Studies of variation in bone robusticity among juvenile hunter-gatherers from specific regions has been limited to Cowgill's (2014a) analysis of Point Hope, Alaska Inuit and Harrington's (2010) research on Later Stone Age South African Cape foragers. Archaeological evidence suggests that foragers from different phases of the Point Hope site exhibited very different foraging patterns. However, no significant differences in the ontogeny of CSG were detected, except for humeral asymmetry (Cowgill, 2014a). This last result, however, was based on small sample sizes (n=2 for one group). Given that activity levels were likely high in both groups, Cowgill (2014a) proposed that analysis of CSG may only detect broad behavioral differences between populations. In other words, bone's response to loading may only vary when differences in strain are large, rendering it blind to small differences in activity. Also, the

complicating effects of genetics, nutrition, and small sample size may further obscure behavioral signatures.

Harrington's (2010) analysis of Later Stone Age South African hunter-gatherer ontogeny did not make geographical or chronological comparisons but focused on the mechanical and biological causes of intra-sample variation. All measures of robusticity and shape exhibited increasing variation with age. This was considered a reflection of increasing heterogeneity in both body mass and activity levels. For example, the youngest children show nearly symmetric humeri and no clear arm dominance. In contrast, most children older than six years have significantly stronger right upper limbs, and asymmetry increases with age. This suggests that a behavioral change occurs in childhood that stimulates increases in bilateral asymmetry. Harrington (2010) further interpreted increased variability in bone strength and limb shape measures in adolescence as reflective of the emergence of greater heterogeneity in behavior as individuals begin to assume adult foraging roles.

The study of the development of sexual dimorphism during growth has also been limited, though the few existing studies have achieved promising results. Ruff and colleagues (1994) showed that among agriculturalists from Pecos Pueblo, sexual dimorphism in femoral shape, which is correlated with levels of terrestrial mobility, was present in late adolescence. Conversely, Harrington's (2010) study of Later Stone Age skeletal development showed little sex related variation in lower limb strength and shape among adolescents, but males had more asymmetric upper limbs. The upper limb asymmetry differences conform to archaeologically inferred differences in tool use between males and females in these groups (Stock and Pfeiffer, 2004). As adult males did not differ from females with respect to femoral CSG, it would appear that sexual differences in mobility observed by Stock and Pfeiffer (2004) were produced by activities that became habitual in late adolescence. Therefore, the small sample size representing this age range in the ontogenetic analysis may have prohibited the detection of differences evident in the larger adult samples.

Overall, examination of postcranial robusticity provides a powerful tool for studying past populations. Inter- and intra- population variability in robusticity predominantly represents differences in how bone was accrued during development, and this process is modulated by activity, health, and genetics. Studies of juvenile bone robusticity, while limited to date, have demonstrated potential for improving understanding of juvenile behavior, developmental health, and genetically modulated differences in growth. More research is needed to determine how much of the variation in CSG between populations is due to differences in genetics and differences in health, as opposed to mechanical adaptation. Inferences about habitual behaviors from long bone cross-sectional geometry must therefore be appropriately contextualized with archaeological evidence and ethnographic analogy. Still, juvenile CSG can provide a wealth of information about health and behavior during the juvenile period, if results are contextualized with other lines of archaeological evidence.

# **Chapter 3: Middle Holocene Cis-Baikal Hunter- Gatherers: A Review of Cultural Chronologies, Behavioral Variation, and Skeletal Growth**

This section reviews previous archaeological research on behavior and health of Middle Holocene populations of the Cis-Baikal region. The first sections describe the region's geography and its ecosystem, and it also provides a summary of the region's Middle Holocene cultural chronology. This provides a background for discussing what is known about population history, behavior, and developmental health during the Middle Holocene. Study of Middle Holocene Cis-Baikal lifeways has detected chronological changes as well as regional variation in population size, genetic structure, foraging strategies, and health. As made clear in the previous chapter, these findings pertain to the current research project, because genetics, health, and behavior regulate the process of bone accrual.

## 3.1 Geography of the Cis-Baikal and Reconstruction of Middle Holocene Environment

A map of the Baikal region is provided in Figure 3.1. Lake Baikal, the world's largest freshwater lake by volume, is located in the South of East Siberia, about 200 kilometers north of the Mongolian border (Weber et al., 2002; Weber and Bettinger, 2010). The term Cis-Baikal refers to the region that lies immediately northwest of the lake (approximately 52-58°N and 101-110°E) (Figure 3.1). Mountains ring the lake, and, to the southwest, the region is bounded by the East Sayany mountain range (Weber et al., 2002). Two large river basins, the Angara and Lena, extend northwards from the lake. As they flow north, these two large rivers intersect with many smaller tributaries.



Figure 3.1.1: Map of the Cis-Baikal with microregions and cemeteries used for this analysis (Lieverse et al., 2016)

Archaeological research has traditionally divided the region into four smaller microregions as listed below. The first three have been the subject of considerable research, while the fourth, South Baikal has not. This reflects that intensive archaeological excavations of the large cemetery in this region, Shamanka II, began only in the 2000s (Bazaliiskii, 2010; Weber and Bettinger, 2010). All definitions of the microregions follow Weber and Bettinger (2010). The locations of the microregions are marked in Figure 3.1.1. **Cis-Baikal Microregions:** 

- 1. **Angara River Valley**: Includes the Angara River and its tributaries from the river's source at the lake and extending north to the Ilim river.
- 2. The Little Sea: The shoreline opposite Ol'khon island as well as the island itself.
- 3. Upper Lena: This region encompasses the upper Lena River Valley to the mouth of the Kirenga River.
- South Baikal: The southwest shore of Lake Baikal from the Selenga delta to the lake's western end.

In general, the environment of the Cis-Baikal can be described as boreal forest interspersed with patches of more open steppe landscape (Weber and Bettinger, 2010; Losey and Nomokonova, 2017). A corridor of steppe connects the Angara and Upper Lena, and steppe also covers most of the Little Sea microregion (Weber and Bettinger, 2010). The Cis-Baikal has a continental and markedly seasonal climate, average January and July temperatures of -26 and 20 degrees Celsius (Weber et al., 2002). Reconstructions of past changes in climate have been an important focus of the Baikal Hokkaido Archaeology Project. Throughout the Early Holocene, eastern Asia generally became progressively warmer and wetter (White and Bush, 2010; Tarasov et al., 2017). This would have lead to gradual increases in the thickness and duration of snow cover and "succession... of forest mosaics during the Early Holocene followed by the wide spread of Scots pine" (Pinus sylvesteris) by ~7,000 years ago (Tarasov et al., 2017). Increased snow cover and decrease in open landscapes may have reduced the quantity and quality of forage for terrestrial ungulates. White and Bush (2010) further hypothesize that a subsequent reversion to more arid conditions between 6,000 to 3,000 years BP would have had several effects on aquatic and terrestrial ecosystems. Firstly, the productivity of aquatic ecosystems may have become increasingly erratic. Simultaneously, greater aridity may also have altered forest coverage in such a way as to increase the abundance and concentration of large ungulates, perhaps making hunting more productive. As discussed below, these environmental changes may correspond to some important changes in diet, population size, and mortuary practices.

## **3.2 Resource Distribution and Subsistence Practices**

Although climate change likely altered the distribution of plant communities and forest coverage throughout the Holocene, modern data provides a reasonable proxy for the past

environment (Weber and Bettinger, 2010). Fish are abundant though variable across all microregions of the Cis-Baikal. Materials recovered from cemeteries and habitation sites indicate that hunter-gatherers employed a variety of fishing technologies including harpoons, fishing lines, and nets deployed either from shore or simple watercraft (Losey et al., 2008; Losey et al., 2012; Weber and Bettinger, 2010).

Lake Baikal and the two large river valleys, the Angara and Upper Lena, differ with regards to aquatic productivity and the availability of fish (Weber et al., 2002; Weber and Bettinger, 2010; Weber et al., 2011; Losey et al., 2012). A wide variety of littoral fish species inhabit the relatively shallow waters along the Lake's shorelines, gulfs, and river mouths (Losey et al., 2012). Reconstructions based on zooarchaeological evidence suggest that lakeshore fishing involved small daily catches of fish throughout the year (Losey et al, 2012). Storage was likely minimal due to the low energy yield and lack of evidence for storage structures (Losey et al, 2012; Weber and Bettinger, 2010). In modern times, the Little Sea appears a much more productive fishery than the South Baikal lakeshore. The lakeshore near the source of the Angara River may have been a high productivity area that attracted South Baikal microregion huntergatherer populations, but a lack of faunal data limits the reconstruction of fishing practices in this microregion (Losey, personal communication, 2013). The lake is also home to the Baikal seal. Archaeological evidence suggests groups that foraged along the lakeshore hunted the seal on a seasonal basis (Weber et al., 1993; Weber et al., 2002; Katzenberg et al., 2009; Katzenberg et al., 2012; Weber et al., 2011; Nomokonova, 2011; Nomokonova et al., 2013a). It is thus an important distinction that only groups whose foraging range included the lakeshore during specific periods of the year would have had access to this resource (Weber et al., 2011; Weber and Goriunova, 2013).

Of the two large rivers, the Angara and its tributaries contain greater quantities of fish than the Lena (Weber and Bettinger, 2010). Large seasonal spawning runs along the Angara river would have been extremely attractive targets for hunter-gatherers, and processing and storing this seasonally available resource may have required substantial organization of labor (Weber and Bettinger, 2010; Losey et al., 2012). Groups may also have had to negotiate access to this resource, particularly during the Early Neolithic, when, as discussed below, the population density of this region is thought to have been especially high (Weber and Bettinger, 2010; Losey et al., 2012).

Large ungulates, such as moose, red deer, and roe deer, the primary terrestrial game in all microregions of the Cis-Baikal, were hunted with spears and bows (Weber et al., 2002; Weber and Bettinger, 2010; Turov, 2010). Birds and small mammals are also abundant (Losey and Nomokonova, 2017). Ethnographically studied boreal forest and arctic hunter-gatherers hunt and trap such small game on a seasonal basis (Tanner, 1979; Smith, 1991; Turov, 2010; Fleming, 2013). Northern hunter-gatherers rely primarily on fish and game, due to the limited availability of plant-foods (Cordain et al, 2000). Thus, while berries, mushrooms, and a few other plant resources were seasonally available in the Cis-Baikal, fish and ungulates were the main components of Middle Holocene diet.

## 3.3 Archaeological Chronology

The cultural chronology of the Cis-Baikal during the Middle Holocene has been the subject of extensive scholarly debate throughout the 20<sup>th</sup> century (Okladnikov, 1950, 1955; Gerasimov, 1955; Gerasimov and Chernykh, 1975; Weber, 1995; Weber et al., 2002; Weber and Bettinger, 2010; Weber et al., 2016a). This section briefly summarizes this literature, focusing on the most recent chronology that has emerged from an intensive program of radiocarbon dating by the Baikal Hokkaido Archaeology Project (BHAP). This has revealed substantial chronological and regional variability in mortuary practices, as well as changes in population size and distribution.

## 3.3.1: Chronologies developed prior to application of Radiocarbon Dating

Archaeological evidence indicates that anatomically modern humans have inhabited the Cis-Baikal region for roughly the last 20,000 years (Michael, 1958; Goebel, 1999). Hunting and gathering persisted as the dominant lifeway in this region from the Paleolithic to the Early Bronze Age (~3725 cal BP). The hunter-gatherer mortuary complexes from the Middle Holocene have been investigated by both Russian and Western scholars. Due to the lack of transition from hunting and gathering to food production, which marks the onset of the Neolithic in other regions, archaeologists have employed changes in technology and mortuary protocols to divide the Middle Holocene cultural sequence (Okladnikov, 1950; Okladnikov, 1955; Weber, 1995; Weber et al, 2002; Weber and Bettinger, 2010). The introduction of pottery, ground stone, and

the bow differentiate the Neolithic from the Mesolithic. The appearance of metal artifacts marks the start of the Bronze Age.

Prior to the work of BHAP, Western scholars published descriptions of Russian research in this region, primarily based on the influential works of A.P. Okladnikov (Okladnikov, 1950, 1955; Michael, 1958, 1992; Chard, 1974; Weber, 1995). Okladnikov defined cultural and chronological units based on mortuary complexes, and this practice has persisted due to the difficulty of correlating mortuary artifacts with material from stratified habitation sites (Mckenzie, 2009; Bazaliiskii, 2010). Influenced by Marxist ideology, Okladnikov's (1950, 1955) chronology ordered mortuary complexes into a sequence that represented a process of unilinear evolution through cultural stages. These represented a progression towards greater cultural and technological complexity and increasing social inequality (Okladnikov, 1950, 1955; Weber, 1995). Absolute dates for each period were derived based on similarities between Cis-Baikal material and the material culture of other regions (Okladnikov, 1950, 1955; Michael, 1958; Weber, 1995). A schematic of the Okladnikov cultural history model is given in Figure 3.3.1.



Figure 3.3.1: Okladnikov cultural history model from Weber, 1995

Okladnikov saw the Early Neolithic (EN) Isakovo mortuary tradition as the product of simple egalitarian hunter-gatherers. While technologically superior to their Mesolithic forerunners, they still focused on hunting large game (Okladnikov, 1950; Weber, 1995). The Middle Neolithic (MN) Serovo mortuary complex saw improvements in pottery production and hunting equipment. These graves also contained a small amount of fishing equipment and fish shaped artifacts, indicating an expansion of the diet to include aquatic resources. Graves of the Late Neolithic (LN) Kitoi culture contained more fishing than hunting equipment, and the fishing gear also appeared more complex. Okladnikov (1950, 1955) interpreted this as evidence of a substantial increase in aquatic resource exploitation related to population growth. He also theorized that supporting a larger population necessitated the organization of labor by powerful individuals. As a result, pronounced social and sexual inequality developed in the LN, as evidenced by greater variation in the richness of burials during this period compared to previous ones. Population and social inequality continued to increase in the Early Bronze Age (EBA), which was represented by the Glaskovo mortuary tradition. Technologically, this period was distinguished primarily by the introduction of metal objects as grave goods.

Since its publication in the 1950s, other Russian scholars proposed extensive modifications to Okladnikov's chronology (Gerasimov, 1955; Weber, 1995 and references therein). Academic debate focused primarily on the position of the Kitoi mortuary complex in the chronology, and its relation to the Isakovo and Serovo cultures. A great deal of the disagreement about cultural chronology resulted from how archaeologists chose to correlate mortuary traditions with material from stratified habitation sites (Weber, 1995; McKenzie, 2009). This reflects a lack of overlap in material culture between burials and settlement sites. For instance, many chronologies have employed pottery styles to aid in relative dating, but pottery from stratified habitation sites is more variable than that found in mortuary contexts (Weber, 1995; McKenzie, 2008). Gerasimov (1955) concluded that more similarities existed between the Isakovo/Serovo and Glaskovo mortuary complexes than between Glaskovo and Kitoi (Gerasimov, 1955; Weber et al., 1995). Furthermore, based on cranial measurements and mortuary data he argued that the Kitoi were culturally and biologically distinct from other groups (Gerasimov, 1955; Gerasimov and Chernykh, 1975).

## 3.3.2 Refinement of Chronology through Radiocarbon Dating

Radiocarbon dating of burials resulted in a major redefinition of Okladnikov's cultural history of the Cis-Baikal region (Mamonova and Sulerzhitskii, 1989; Weber, 1995). Radiocarbon dating by Russian scholars confirmed that Glaskovo burials were the youngest in the sequence (Mamonova and Sulerzhitskii, 1989; Michael, 1992). Conversely, radiocarbon dating of the Kitoi clearly contradicted Okladnikov's chronology, as these graves now appeared indisputably older than those belonging to other mortuary traditions (Mamonova and Sulerzhitskii, 1989; Weber, 1995). Based on this result, Kitoi graves were reclassified as belonging to the EN period. Based on the dates available by the early 1990s, Weber (1995) first suggested the presence of a

chronological discontinuity in mortuary traditions during the MN, between the EN Kitoi and the LN Isakovo and Serovo mortuary complexes.

Subsequently, the Baikal Archaeology Project carried out radiocarbon dating of human remains from new and previously excavated cemeteries (Weber et al., 2002; Weber et al., 2006; Weber et al., 2010; Weber and Bettinger, 2010). Within the last few years, the chronology has undergone further revision to account for the discovery of a Freshwater Reservoir Effect (FRE) (Nomokonova et al., 2013b; Ramsey et al., 2014; Schulting et al., 2014; Weber et al., 2016a). Bodies of water contain dissolved Carbon 14, which remains for many years. Thus, bodies of water serve as a reservoir for old carbon that is subsequently incorporated into extant aquatic organisms (Philippsen, 2013, 2015). Consequently, human consumption of aquatic foods results in the incorporation of old radiocarbon into their tissues, making their remains appear older than they truly are. The magnitude of the FRE depends on numerous environmental and geological factors (*e.g.* depth of the lake, temperature, leaching of old carbon from limestone) as well as the amount and type of aquatic resources in the diet (Philippsen, 2015). For a more in-depth explanation of the specific factors affecting the magnitude of the FRE within the Cis-Baikal region see Schulting et al. (2014).

Using paired dating of human and terrestrial mammal remains from the same grave, BHAP researchers developed calibration equations that correct for the FRE (Ramsey et al., 2014; Schulting et al., 2014; Weber et al., 2016a). The terrestrial mammal bone allowed correction, because these organisms did not consume aquatic resources. Therefore, the difference between human and animal radiocarbon dates approximates the magnitude of the FRE. The new chronology is provided in Table 3.1 and discussed in detail below. The determinations of the duration and chronological boundaries of each period were made using Bayesian modeling of FRE corrected radiocarbon dates as described in 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) <sup>1</sup>	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	Glaskovo

Table 3.1: Chronology of Cis-Baikal archaeological periods corrected for the freshwater reservoir effect (after Weber et al., 2016a)

1: Microregional differences exist in chronology of cemetery use between the Angara River Valley and South Baikal microregions (see text).

Whether some burials or mortuary cultures date to the Late Mesolithic (LM) has been the subject of previous debate (Bazaliiskii, 2010; Weber et al., 2010). Accounting for the FRE confirms the presence of LM burials, dating between 8277 +/- 176 to 7503 +/- 14 mean HPD cal BP (Weber et al., 2016a). Several have been described as belonging to the Khin' mortuary tradition (Bazaliskii, 2010). However, the small overall number of LM graves makes interpreting variability in burial practices difficult, especially since analysis of these burials "has barely reached the stage of initial accumulation of empirical evidence" (Bazaliiskii, 2010, p. 54). Mortuary architecture and grave good assemblages from this period are highly variable (Bazaliiskii, 2010; Weber et al., 2016a). Despite substantial intra-LM variability in burial forms, one can distinguish Mesolithic burials from EN interments based on differences in grave goods and architecture. Furthermore, LM cemeteries are invariably smaller than EN cemeteries, which exhibit far more variability in size (Bazaliiskii, 2010; Weber et al., 2016a). Some EN cemeteries contain only a few individuals, others over a hundred (Bazaliiskii, 2010).

The EN period lasts from 7503 +/- 14 to 7027 +/- 33 mean HPD cal BP (Weber et al., 2016a). This represents a rather brief period of formal burials, 476 +/- 37 years. Graves from this period are ascribed to the Kitoi mortuary tradition, though, as discussed below, substantial geographic variation exists in burial practices (Bazaliiskii, 2010; Weber and Bettinger, 2010). Importantly, microregional variation also exists in EN cemetery use. Burial begin ~80 years earlier and end ~270 years later in the South Baikal compared to the Angara River Valley microregion (Weber et al., 2016a,b). Furthermore, radiocarbon dates from the EN South Baikal cemetery of Shamanka II suggest two phases of burial, separated by a discontinuity of ~97 years (Weber et al., 2016b). Burials in the neighboring Angara River Valley do not show a similar

hiatus in formal interments. Prior to and during the EN period, the environment underwent important changes, but if this relates to changes in mortuary practices remains unclear. It has been hypothesized that the trend towards warmer and wetter conditions, which began in the Early Holocene, affected the abundance of terrestrial game. Continual increases in snow cover and the eventual transition from more open landscape to Scots pine forest would have decreased the amount of forage available for ungulate species (red deer, roe deer, moose) by approximately 7,000 years cal BP, which corresponds to the EN period (White and Bush, 2010; Tarasov et al., 2017). However, decreases in ungulate populations may not have been linear. Indeed, prior to the spread of Scots pine, the succession of forest mosaic communities may have initially stimulated increases in herbivore populations (Weber, personal comm.). Furthermore, it should be noted that within boreal forest environments, considerable and unpredictable fluctuations in large game populations are the norm, and these cycles can affect hunter-gatherer population sizes and foraging strategies in complex ways (Belovsky, 1988; Weber and Bettinger, 2010). Second, a subsequent shift towards more arid conditions towards the end of the EN may have had a destabilizing effect on aquatic ecosystems (White and Bush, 2010). Thus, whether the Early Holocene environmental changes explain the development of large cemeteries in the EN, or whether the second period of increased aridity triggered changes in foraging strategies and population size responsible for the end of EN cemetery use remains unclear (White and Bush, 2010; Weber and Bettinger, 2010; Tarasov et al., 2017).

A discontinuity in use of formal cemeteries occurred during the MN, from 7027 +/- 33 to 5571 +/- 88 mean HPD cal BP in every microregion of the Cis-Baikal. This has been associated with marked reduction in population size at the end of the EN, because, as discussed in detail below, EN and Late Neolithic/ Early Bronze Age (LN/EBA) populations differ genetically (Mooder et al., 2006; Mooder et al., 2010; Moussa et al., 2016). However, it is unlikely that the Cis-Baikal was completely depopulated during the Middle Neolithic (Weber and Bettinger, 2010). More probably, either descendants of the Kitoi or newly arrived groups foraged in this area. Perhaps the lack of formal burials indicates more mobile and dispersed groups than in the EN and LN/EBA, but the exact nature of foraging behavior during this period remains unclear (Weber et al., 2002; Weber and Bettinger, 2010).

The LN saw the resumption of burial in formal cemeteries and dates from 5571 +/- 88 to 4597 +/- 76 mean HPD cal BP (Weber et al., 2016a). The Isakovo and Serovo mortuary traditions date to this period, and they appear contemporaneous rather than sequential (Weber et al., 2008; Bazaliiskii, 2010; Weber and Bettinger, 2010). However, while graves from both traditions are found in the Angara River Valley, only Serovo graves have been recorded in the Little Sea and Upper Lena (Weber and Bettinger, 2010; Weber et al., 2016; Weber et al., 2016; Weber et al., 2010; Weber et al., 2016a).

The EBA dates from 4597 +/- 76 to 3726 +/- 34 mean HPD cal BP. Burials from this period belong to the Glaskovo mortuary tradition, and the development of this mortuary tradition coincided with the appearance of metal objects (Weber, 1995; Weber and Bettinger, 2010; Weber et al., 2016a). Bayesian modelling of radiocarbon dates indicate continuity and overlap between the LN and EBA mortuary traditions (Weber et al., 2010; Weber et al., 2016a). Thus, while typological criteria reliably differentiate the Glaskovo from preceding mortuary traditions, the radiocarbon dates and some aspects of material culture suggest cultural continuity and rapid transition between Isakovo/Serovo and Glaskovo mortuary traditions (Weber and Bettinger, 2010; Weber et al., 2010). For instance, LN and EBA graves are frequently found in the same cemetery (Weber and Bettinger, 2010). Furthermore, EBA graves are found in the same rows and clusters as LN graves within cemeteries. This implies that Glaskovo burials are placed in a way that recognizes and respects LN graves (Weber and Bettinger, 2010). Given the evidence for cultural continuity between the LN and the EBA, most bioarchaeological analyses of Baikal skeletal material have treated LN and EBA burials as manifestations of the same archaeological horizon referred to as Isakovo/ Serovo/ Glaskovo (ISG) (Lieverse et al., 2007a,b; Lieverse et al., 2009; Stock et al., 2010; Lieverse et al., 2011; Waters-Rist, 2011; Stock and Macintosh, 2016). This approach increases sample sizes, but may obscure important chronological differentiation in behavior, health, diet, and social structure between the LN and EBA periods (e.g. Waters-Rist, 2011; Shepard, 2012).

A consideration of both geographic as well as temporal distribution of burials produces further insight into regional and chronological variation in Middle Holocene population size. How changes in the number and style of formal burials between the LM and EN periods correlates with changes in population size and distribution remains unclear. However, if, as suggested by Weber and Bettinger (2010), one uses the number of burials as a proxy for population size, it would be reasonable to suggest that population grew substantially. It should be noted that there are limitations to the use of burials as proxies for population size. For instance, the differential extent of archaeological survey throughout the Cis-Baikal may introduce some bias into how many burials have been recorded in each microregion. At best, burial number serves as only a general proxy for population size. Indeed, formal interment is a discontinuous variable. People either bury their dead in visible cemeteries or they do not (Weber and Bettinger, 2010). There may be some level of population size above which hunter-gatherers construct cemeteries to delineate territorial boundaries and group belonging. Reconstructions of finer changes in population size based on burial numbers are more tentative. However, careful consideration of burial distribution and frequency, as well as variance in mortuary traditions can offer insights into population size, distribution, and the extent of contact between groups (Weber and Bettinger, 2010). For a further consideration of assumptions made using this method see Weber and Bettinger (2010).

The greatest variation in Cis-Baikal mortuary traditions occurred in the EN (Bazaliiskii, 2010; Weber and Bettinger, 2010). Most EN burials were located in the Angara River Valley and adjoining South Baikal microregion. These adjacent microregions also displayed the greatest similarities in grave structure and material culture, but each one also had idiosyncratic characteristics (Bazaliiskii, 2010). Fewer EN burials have been recorded in the Little Sea and Upper Lena microregions, and these do not consistently demonstrate features diagnostic of "classic" Kitoi burials in the Angara and South Baikal microregions (Bazaliiskii, 2010; Weber et al., 2010; Weber and Bettinger, 2010; Weber et al., 2016a). This suggests that EN populations were concentrated in the Angara and adjoining South Baikal microregions, and mortuary practices differed substantially across microregions. Following the discontinuity in formal burials during the MN, less regional heterogeneity existed in LN and EBA mortuary characteristics. No aspect of burial form or mortuary ritual was endemic to a single cemetery or region, implying greater contact between populations within and between microregions than during the EN (Weber and Bettinger, 2010). Still, as evidenced by the lack of Isakovo graves in the Little Sea and Upper Lena microregions, implying at least some heterogeneity in culture during the LN. The LN/EBA population of the Angara was about the same size as the EN, but population grew more in other microregions, "most notably the Little Sea" (Weber and Bettinger, 2010, 499).

The program of radiocarbon dating corrected for the FRE has clarified Cis-Baikal cultural chronology and offered new insights into population size distribution during the Middle Holocene. Cemeteries first appeared in the LM, but the frequency of burial and population size increased in the EN. Furthermore, the EN population appear to have been most concentrated in the Angara and South Baikal microregions. The discontinuity in the use of formal cemeteries during the MN likely correlated with a decrease in Cis-Baikal population and changes in foraging strategy. Use of formal cemeteries resumed in the LN. Compared to the EN, population appears to have been larger in the LN and EBA, and it was more evenly distributed between microregions.

## 3.4 Description of Mortuary Cultures and Sites Analyzed in this Investigation

Although a multitude of small cemeteries have been excavated in the Cis-Baikal, most osteological analyses have been conducted on material from large cemeteries. For a comprehensive list of large and small Cis-Baikal cemeteries and their locations, see Weber and Bettinger (2010). Juvenile remains suitable for biomechanical analysis are only available for three cemeteries, Lokomotiv, Shamanka II, and Ust-Ida I. Consequently, this overview of archaeological background focuses specifically on these cemeteries. For convenience, Shamanka II and Ust-Ida I are referred to as Shamanka and Ust-Ida for the rest of this study. The following descriptions only describe aspects of mortuary tradition and cemetery structure. Bioarchaeological analyses of the behavior, diet, genetics, and health of individuals buried at these sites are discussed in the following section. A list of these cemeteries, as well as their archaeological age and cultural affiliation, is given in Table 3.2. Their location is given on the map in Figure 3.1.

Cemetery	Microregion	Archaeological Period	<b>Mortuary Tradition</b>	
Lokomotiv	Angara	Early Neolithic	Kitoi	
Ust-Ida I	Angara	Late Neolithic/ Early	Isakovo, Glazkovo	
		Bronze Age		
Shamanka II	South Baikal	Early Neolithic	Kitoi (n.b. several Early Bronze	
			Age Glazkovo juvenile/ young	
			adult burials)	

Table 3.2: List of cemeteries used for this analysis

#### 3.4.1 Shamanka II

The Lokomotiv and Shamanka cemeteries date to the EN, and burials are attributed to the Kitoi mortuary tradition (n.b. some EBA burials are present in the Shamanka cemetery). Kitoi graves rarely have stone architecture on the surface and few stones within the graves (Bazaliiskii, 2010). However, some graves were reused or opened during ritual activity, which implies they were marked in some way (Bazaliiskii, 2010; Losey et al., 2011, 2013). Bodies were placed in the graves in an extended position with the head oriented to the north (Weber et al, 2016a). Graves containing multiple individuals were common (Bazaliisky and Saveylev, 2003; Bazaliiskii, 2010). Kitoi grave goods assemblages exhibit the greatest number of artifact types of any Middle Holocene mortuary tradition (Bazaliiskii, 2010). However, the richness of burials also varies markedly. Some individuals were buried without grave goods, others a few, and some with a hundred items or more. The diagnostic composite Kitoi fishhooks and bifacial arrowheads are the most common artifacts recovered. Other stone and bone tools are also found. Ornamental grave goods include green nephrite knives, calcite rings, beads and pendants made of animal bones and teeth, zoomorphs depicting moose, fish, and seal, and anthropomorphs (Bazaliiskii, 2010). Pottery is rare at cemetery sites (McKenzie, 2009). Copious amounts of red ochre were applied to the body (Bazaliiskii, 2010).

Shamanka is one of two cemeteries currently known from the South Baikal microregion, the other being the Fofanovo cemetery on the lower Selenga River (Gerasimov and Chernykh, 1975; Bazaliiskii, 2010; Weber et al., 2016a). Shamanka was discovered in 1962, and sporadic excavation of a handful of graves occurred in the 1990s (Losey et al., 2013; Weber et al., 2016b). Large scale excavations were undertaken from 2001-2008, and the remains of at least 165 individuals have been recovered (Losey et al., 2013; Weber et al., 2016b). 56 EN graves contain single interments, and the remaining 41 graves contain more than one individual. Most of the individuals are oriented with the head pointing north. Bazaliiskii (2010) notes that, within graves containing multiple burials, a greater proportion of interments are asynchronous (individuals buried at different times) than at Lokomotiv, where most multiple burials are synchronous. Eleven other individuals were interred during the EBA. A description of Glaskovo grave architecture and grave goods is given in the section below dealing with Ust-Ida. These later burials are not integrated into the spatial organization of Early Neolithic graves (Weber et al.,

2016b). The EBA individuals are also distinguished by the fact that most of them display evidence of perimortem injury (Losey et al., 2017).

The EN graves exhibit clear spatial patterning, with distinct North and South sectors (Weber et al., 2016b). The Northern sector exhibits a further subdivision into Northwest and Southeast clusters. A substantial number of the graves are arranged in twelve rows, and all rows, save one in the South sector, run along the NW-SE axis. The anomalous row runs along the NE-SW axis. Graves not arranged side by side have been classified as scattered graves. As has been discussed in the preceding section on cultural chronology, EN Shamanka burials took place in two distinct phases. The first period of use lasted approximately 273 +/- 43 years. A discontinuity of 400 +/- 56 years separates this phase from the second shorter phase that lasted 122+/- 82 years. It appears that both sectors of Shamanka II were used in both EN phases (Weber et al., 2016b). However, all rows were established in the first phase of cemetery use, and burials were only added to some of the rows after the intra-EN discontinuity. Graves with between one to three burials were constructed in both the first and second phase, but the majority of phase two burials were secondary interments in graves created during phase one.

Several studies have commented on the symbolic significance of Shamanka II's location, and the unique ritual treatment of human remains that occurred at this cemetery (Losey et al., 2013; Weber et al., 2016b). The cemetery is situated on a hillside that provides an arresting view of the lake and its surroundings, and below it a narrow peninsula runs into Kultuk Bay. The location may thus have been chosen for its ceremonial significance. Graves provided a nexus for interactions between the living and the dead (Losey et al., 2013; Weber et al., 2016b). At least 60 graves were reopened (Losey et al., 2013). Bodies were either moved to make space for other burials or they were ritually manipulated. As some burials consist of only isolated elements, large portions of the body may have been removed. Alternatively, only select portions of a body were transported to Shamanka II for burial. Analysis of the graves indicates the ritual use of fire, and bear crania, teeth, and penis bones were placed in some graves (Losey et al., 2013). At no other Middle Holocene Cis-Baikal cemetery is ritual use of this animal so extensive. Otherwise the tools and faunal remains found in graves resemble those from the Lokomotiv cemetery (Losey et al., 2017).

#### 3.4.2 Lokomotiv

The Lokomotiv cemetery is located near the confluence of the Angara and Irkut rivers in the present-day city of Irkutsk. The site was discovered in 1897 and first excavated in 1927. Subsequent excavations were conducted in the 1940s, 1950s, 1980s, and 1990s (Bazaliisky and Savelyev, 2003). The site has still not been completely excavated, and over 100 graves may have been destroyed by construction (Bazaliiskii and Savelyev, 2003).

Reliable skeletal and archaeological data is only available for 71 graves (Bazaliisky and Savelyev, 2003). The sole LM grave is the most famous, and it contains the remains of a tundra wolf and a human skull (Losey et al., 2011). The other 70 graves contain 124 EN individuals. Forty-three of these graves contain one person, fifteen were double burials, five triple burials, and seven graves contained between four to eight individuals (Bazaliiksy and Savelyev, 2003; Mooder et al., 2006). All juveniles except one were buried in a multi-person grave, and an adult was always present in these graves. In multiple burials, individuals were most commonly arranged on top of each other facing head to toe, though placement in the same orientation does occur. Interestingly, the individuals in graves containing more than two people appear, except for one double burial, to have been interred simultaneously (Bazaliisky and Saveylev, 2003). This includes the large graves containing four to eight individuals. The heads of 29 individuals, or roughly a quarter of all those buried at the cemetery, were removed. Osteological analysis indicates that decapitation occurred before burial (Bazaliisky and Saveylev, 2003; Losey et al., 2011).

As was the case at Shamanka, there were considerable disparities in the number of grave goods between individuals (Bazaliisky and Saveylev, 2003). Several of the richest adult male and female graves contain between 200-300 objects, while others contain no grave goods. On average, graves contained between 10-80 objects. No juvenile burials contained grave goods.

## 3.4.3 Ust-Ida I

The site of Ust-Ida was first documented in the 1950s, and some rescue excavations took place during the 1980s. Systematic excavations were carried out from 1987 to 1995 by V.I. Bazaliiskii (Tiutrin and Bazaliiskii, 1996; Bazaliiskii, 2010). The site contains one EN Kitoi grave, 31 LN Isakovo graves, and 20 EBA Glazkovo graves. In total, the skeletal remains of 42 LN and 20 EBA individuals have been recovered from this site (Lieverse, 2005; Weber et al., 2006). The LN sample is exclusively Isakovo, with no burials ascribed to the contemporaneous Serovo mortuary tradition. Single and multiple interments are known from the LN component of the cemetery. There is only one multiple interment in the EBA component.

Ust-Ida is spatially divided into two distinct clusters of 20-25 graves each (Weber et al., 2006). Both clusters have approximately equal numbers of LN and EBA graves. Some graves are scattered, and others are arranged into rows. These run west to east and contain burials from both phases of burial. As discussed above, radiocarbon dating is consistent with chronological overlap between LN and EBA burials (Weber et al., 2010; Weber et al., 2016a). However, this finding is tentative, because very few EBA graves from this cemetery have been both dated and corrected for the FRE.

LN Isakovo graves are covered by oval stones, and they are oriented parallel to the Angara River with the head pointing upstream (southwest) (Bazaliiskii, 2010; Weber and Bettinger, 2010). The graves contain a less diverse assemblage of grave goods than typically found in EN Kitoi graves, 20-25 categories versus 60-65 (Bazaliiskii, 2010). Points, daggers, and harpoons are the most common items. Pottery is more common than in EN graves, and it is present in over half of Isakovo graves (McKenzie, 2009; Bazaliiskii, 2010). A few bone and stone pendants as well as anthropomorphs have also been recovered. Red ochre is much less copious than in Kitoi burials, visible only as "spots" on the skeleton. Previous analyses of two types of artifact merit specific mention as they are found interred with juveniles. The graves of adults identified as males contained large spearheads. These artifacts were also found in some of the child burials, and, for this reason, Bazaliiskii (2010) hypothesized that these children were also males. Bird bone needle cases are also found in most juvenile graves at Ust-Ida (Fleming, 2013). Fleming (2013) interpreted this as a potential indicator of hide-processing by juveniles in groups using this cemetery.

The EBA Glaskovo graves at Ust-Ida are differentiated from LN Isakovo graves by the orientation of the body, parallel to the river but head facing downstream or northwest (Weber et al., 2002; Weber and Bettinger, 2010; Weber et al., 2016a). Metal and white nephrite artifacts are unique to EBA burials, but not every individual from this period was buried with these objects (Weber et al., 2002; Weber and Bettinger, 2010; Weber et al., 2016a). Two additional features distinguish the LN and EBA components. LN graves commonly contain multiple individuals, but

most EBA graves do not (Weber et al., 2006; Weber et al., 2016a). More pertinent to studies of growth is that fact that 60% of LN individuals are juveniles, while only a few juveniles were buried during the EBA (Weber et al., 2006).

## **3.5 Analyses of Biology and Past Lifeways of Middle Holocene Cis-Baikal Hunter-Gatherers**

Analyses of skeletal material have primarily focused on comparing the Early Neolithic (EN) Kitoi to the Late Neolithic/ Early Bronze Age (LN/EBA) Isakovo/Serovo/ Glaskovo (ISG) groups. Before discussing the findings in more detail, I briefly summarize the general understanding of variation in genetics, behavior, and health that has emerged from recent studies. EN and LN/EBA populations are genetically distinct (Mooder et al., 2006; Mooder et al., 2010; Moussa et al., 2016). Analyses of skeletal remains demonstrate that the EN was characterized by greater reliance on fish, heavier workloads, and poorer developmental health (Weber et al., 2002; Lieverse et al., 2007 a,b; Lieverse et al., 2010; Stock et al., 2010; Weber and Bettinger, 2010; Lieverse et al., 2011; Waters-Rist, 2011; Waters-Rist, et al., 12011; Weber et al., 2011; Lieverse et al., 2013; Temple et al., 2014; Stock and Macintosh, 2016). LN/EBA groups exhibited a greater reliance on terrestrial game, improved developmental health, and lower workloads. Additionally, multiple lines of evidence are consistent with greater terrestrial mobility in the EN compared to the LN/EBA (Stock et al., 2010; Lieverse et al., 2011; Stock and Macintosh, 2016). More recent analyses have suggested that, in addition to chronological differences in behavior, diet, and health, the skeletal data also support the existence of geographic variation in these variables (Weber and Bettinger, 2010; Waters-Rist, 2011; Weber et al., 2011; Lieverse et al., 2013, 2016; Weber et al., 2016a). The remainder of this chapter considers variation in genetics, behavior, and developmental health in greater detail to provide a background for interpreting patterns of bone robusticity accrual.

## **3.5.1 Genetic Analysis of Population History**

As first suspected based on craniometric studies, genetic analysis of mitochondrial and Y-chromosomal DNA demonstrates that EN populations were biologically distinct from LN/EBA populations (Gerasimov, 1995; Weber et al., 1995; Mooder et al., 2006; Mooder et al., 2010; Moussa et al., 2016). Based on differences in mtDNA haplotypes, it has been hypothesized that EN populations belong to an older West Siberian stratum of populations, which arrived in the Cis-Baikal potentially as far back as the Paleolithic period (Mooder et al., 2010). Significant movement of peoples during the Neolithic introduced new haplotypes into the region, and the LN/EBA populations belong to this newer genetic stratum (Mooder et al., 2010; Schurr et al., 2010). Compared to modern Siberian Indigenous groups, the Kitoi appear most genetically similar to the geographically distant Kets and Shorians (Mooder et al., 2010; Schurr et al., 2010). The Kets currently inhabit the middle and lower Yenisei River Basin (~1,800 km from Lake Baikal), and modern day Shorian populations are located in the middle Tom River basin and along its tributaries, the Kondoma and Mrass-Su Rivers (~1,600 km from Lake Baikal) (Derbeneva et al., 2002; Ulyanova et al., 2010) Whether this implies that ancestors of the Kets and Shorians once had a much larger distribution or that their progenitors migrated out of the Cis-Baikal at the end of the EN or during the MN remains unclear. The LN/EBA populations cluster closely with contemporary native Siberian populations inhabiting the Baikal region and Iron Age (2,300-1,800 years BP) Mongolians from the Egyin Gol cemetery (Mooder et al., 2010).

Importantly, the chronological change in haplotype frequencies does not mean a total lack of gene flow between EN and LN/EBA populations. Indeed, analysis of dental and cranial non-metric traits implies some degree of genetic continuity between these groups (Waters-Rist, 2011; Movsesian et al., 2014; Waters-Rist et al., 2016). Notably, EN individuals from the Lokomotiv cemetery show a closer relationship to LN/EBA populations than EN South Baikal individuals buried at Shamanka II. Thus, despite substantial genetic change across the MN, the EN population, particularly the groups inhabiting the Angara River Valley, appear to have made some genetic contribution to LN/EBA populations.

This partial biological discontinuity between EN and LN/EBA populations combined with a lack of formal burials in the Middle Neolithic can be interpreted in the following way. The end of the EN coincided with either a migration out of the Cis-Baikal region or a drastic reduction in population size (Weber, 1995; Mooder et al., 2010). By the end of the Middle Neolithic, genetically distinct groups settled in the Cis-Baikal. The decrease in population towards the end of the EN may correlate with environmental change. The termination of EN cemetery use occurs after the spread of Scots pine and increased snow cover would have potentially lead to a decrease in the abundance of terrestrial game. Furthermore, the subsequent onset of more arid conditions occurs close to the end of the EN period, and this may have had a destabilizing effect on aquatic productivity (White and Bush, 2010). Both changes in the abundance of terrestrial game and aquatic productivity may have led to decreases in human population size or triggered migration. The onset of more arid conditions would have also extended areas of desert and semi-desert in northern China and Mongolia, leading to a displacement of hunter-gatherer populations there. These groups may have migrated northwards into the recently depopulated and more hospitable Cis-Baikal region (White and Bush, 2010). However, Weber and Bettinger (2010) caution that, due to the difficulties of reconstructing climate history, it remains unclear if the shift to greater aridity occurred before or after the end of EN cemetery use. Alternatively, decline in population size at the end of the EN may have had nothing to do with a specific environmental change. Weber and Bettinger (2010) hypothesize that a foraging strategy combining hunting and fishing "can be fragile, volatile, and vulnerable in the environment lacking suitable plant foods as a reliable source of alternative food in times of game shortage which is the case in the Baikal region" (p.504). Populations of terrestrial ungulates routinely undergo marked fluctuations, resulting in periods of pronounced resource scarcity. Consequently, considerable oscillations in population size may be a characteristic of boreal forest hunter-gatherer demographics. The genetic history of Middle Holocene populations has relevance to the current investigation, because genetic diversity may account for some chronological variation in skeletal robusticity (Stock et al., 2010).

## **3.5.2 Dietary Reconstructions**

Understanding of chronological and regional variation in diet is also important for studies of bone robusticity. Regional and chronological differences in diet may have coincided with variation in the type of subsistence behaviors that children and adults engaged in, and how frequently they did so. Overall stable isotope analyses indicate that populations from all microregions and archaeological periods relied on a combination of fish and terrestrial game (Weber et al., 2011). Katzenberg and Weber (1999) and Weber et al. (2002) proposed that isotope values from human bone indicated a greater reliance on fish in the EN Kitoi populations and a greater reliance on terrestrial game in the LN/EBA Isakovo/Serovo/Glaskovo. Lumping populations into these two groups obscures geographic heterogeneity in the data. Individuals buried in different microregions exhibit different ranges of carbon and nitrogen isotope values (Weber et al, 2011). This means that individuals foraged primarily in the microregion they were buried in (Weber et al, 2011). Undoubtedly travel between microregions still occurred, and

burials with non-local dietary signatures are present in several microregions, especially the Little Sea (see below).

Study of Little Sea microregion isotopic signatures found that diet showed little change between archaeological periods (Katzenberg et al., 2012). However, individuals from this microregion display two distinct diets during both the EN and LN/EBA (Weber and Bettinger, 2010; Weber et al., 2011; Weber and Goriunova, 2013). One group incorporated terrestrial game, fish, and seals (GFS). The other subsisted only on game and fish (GF). Interestingly, all individuals with local strontium isotope signatures belonged to the GFS group (Weber et al., 2011; Weber and Goriunova, 2013). Non-local individuals exhibited both the GFS and GF diets. Seal appears to have been primarily harvested during the spring, when this animal was sun basking on the lake ice (Weber et al., 1998; Nomokonova, 2011). Thus, the existence of two different non-local diets highlights the potential existence of "two different rounds of seasonal migration" (Weber and Goriunova, 2013, 341).

As was the case for Little Sea populations, Upper Lena individuals show no evidence for greater consumption of aquatic resources during the EN than the LN or EBA (Weber et al., 2011). Recall that fish are less plentiful in this river than in the Angara. This may have precluded an extensive reliance on local fish in either period. Indeed, individuals from this region may have sought out aquatic resources elsewhere. For instance, it has been hypothesized that non-locals interred in the Little Sea spent significant portions of their lives in the Upper Lena (Weber et al., 2011; Weber and Goriunova, 2013).

Only in the Angara microregion does stable isotope analysis offer convincing evidence for a chronological shift in diet towards a decreased reliance on fish in the LN/EBA compared to the EN (Weber and Bettinger, 2010; Weber et al., 2011). As previously discussed, this may reflect greater dependence on terrestrial prey during the LN/EBA due to climate change (White and Bush, 2010; Tarasov et al., 2017). It is equally possible that, in the EN, greater population size and density lead to terrestrial prey depletion, necessitating a greater reliance on aquatic food. Aside from stable isotope data, there is only limited zooarchaeological evidence to support this hypothesis. Only a few Angara habitation sites have been systematically excavated, dated, and analyzed. However, analyses of faunal assemblages from these sites are consistent with human activity depleting prey stocks (Losey et al., 2017). Beginning in the LM period, roe deer remains are more frequent than red deer remains. Roe deer are more resistant to prey depression, but smaller and thus less highly valued game than red deer. Consequently, the increased reliance on roe deer is consistent with prey depression leading to a decrease in hunting efficiency beginning in the LM and extending into the EN. Environmental change can not explain this as both deer species utilize similar habitats (Losey et al., 2017) It is unclear if EN South Baikal microregion populations were also more dependent on fish than terrestrial game compared to LN and EBA groups inhabiting this microregion. Stable isotope analysis of human remains from this microregion has only been carried out for one cemetery, Shamanka II, predominantly composed of Early Neolithic burials (Weber and Bettinger, 2010; Weber et al., 2011; Weber et al., 2016b). Isotopic values of EBA burials have not been compared to those from the EN, precluding analysis of chronological change in diet between archaeological periods. Although chronological change in South Baikal diet has not been directly analyzed, EN South Baikal and Angara River Valley groups appear to have depended on aquatic resources to a similar extent. The abundance of fishing equipment in burials and the positioning of cemeteries near river mouths demonstrates the importance of aquatic food in both regions (Weber and Bettinger, 2010). As "classic" Kitoi burials, defined partly by the presence of abundant fishing equipment, are rare in the two eastern microregions, the greater dependence on fish seen in EN relative to LN and EBA populations may have been limited to the Western Cis-Baikal (Bazaliiskii, 2010).

Furthermore, analysis of the FRE indicates that dependence on aquatic resources increased during the EN in both the Angara and South Baikal microregions (Weber et al., 2016 a,b). This may relate to a reduction in the abundance of terrestrial game during this period, due to either environmental change, prey depression, or a combination of these factors. Despite a chronological change in diet in both the Angara and South Baikal microregions, Shamanka individuals shows more complex patterning with regard to chronological change in diet than Angara individuals. During the EN, this cemetery was used in two discontinuous phases. During the first phase, most individuals with signatures indicating consumption of local lakeshore fish were buried in the NW and SE cluster of the North Sector, as well as in the South Sector (Weber et al., 2016b). While SE cluster individuals with local diets showed increased dependence on fish with time, local diet individuals buried in the NW cluster and South Sector did not. Reliance on aquatic resources also increased in individuals consuming non-local fish. The sole dietary group

representing the second phase of burial also increased their consumption of local lakeshore fish over time.

Although stable isotope analysis and similarities in mortuary practices support dietary similarities between EN Angara and South Baikal populations, there were also some differences. The isotopic range of Shamanka individuals partially overlaps that of EN Angara microregion individuals. The overlap probably results from similarity in the isotopic values of food sources. The geographic proximity of EN cemeteries in these two microregions also makes it very likely that foraging ranges overlapped to some extent (Weber and Bettinger, 2010; Weber et al., 2011; Weber et al., 2016). Still, Shamanka II diets are distinct. Isotope values skew towards the "light end of the carbon axis," and they show a weaker correlation between carbon and nitrogen isotope values than the Angara data set (Weber et al., 2011, 542). This suggests individuals buried at Shamanka incorporated lake fish and seals into their diets, while their Angara contemporaries obtained fish from the Angara River and its tributaries (Weber et al., 2011).

It is equally important that Shamanka individuals show almost twice as much variation in stable carbon and nitrogen isotope values as EN Angara individuals (Weber et al., 2016b). It has been proposed that the wider range of isotope values indicates that individuals buried at Shamanka "constitute a more heterogenous group in terms of their places of origin, and hence with respect to their diets than the Angara groups" (Weber et al., 2016b, p.248). Indeed, more detailed analysis of Shamanka individuals has lead to the identification of dietary groups with distinct isotope values (Weber et al., 2016b). In other words, multiple groups, which obtained fish from different locations, buried their dead at Shamanka. While some individuals consumed local lakeshore fish and seals, others may have acquired fish from the Irkut River to the west, the Angara to the north, Selenga River to the east (the location of the other large cemetery in this region, Fofanovo), or other locations not yet isotopically sampled (Weber et al., 2016b). This data suggests that Shamanka may have served as an important ceremonial and mortuary site for both local groups as well as groups that spent a significant amount of time elsewhere. Therefore, individuals buried here may have differed more with regards to behavior, genetics, and health than individuals buried at contemporaneous cemeteries in the Angara River Valley.

Overall, the prior analysis of stable isotope values has indicated that individuals buried in different microregions utilized distinct foraging ranges. A greater focus on aquatic resources

during the EN appears quite convincing, especially in the Angara and South Baikal microregions. Here dependence on aquatic resources increased throughout the EN. Shamanka individuals show more dietary diversity, implying heterogeneity in the foraging ranges of the groups utilizing this cemetery. In other microregions, diets show little sign of temporal variation, and, in the Little Sea, variation in dietary signatures appears related to differences in seasonal migration that operated throughout the Middle Holocene. All the variation in diet discussed may have correlated with differences in workload and foraging behaviors. This would have altered the mechanical environment that the skeleton adapted to throughout life.

#### 3.5.3 Analyses of Behavior using Skeletal Remains

Analyses of skeletal remains provide direct evidence of both chronological and regional variation in adult behavior. Prior study of adult robusticity is of primary concern to the proposed ontogenetic study, as this data represents the "endpoints" in bone robusticity and shape towards which juveniles grew in different archaeological periods. This section discusses patterning in adult robusticity, in concert with additional insights into behavior produced through studies of osteoarthritis and muscle markers.

The study of adult postcranial robusticity among Middle Holocene hunter-gatherers of the Cis-Baikal region has been the subject of three research articles (Stock et al., 2010; Lieverse et al., 2011; Stock and Macintosh, 2016). These have compared EN and LN/EBA populations to each other and other hunter-gatherer populations. These comparisons support sexual differences in behavior throughout the Middle Holocene, and EN and LN/EBA populations differed with regards to activity levels and levels of terrestrial mobility. To date, no study has separately analyzed the LN and EBA populations (Stock et al., 2010; Stock and Macintosh, 2016).

Throughout the Middle Holocene, males had stronger upper and lower limbs for their body size compared to females (Stock et al., 2010; Stock and Macintosh, 2016). This has been attributed to the sexual division of labor. Specifically, sexual variation in lower limb shape and robusticity has been linked to differences in distance traveled. Greater terrestrial mobility results in a more anteroposteriorly elongated diaphysis due to the greater levels of strains engendered along the anteroposterior axis during locomotion. It also leads to increases in lower limb robusticity. As males have more anteroposteriorly expanded and robust lower limbs in both time periods, it has been hypothesized they engaged in more logistic mobility while females practiced residential mobility (Stock et al., 2010; Lieverse et al., 2011; Stock and Macintosh, 2016). Logistic mobility refers to long distance travel out and back from a base camp by small groups to acquire and return resources. Conversely, residential mobility describes a foraging strategy in which entire groups relocate their residence during moves between resource patches (Kelly, 1995). Cis-Baikal males are specifically thought to have undertaken greater logistic mobility during big game hunting (Weber et al., 2002; Stock et al., 2010; Lieverse et al., 2011; Stock and Macintosh, 2016).

Comparisons of the lower and upper limb across archaeological periods indicate that EN individuals were generally more robust than LN/EBA individuals, which was interpreted to mean that workloads decreased between the EN and LN periods (Stock et al., 2010; Stock and Macintosh, 2016). Chronological reduction in humeral robusticity indicates a general reduction in the loads engendered during manipulative behavior (Stock et al., 2010). The more circular and less reinforced lower limb shafts of LN/EBA males and females relative to their EN predecessors indicate chronological reduction in the distance traveled during either residential or logistic forays, and this decrease appears especially pronounced among females (Stock et al., 2010; Lieverse et al., 2011; Stock and Macintosh, 2016). This change in mobility and workloads has tentatively been linked to game populations being either more dispersed in the EN or the depletion of local game stocks by more concentrated EN populations (Weber et al., 2002; White and Bush, 2010; Stock et al., 2010; Lieverse et al., 2011; Lieverse et al., 2013; Losey et al., 2017). The growing dependence on fish throughout the EN would support either scenario, especially if population increased during this period (Weber and Bettinger, 2010; Weber et al., 2016a,b). Differences in lower limb robusticity and shape cannot distinguish between logistic or residential mobility (Stock and Macintosh, 2016). They merely indicate differences in habitual loading regimens. Studies have therefore relied on ethnographic analogy and comparisons to other archaeological samples to make hypotheses about the extent to which levels of logistic and residential mobility changed between archaeological periods. Several studies have proposed that male hunters may have traveled greater distances to acquire game in the EN than the LN/EBA due to depletion of terrestrial ungulates close to group residences (Lieverse et al., 2007a; Stock et al., 2010; Lieverse et al., 2011; Stock and Macintosh, 2016). Depletion of local terrestrial resources would also account for greater EN female mobility, as they would have had to engage in more intensive localized foraging. Alternatively, one cannot exclude the possibility that entire

EN groups may either have moved residences more frequently or over longer distances than LN/EBA groups (Lieverse et al., 2011; Stock and Macintosh, 2016). These hypotheses are tentative and raise the issue of equifinality. The data most directly support greater workloads and terrestrial mobility in the EN period, but it is unclear if levels of logistic or residential mobility differed between periods.

Examinations of interlimb robusticity ratios and levels of humeral bilateral asymmetry are consistent with the employment of watercraft throughout the Middle Holocene, though, as discussed below, the frequency with which boats were employed remains unclear. Interlimb robusticity ratios, which measure the strength of the upper limb relative to the lower limb, can provide evidence of boat use, because this activity generates high levels of upper limb loading that completely terrestrial hunter-gatherers will not experience. Cis-Baikal values for this ratio fall within the range of other populations known to utilize watercraft (Stock et al, 2010; Lieverse et al, 2011; Osipov et al., 2016). The only exception to this pattern is LN/EBA females, who exhibit reduced ratios of upper to lower limb robusticity compared to EN females and females from other aquatic hunter-gatherer populations (Lieverse et al., 2011). Either LN/EBA females employed watercraft less than their predecessors, or EN females practiced additional behaviors that engendered increased cortical bone apposition in the upper limb (Lieverse et al., 2011). Humeral asymmetry can also be indicative of differences in aquatic mobility. Terrestrial groups more focused on hunting tend to have more asymmetric upper limbs due to the repetitive use of bows and spears (Stock et al., 2010). Aquatic foragers also employ such technology, but the even strains engendered by boat use reduce levels of asymmetry. Fairly equivalent loads appear to have been placed on both arms throughout the Middle Holocene. There is no difference in asymmetry between EN and LN/EBA groups, and the range of percent asymmetry is between the high values exhibited by terrestrial hunter-gatherers that did not employ watercraft and the lower values of aquatic hunter-gatherers.

While boats were likely used in the Middle Holocene, it remains unclear how important they were for subsistence or travel. The biomechanical data consistently shows that Cis-Baikal individuals produce values *between* those of oceangoing and completely terrestrial huntergatherer groups (Stock et al., 2010; Lieverse et al., 2011; Osipov et al., 2016). Thus, boats were likely not as important for fishing or transport as in the oceangoing populations to which the CisBaikal samples have been compared. Zooarchaeological evidence supports only a minor role for boats in subsistence practices. Analysis of fish remains shows that Cis-Baikal hunter-gatherers did not target deep water fish, so, if watercraft were used, they were likely simple craft built for fishing in the shallows or transport along rivers (Losey et al., 2008; Losey et al., 2012). Indeed, there is no archaeological evidence consistent with the construction or storage of larger, more complex craft (Ames, 2002; Scharlotta et al., 2016). Furthermore, other activities associated with aquatic foraging, such as the use of fishing gear and the processing of fish and seals also contribute to humeral hypertrophy characteristic of aquatic hunter-gatherers (Weiss, 2003; Ruff, 2005; Stock et al., 2010). These sources of loading may be as viable an explanation for the "aquatic" signature of Cis-Baikal groups as boat use (Stock et al., 2010; Lieverse et al., 2011).

Studies of osteoarthritis and muscle markers support the existence of chronological changes in terrestrial mobility and workloads (Lieverse et al., 2007a; Lieverse et al., 2009; Lieverse, 2010; Lieverse et al., 2011; Lieverse et al., 2013). Studies of osteoarthritis are based on the premise that repeated activity can cause degeneration of the joint surfaces (Lieverse et al., 2007a). Therefore, variation in osteoarthritis prevalence and distribution may reflect behavioral differences. In Cis-Baikal populations, EN males exhibit osteoarthritis more frequently on the knee joint than EN females and LN/EBA males and females (Lieverse et al., 2007a; Lieverse, 2010). EN females exhibit less vertebral osteoarthritis than LN/EBA females, and LN/EBA populations show no sexual disparity in osteoarthritis distribution. This patterning is consistent with a reduction in male mobility between archaeological periods. Conversely, the chronological increase in spinal degeneration among females suggests greater female mobility or workloads in the LN/EBA. Problematically, the latter conclusion disagrees with studies of lower limb robusticity and shape, which suggest that EN females were more mobile than LN/EBA females (Stock and Macintosh, 2016). Thus, one cannot exclude the possibility that factors other than mobility and workloads determine osteoarthritis prevalence, especially in the vertebral column (Lieverse et al., 2007a).

Analysis of muscle markers proceed from the premise that more frequent or intense activity makes muscle attachment sites on the skeleton, also known as entheses, more prominent (Weiss, 2014). Studies of muscle markers add further nuance to behavioral reconstructions in two ways. Firstly, Lieverse and colleagues (2009, 2011) considered which upper limb muscles were used most extensively. Upper limb muscles involved in boat use were well developed in all Cis-Baikal populations (Lieverse et al, 2009; Lieverse et al, 2011). However, rank patterning, a measure of which upper limb muscle attachments were most developed, were equivalent for EN males, EN females, and LN/EBA males but not LN/EBA females. This, in conjunction with the distinctive inter-limb robusticity ratios of LN/EBA females discussed above, suggests that they engaged in different upper limb activities than their male counterparts or female predecessors (Lieverse et al., 2009, Lieverse et al., 2011).

Second, study of lower limb muscle markers called attention to geographic variation in behavior (Lieverse et al., 2013). This is an important finding since prior studies have focused primarily on chronological change. The EN Angara microregion sample exhibits the highest male and female scores for lower limb muscle marker development, even compared to contemporaries from the South Baikal Shamanka site. LN/EBA Angara individuals demonstrated the third highest values, and their Little Sea contemporaries exhibited the least developed muscle markers. The degree of muscle marker development may correlate with depletion of local terrestrial resources due to differences in population size (Lieverse et al., 2013). For example, the presence of several large EN cemeteries in the Angara microregion may have necessitated greater male travel than in other microregions or archaeological periods due to the depletion of local game populations. The more pronounced muscle attachments of EN Angara females compared to females from other microregions and archaeological periods also suggests higher female workloads or greater travel to access more scarce or distant resources. Like studies of postcranial robusticity, the subsequent reduction in muscle marker development in the LN/EBA Angara sample indicates reductions in workloads. This may reflect less depletion of local terrestrial resources due to reductions in population density or environmental change (White and Bush, 2010; Lieverse et al., 2013). Thus, while previous studies of robusticity have pooled samples by archaeological period, individuals from different microregions and cemeteries may also demonstrate behavioral differences. These findings echo studies of dietary variation, which showed chronological and regional variation in the proportion of terrestrial and aquatic food in the diet.

The exploration of adult long bone robusticity and other skeletal indicators of behavior constitutes important background for a growth study of bone robusticity. In conjunction with

studies of diet, these explorations make clear that behavior exhibited considerable variation chronologically and geographically. Workloads decreased between the EN and LN, and, in the Angara and South Baikal microregions, this was accompanied by a decrease in dependence on aquatic resources. How increased reliance on aquatic food within the EN period affected workloads and behavior remains unclear. There is also strong evidence for a decrease in terrestrial mobility between the EN and LN/EBA. Whether the relative proportion of logistic and residential mobility varied over time or between microregions remains unclear. While sexual disparity in behavior existed in both archaeological periods, differences between the sexes appear to have been especially pronounced in the LN/EBA. Therefore, any future study of Middle Holocene Cis-Baikal behavior should consider both chronological and microregional variation.

#### 3.5.4 Variation in Growth and Developmental Health

An understanding of how developmental health varied during the Middle Holocene also proves pertinent to an examination of bone robusticity during development. Variation in health and nutrition can affect growth in body mass, a major determinant of skeletal load. Studies of this topic in the Cis-Baikal have compared EN, LN, and EBA populations, though these analyses also show some evidence for regional variation. The entire Cis-Baikal skeletal sample exhibits only five cases of metabolic disorders, indicating a low incidence of chronic nutritional deficiency (Lieverse, 2010). Low prevalence of periostitis also testifies to a low level of chronic infections among Middle Holocene populations (Lieverse, 2010). More nuanced insight into stress during the growth period comes primarily from studies of linear enamel hypoplasia (LEH) and skeletal growth.

Enamel hypoplasia is a deficiency in tooth enamel thickness caused by disruptions in the process of enamel secretion, one form of which takes on the appearance of linear or furrow-form defects (LEH) that run around the crown surface (Hillson, 2008). Growth disruptions can result from many factors, but research has demonstrated that hypoplastic defects primarily result from generalized growth stress produced by illness or poor nutrition (Hillson, 2008). As enamel forms during development and cannot be remodeled afterwards, LEH provides a permanent record of episodes of non-specific stress during the growth period when tooth enamel is secreted. Stressors

powerful enough to disrupt enamel secretion may also compromise the accrual of body mass and longitudinal growth (Hillson, 2008).

Analysis of LEH revealed chronological and geographic patterns in the prevalence of enamel defects (Lieverse et al., 2007b; Lieverse, 2010; Waters-Rist, 2011). Children and adults interred in EN cemeteries displayed significantly higher frequencies of LEH than individuals from LN/EBA cemeteries, suggesting higher levels of developmental stress (Lieverse et al, 2007b; Waters-Rist, 2011). Waters-Rist's (2011) analysis of LEH suggests some additional variation between LN and EBA populations. In her study, defect prevalence decreased between the EN and LN before rising again during the EBA. The EN and EBA populations also have similar frequencies of individuals with multiple enamel defects, which indicates multiple incidents of developmental disruption throughout the life course (Waters-Rist, 2011). The LN sample had a significantly lower number of individuals with multiple enamel defects.

Both Waters-Rist (2011) and Lieverse and colleagues (2007b) have pointed out that seasonal food shortages constitute a major challenge for ethnographically documented boreal forest and arctic hunter-gatherers. As the Cis-Baikal also exhibits marked seasonal fluctuation in resource abundance, seasonal food shortages may have been a major cause of developmental stress in the Cis-Baikal populations, where repetitive hypoplasia, when present, occurs on roughly a yearly basis (Waters-Rist, 2011). Following this line of reasoning, it appears that LN populations experienced stress episodes due to seasonal resource shortfalls less frequently than EN populations and EBA populations, perhaps due to lower population densities (Waters-Rist, 2011). Thus, levels of developmental stress may have fluctuated throughout the Middle Holocene. Such an interpretation contrasts with the older view that LN and EBA populations were more like each other than their predecessors in terms of developmental stress (Lieverse et al., 2007b). On the other hand, the LN sample in Waters-Rist's (2011) study was comprised of only individuals from the Angara microregion cemetery of Ust-Ida. Foraging in the ecosystem surrounding Ust-Ida may have "resulted in fewer or less intense food shortages" than experienced by EN and EBA individuals from other areas of the Cis-Baikal (Waters-Rist, 2011, 166). This suggestion of regional variation in health echoes Lieverse et al.'s (2013) study of muscle markers, which found patterning consistent with both regional and chronological variation in behavior. As discussed above, EN populations may have had poorer developmental

health than LN individuals due to their "geographically restricted emphasis on aquatic resources" especially in the Angara and adjoining South Baikal microregions (Lieverse et al., 2007b, 336). The fact that populations in these microregions became more dependent on aquatic resources throughout the EN supports this hypothesis. The rise in hypoplasia during the EBA period may likewise reflect population growth putting renewed pressure on resources, particularly in the Little Sea (Weber and Bettinger, 2010; Waters-Rist, 2011)

Analysis of stature and body mass accrual during growth augments interpretations of enamel defects. LN/EBA adults exhibit higher stature and body mass relative to EN adults (Stock et al., 2010). While genetic differences may play some role, the difference suggests better developmental health during the LN/EBA. Ontogenetic analysis of growth using juvenile remains confirms reduced EN stature and body mass manifests in late infancy and persists into adulthood (Temple et al., 2014). This generally agrees with the finding of hypoplasia research that developmental disturbance was more frequent or more severe during the EN than the LN. However, this growth study only included EN and LN populations from the Angara and South Baikal microregions. A lack of juvenile remains from other microregions and the EBA sufficiently preserved enough to allow stature and body mass estimation preclude wider study of geographic and chronological variation in developmental stress.

Interestingly, differences in body mass and stature between EN and LN juveniles appear around the age of weaning, as determined using isotopic analysis (Waters-Rist et al., 2011; Temple et al., 2014). Weaning is a vulnerable time, because the removal of passive immunity provided by breast milk makes the infant more vulnerable to pathogens. They are also vulnerable to shortages or insufficiencies in solid weaning food. During the EN, the process of weaning also appears to have been more abrupt than in the LN, which would have made individuals more vulnerable to growth disturbances (Waters-Rist et al., 2011). The more gradual weaning of LN infants would have made them less likely to suffer from illness or nutritional shortfall, even though this process occurred at an earlier age in the LN period (Waters-Rist et al., 2011). It is also significant that the majority of EN infants buried in the South Baikal appear to have died while breastfeeding. Mothers milk should have buffered them from resource scarcity or illness, unless these stressors were especially severe (Waters-Rist et al., 2011). Waters-Rist and colleagues (2011) see this, along with the hypoplasia data previously discussed, as evidence for
higher levels of developmental stress compromising the health of EN populations. LN juveniles appear to have been less affected by seasonal stressors that could compromise growth in size and stature than EN juveniles.

Health and behavior both influence skeletal growth. Thus, analysis of the ontogeny of long bone robusticity can yield results that speak to variation in both behavior and developmental stress. Studies of growth and enamel defects in Cis-Baikal populations indicate greater developmental disturbance in the EN than the LN. Developmental stress may also have increased from the LN to the EBA. These differences in developmental health appear to be correlates of changes in foraging strategy, population size, and differences in ecology. Analyses of adult limb robusticity and diet suggest chronological and regional differences in behavior. The long bones of EN adults appear adapted to higher workloads and greater terrestrially mobility than LN/EBA adults. In addition, EN populations that foraged in the Angara River Valley and South Baikal microregion, appear to have depended more on aquatic resources than LN/EBA populations. Regional differences in behavior, and health have not received as much attention as chronological change. However, isotopic analysis indicates that individuals from different microregions utilized distinct foraging ranges, which varied with regards to the abundance of fish and game. Furthermore, EN Angara individuals may have habitually placed higher loads on their skeleton than contemporaneous EN South Baikal individuals. Consequently, there remains much to learn about how behavior and health differed between archaeological periods and in different microregions of the Cis-Baikal during the Middle Holocene. Little is known about the economic role of juveniles and how they learned adult behaviors. As discussed in Chapter 2, it is precisely during this period that adult levels of long bone robusticity and shape become established. Study of the ontogeny of long bone robusticity builds upon prior research concerning diet, health, and behavior to address this important gap in knowledge of Middle Holocene Cis-Baikal life history.

# **Chapter 4: Materials and Methods**

# **4.1 Sample Provenience**

In total, 114 Middle Holocene Cis-Baikal individuals were included in this analysis. The skeletal material exhibited varying degrees of preservation and completeness. To maximize sample size, individuals were included in the analysis if the position of at least one cross-section location of interest could be identified. The definition of these locations and how their position was identified is given in Section 4.5.1 and Table 4.13.

Table 4.1 gives the number of juveniles of indeterminate sex and females and male adolescents and young adults from each cemetery and archaeological period. The reasons that samples are divided into two groups, indeterminate sex juveniles younger than 16 years old and adolescent/young adult females and males, are discussed in the following sections. For detailed descriptions of mortuary traditions and cemeteries see Chapter 3, which deals with archaeological background.

Due to poor skeletal preservation, juvenile long bones from Little Sea cemeteries were unavailable for analysis, and no juvenile burials were available from the Upper Lena microregion. Therefore, this study directly compares ontogenetic patterns of bone robusticity only in Early Neolithic (EN) and Late Neolithic (LN) populations from the Angara River Valley and South Baikal microregions. The EN individuals come primarily from the Lokomotiv and Shamanka II cemeteries. The former cemetery is in the Angara River Valley microregion, the latter in the South Baikal microregion. LN individuals come from the Angara River Valley microregion cemetery of Ust-Ida I. For convenience, Shamanka II is abbreviated as Shamanka and Ust-Ida I as Ust-Ida.

Several individuals were excluded from sample comparisons, but biomechanical properties were calculated and utilized for the analysis of general ontogenetic trends. Four Early Bronze Age (EBA) juveniles from Ust-Ida and Shamanka younger than 16 years were excluded from sample comparisons, because they are unlikely to provide a good approximation of EBA growth. The two EBA Ust-Ida individuals are perinates, exhibiting a level of skeletal maturity consistent with them having died around the time of birth. The EBA Shamanka individuals have estimated ages of 7.5 and 14.5 years. In addition, data was also collected for a single Early

Neolithic individual from the Ust-Belaia cemetery, located in the Angara River Valley microregion. Based on dental development, age was estimated at 1.5 years old. The age and body mass estimations for these individuals are given in Appendix 1 as they may be of benefit for future research. The exclusion of these individuals means that assessment of chronological and inter-cemetery variation in the development of postcranial robusticity prior to the age of 16 years is limited to comparisons of EN Lokomotiv, EN Shamanka, and LN Ust-Ida individuals. However, one should note that graphical and statistical comparisons of all EN individuals to a combined LN/EBA sample produced the same results.

Lastly, the analysis included four EBA adolescents/young adults older than 16 years, for which morphological sex estimation was possible. Their inclusion is necessary to make the current study relatable to prior studies. Past examinations of adult robusticity has predominantly amalgamated adult LN and EBA individuals for comparisons of health and behavior (Lieverse et al., 2007; Lieverse et al., 2009; Stock et al., 2010; Lieverse et al., 2011; Stock and Macintosh, 2015). Conversely, comparisons of juvenile diaphyses have utilized only EN and LN juveniles (Waters-Rist et al., 2011; Temple et al., 2014). To determine if previously observed adult differences are established by the end of adolescence, LN and EBA older adolescents and young adults were combined into a single unit of analysis.

Cemetery	Archaeological period	Indeterminate Sex Juveniles <16 Years Old	Adolescent/ Young Adult Females	Adolescent/ Young Adult Males
Lokomotiv	Early Neolithic	17	8	4
Shamanka H	Early Neolithic	27	5	9
Shamanka II	Early Bronze Age	2	0	3
Ust Ido I	Late Neolithic	30	1	4
Ust-Ida I	Early Bronze Age	2	1	0
Ust-Belaia	Early Neolithic	1	0	0
	Early Neolithic	45	13	13
N by	Late Neolithic	30	1	4
periods	Early Bronze Age	4	1	3
-	Total	79	15	20

Table 4.1: Sample size organized by cemetery, archaeological period, and age cohort

## 4.2 Age Estimation

The sample under study encompasses the age-range over which developmental changes in bone robusticity occur. The youngest individuals are perinates and infants less than one year old. The oldest individuals are young adults; individuals in which dental development and long bone growth is complete, but whose skeletons still show some sign of skeletal immaturity (*e.g.* unfused epiphyses). The growth and maturation of the dentition and skeletal elements proceeds in a predictable sequence that, despite individual and population level variation, shows a strong association with chronological age (Scheuer and Black, 2004; Saunders, 2008). Therefore, assessment of dental and skeletal maturation can provide an estimate of true chronological age for each individual. In this study, age was primarily estimated from dental development. Individuals aged using this method were then used to create standards for age estimation based on bone length. Individuals without preserved teeth or long bones were aged using skeletal fusion. Age estimates, and the method used to calculate them for each individual are provided in Appendix 1. The following sections discuss the techniques employed for age estimation in greater detail.

#### 4.2.1 Dental Age Estimation

Age estimates based on dental development are preferred, because they show the strongest correspondence with chronological age (Liversidge and Molleson, 2004). Dental maturation also varies less due to individual and population level differences in genetics, health, and nutrition than long bone growth and epiphyseal fusion (Tompkins, 1996; Liversidge and Molleson, 2004; Cardoso, 2007; Conceição and Cardoso, 2011; Elamin and Liversidge, 2013). Seventy-five of the Cis-Baikal individuals had a dentition suitable for age estimation. This included 64 individuals with an immature dentition and 11 young adults whose dental development was complete.

Dental age was estimated using the Queen Mary University of London (QMUL) Atlas of Dental Development (Al Qahtani et al., 2010). A dental atlas uses illustrations and charts to record the extent of dental maturation achieved by all teeth within a dentition at fixed chronological intervals. The QMUL atlas was constructed using radiographs of living children and direct observation of the skeletal remains of children of known age. The individuals used to create this atlas ranged in age from 28 weeks in-utero to 23 years old. 176 individuals were younger than two years of age. Fifty of these came from the Spitalfields, London archaeological collection. The other 126 were part of the Maurice Stack collection housed at the Royal College of Surgeons. 528 individuals were available for observation after age two years, and 12 males and 12 females were selected to represent each chronological year. Half of these individuals were Europeans, and the other half were of Bangladeshi ancestry. To create the atlas, individuals were sorted into the following age groups "the seventh, eighth, and ninth month of gestation; birth at midpoint of 2 weeks; the first, second, third, and fourth 3 months of life; and for each chronological year over the age of 1 up to the age of 23 years" (AlQahtani et al., 2010). Minimum, maximum, and median stages of tooth development were recorded for each age group using Moorrees et al. (1963 a,b) developmental stages, and diagrams were created illustrating the median tooth development and eruption stages for each age class.

While many other standards exist for estimating age from whole or partial dentitions (*e.g.* Ubelaker, 1978; Smith, 1991), the QMUL atlas was considered the best choice for several reasons. First, this atlas was employed in Temple et al.'s (2014) growth study of Cis-Baikal juveniles. Using the same standards maximizes compatibility with this earlier work. Second, the QMUL atlas was specifically designed for age prediction, and, unlike other standards, it is based on a reference sample of uniform age and sex distribution (AlQahtani et al., 2014). Finally, the tables providing minimum, median, and maximum developmental stages achieved at each chronological interval aid in determining the best age class for dentitions that could be considered a good fit to two adjacent stages.

To apply the QMUL atlas to the Cis-Baikal sample, dental development was recorded and then matched to the best age class as follows. Moorrees et al. (1963 a,b) dental formation stages, as described and illustrated in AlQahtani et al. (2010) were used to assess the stage of crown and root formation for each permanent and deciduous tooth. Deciduous root resorption was not scored. Teeth embedded in the mandible and maxilla were radiographed using a Nomad GoPro dental X-ray machine and Suni Ray sensor kit. Teeth that had fallen out of alveolar sockets post-mortem were scored visually. If the same tooth from both sides of the jaw was present, the side best visualized in radiographs or visually observed was scored. Thus, scores were recorded for a composite lower and upper quadrant. The number of teeth that could be scored for each individual varied due to differences in preservation. The developmental scores for all available teeth were then matched to the closest age group in the atlas using the tables and charts provided (AlQahtani et al., 2010). To evaluate the consistency of dental age estimation, tests of intra- and inter-observer reliability were conducted using weighted Cohen's Kappa (Cohen, 1960). This follows the methodology employed by numerous studies that score dental maturation stages (AlQahtani et al., 2010). The Kappa statistic (K) measures the agreement between observers for discrete variables (Cohen, 1960). The test rates the strength of agreement between two rounds of observation for the same sample, factoring in the probability that agreement would occur purely by chance. This produces a K value between 0 and 1. A score of 1 indicates perfect agreement, while scores close to 0 indicates a level of agreement which would result due to chance (Cohen, 1960; Landis and Koch, 1977; Sim and Wright, 2005). The commonly utilized standards for assessing the strength of agreement indicated by different ranges of K in biomedical contexts are given in Table 4.2

Table 4.2: Levels of agreement indicated by the Kappa statistic (Landis and Koch, 1977)

Kappa Score	Agreement
0.0-0.2	Slight
0.21-0.4	Fair
0.41-0.6	Moderate
0.61-0.8	Substantial
0.81-1.00	Almost Perfect

Kappa tests can be unweighted or weighted. In unweighted Kappa a disagreement between raters by one stage or rank is considered as serious as a disagreement by multiple ranks. In weighted Kappa the effect of the disagreement depends on the number of categories that raters disagree by. Assigning a greater weight to larger disagreements is desirable for assessment of an ordinal variable such as Moorrees et al. (1963a, b) crown and root stages (Sim and Wright, 2005). Seriation of a continuous process will inevitably lead to borderline cases that observers could legitimately place into one of several consecutive stages. Following the standards commonly employed in medical literature for assessing error in ordinal classification, a quadratic weighting scale was used (Sim and Wright, 2005). This treats misclassification by more than one stage as more serious than disagreement by a single stage. Linear weighted K scores, which treat all disagreements equally, no matter the magnitude of disagreement, are also reported to ensure consistency with other studies. For assessment of intra-observer error, teeth were scored two times a month apart. These rounds were then compared to each other and to scores produced by two other observers (Drs. D. Temple and L. Harrington) for a smaller subset of teeth. There is a small variation in number of teeth scored between scoring rounds due to differences in which teeth it was felt could be confidently scored due to X-ray quality or overlap with other teeth. Results for all comparisons are given in Table 4.3.

Table 4.3: Results of weighted and unweighted kappa tests of intra-observer and inter-observer agreement for classifying tooth stages: (B1-B2: Scoring rounds by Benjamin Osipov; DT: Scoring by D. Temple; LH: Scoring by L. Harrington)

Comparison	Ν	Kappa	Weighted Kappa	% disagreements greater than one stage				
	Intra-Observer error							
B1-B2	223	0.63	0.78	3.59				
Inter-Observer Error								
B1-DT	101	0.49	0.61	2.97				
B2-DT	103	0.5	0.63	2.91				
B1-LH	107	0.21	0.55	14.02				
B2-LH	126	0.52	0.84	7.14				
DT-LH	49	0.2	0.39	18.37				

Overall the tests indicate substantial intra-observer agreement and moderate to substantial inter-observer agreement between myself and other raters according to the standards in Table 4.2. Intra-observer agreement was stronger than inter-observer agreement. Disagreements by more than one stage occurred in less than ten percent of the cases for all but two inter-observer comparisons (Table 4.3). This result further demonstrates the close correspondence between observations. As previously stated, disagreements by one or two stages may reflect the ambiguities involved in scoring borderline cases. They may also result from differences in training and prior experience, particularly the familiarity of each observer with radiographs. The lower levels of agreement between the other two observers may also reflect the smaller sample size of this comparison. Overall, these statistical tests indicate reasonable intra and inter-individual reliability in tooth stage classification. Therefore, any variation between age estimates

would primarily result from differences in the number of teeth scored. Scores from the second round of scoring (B2) were employed for age estimation, because they show the highest interobserver agreement (Table 4.3).

An additional test of intra-observer agreement evaluated the accuracy with which dentitions could be assigned to the age categories in the AlQahtani et al. (2010) tooth atlas. Such a test proved necessary, because, in many cases, dentitions will exhibit characteristics of two or three consecutive atlas diagrams (Liversidge, personal comm, 2015). The observer must therefore decide which age category constitutes the "best" match. Dentitions were assigned an atlas stage three times, and the scores were then compared using Cohen's Kappa. Results are given in Table 4.4. The test indicates near perfect agreement between observations, and differences never exceeded one atlas stage, which corresponds to a difference of one calendar year. In cases of disagreement, it was always the case that two observations agreed and one disagreed. Therefore, the stage chosen twice was used as the final age estimate in these cases. As with the scoring of tooth formation stages, minor differences are expected between observations. Dentitions will often partially match adjacent atlas stages, and the lack of complete dental quadrants contributed to the uncertainty of classifications.

 Table 4.4: Results of weighted kappa of intra-observer error in assigning dentitions to atlas stages

 Test
 N
 Kappa
 Weighted Kappa

1050	1	карра	weighten Kappa
Observation 1-2	64	0.814	0.787
Observation 1-3	64	0.795	0.932
Observation 2-3	64	0.712	0.846

# 4.2.2 Non-Dental Age Estimation

Dental maturation could not be assessed for 36 individuals with unfused long bone epiphyses. The teeth of these individuals were missing, or only fully mature teeth were observed. When developing teeth are not present, age can be predicted from long bone length or skeletal maturation (the appearance and fusion of skeletal epiphyses). Studies comparing long bone growth and skeletal maturation have not produced a clear consensus as to which shows the closest correspondence to chronological or dental age (Conceição and Cardoso, 2011).

For this study, the age of individuals without developing teeth was primarily estimated from long bone length. Length was favored over skeletal fusion for the following reasons. Unlike

long bone length, skeletal fusion is a discrete rather than continuous variable, either fusion has occurred, or it has not. Furthermore, the fusion of the most commonly preserved epiphyses occurs in punctuated bursts (Scheuer and Black, 2004). This means that individuals exhibiting the same "stage" of skeletal maturation may differ widely in chronological age. The extent to which individuals can be seriated based on skeletal maturation also depends on the degree of skeletal preservation. The more epiphyses and metaphyses present for scoring, the more refined the seriation of the sample will be. Consequently, the variable completeness of Cis-Baikal individuals also favors the employment of long bone length rather than skeletal fusion for age estimation.

To create estimates of dental age, Ordinary Least Squares (OLS) regression equations were constructed with dental age as the dependent variable and diaphyseal length of the femur, tibia, humerus, ulna, and clavicle as the independent variables. In cases where only one of the epiphyses had fused to a metaphyseal surface, diaphyseal length was estimated. Fully fused bones were not included in OLS regressions. Temple et al.'s (2014) study of lower limb bone growth found that EN individuals from the Angara River Valley and South Baikal juveniles had significantly shorter femora but not tibiae for age than LN juveniles. Differences in upper limb bone growth were not examined. For the current study, three sets of equations for predicting dental age from bone lengths were created. The first utilized individuals from all archaeological periods. The other two sets were archaeological period specific. One was generated using only EN individuals, and the other utilized LN individuals. The sole EBA individual with complete long bones and a dentition for which maturation could be assessed was also included in this regression analysis.

The equations, R<sup>2</sup> coefficients, and SEE (Standard Error of the Estimate) for equations are reported in Table 4.5. The combined sample and archaeological period specific equations show only small differences in slope, intercept, and SEE. A comparison of the age estimates produced by combined sample and archaeological period specific equations (Table 4.6) indicates small but consistent differences in the relationship between dental age and long bone length between individuals from different archaeological periods. The difference between combined and archaeological period specific age estimates generated by the femur, tibia, and humerus equations is negative for EN individuals and positive for LN/EBA individuals. This means that the EN equations produce higher age estimates and the LN/EBA equations produce lower estimates than those obtained from combined sample equations. This concurs with Temple et al.'s (2014) finding of slower longitudinal bone growth among Early Neolithic individuals. The slightly smaller bone lengths for age of EN individuals leads to systematic underestimation by the combined sample equations, and the opposite trend occurs in the LN/EBA sample. Both the EN and LN/EBA estimations based on the clavicle and ulna show a small negative difference between combined and sample specific equations. This may mean that smaller elements do not show the same differences in growth, or that the differences between individuals from different archaeological periods are too small to affect age predictions.

Table 4.5: Combined sample and archaeological period specific equations for predicting dental age from bone length

Element	N	R <sup>2</sup>	SEE	Equation	
	(	Combin	ed Sam	ple	
Tibia Diaphysis	46	0.94	1.10	Dental Age= .072(x)-6.938	
Femur Diaphysis	46	0.93	1.25	Dental Age= .059(x)-7.119	
Ulna Diaphysis	28	0.95	1.23	Dental Age=.108(x)-8.489	
Humerus Diaphysis	45	0.93	1.30	Dental Age= .090(x)-8.621	
Clavicle Max Length	42	0.92	1.38	Dental Age= .204(x)-10.58	
Early Neolithic					
Tibia Diaphysis	23	0.95	1.19	Dental Age= .074(x)-7.109	
Femur Diaphysis	24	0.96	1.00	Dental age= .060(x)-6.927	
Ulna Diaphysis	19	0.95	1.28	Dental Age= .106(x)-8.046	
Humerus Diaphysis	23	0.95	1.26	Dental Age= .091(x)-8.392	
Clavicle Max Length	20	0.94	1.34	Dental Age=.197(x)-9.787	
Lat	e Neo	olithic/	Early B	Bronze Age	
Tibia Diaphysis	22	0.94	0.92	Dental Age= .070(x)-6.841	
Femur Diaphysis	21	0.89	1.46	Dental Age= .061(x)-7.878	
Ulna Diaphysis	8	0.94	1.11	Dental Age= .124(x)-11.381	
Humerus Diaphysis	21	0.93	1.19	Dental Age=.092(x)-9.565	
Clavicle Max Length	21	0.89	1.43	Dental Age= .219(x)-12.027	

Table 4.6: Average difference in age estimates between combined sample and archaeological period specific regression equations for estimating dental age from diaphyseal length

Archaeological period	Tibia	Femur	Humerus	Ulna	Clavicle
Early Neolithic	-0.321	-0.287	-0.480	-0.042	-0.011
Late Neolithic/Early Bronze Age	0.343	0.317	0.488	-0.033	-0.005

Given the difference in age estimates produced using the largest skeletal elements and to ensure methodologically consistency with a previous publication, the archaeological period specific equations are used to estimate dental age (Osipov et al., 2016). For each individual, the available bone for which the equation had the lowest SEE was used to estimate age. A catalogue listing the age estimation method used for each individual can be found in Appendix 1.

OLS equations produce negative age estimates for several of the youngest individuals. Estimates of age based on skeletal fusion provided by Dr. Angela Lieverse (Lieverse, 2010; Lieverse et al., in press) indicate that these individuals are less than a year old. Thus, the negative age estimates most likely result from using the long bone equations to extrapolate below the age range of the sample with scoreable dentition. For these individuals, age estimates were based on skeletal fusion, because the timing of fusion events in the first year of life has been extensively studied and diagnostic parts of the cranium are often well preserved (Scheuer and Black, 2004). Estimates derived from skeletal fusion were rounded to the nearest half year: zero, one-half, or one year old. Rounding ages to the nearest half year allows these individuals to provide an adequate baseline from which subsequent increases in bone robusticity can be tracked.

## 4.2.3 Young Adults

In this study, the term young adult refers specifically to individuals in which longitudinal bone growth has completed, but their skeletons still show some signs of immaturity (*e.g.* unfused epiphyses and limited dental wear). Studies of bone robusticity accrual must track populations into young adulthood, because, as previously discussed in the literature review on bone functional adaptation (Ch.2), the skeleton gradually loses its heightened "juvenile-like" sensitivity to skeletal loading after adolescence (Sumner and Andriacchi, 1996; Ruff, 2003a, 2003b). Marked increases in body mass and muscle size as the body "fills out" drive continued

accrual of cortical bone. In addition, workloads may change throughout the third decade of life as foraging skills develop. As discussed in greater detail in Chs.8 and 9, some tasks, such as hunting and manufacture of complex tools, are extremely difficult. Proficiency requires not only a requisite amount of physical strength but also many years of training (Sugiyama and Chacon, 2005; Guerven and Kaplan, 2006). Thus, during late adolescence and young adulthood, both physical and behavioral changes may play a role in modulating the final phase of bone accrual towards the adult "endpoint." Therefore, an ontogenetic sample must include young adults to approximate this final stage of growth.

In this study, individuals were classified as young adults if dental development was complete, but epiphyses that fuse in late adolescence or the first half of the third decade remained open. These include the medial clavicle, portions of the iliac crest, the juncture between the first and second sacral centra, and the spheno-occipital synchrondosis. Additionally, to be considered young adults, individuals had to display only slight wear on the canine, premolars, and second molars. The high rate of dental attrition observed in Cis-Baikal populations makes this a valid criterion for identifying young adults (Lieverse et al., 2007b). If dental attrition could not be observed, they had to exhibit pubic symphysis morphology consistent with an age of 18-25 (Haas et al., 1994). A total of 28 individuals fell into this category. Late fusing epiphyses close over a broad age range. For example, the medial clavicle fuses between 20-25 years (Scheuer and Black, 2004). Therefore, it proves impractical to seriate young adults from youngest to oldest. Instead, they were all set equal to the age of 22.5 years old. While this may obscure some age-related variation, what is important for this sample is that they provide a mean "endpoint" and range for ontogenetic series.

## 4.3 Sex Estimation

The study of bone robusticity has the potential to shed light on sexual differences in juvenile behavior and developmental health. However, only DNA analysis can produce reliable sex determinations prior to puberty. This reflects the fact that, because of low levels of sex hormone production, only minor sexual differences in skeletal growth exist prior to adolescence (Grumbach and Kaplan, 1974 cited in D.S. Weaver, 1980; Humphrey, 1998; Scheuer and Black, 2004). Furthermore, the metric and morphological methods for sub-adult sex estimation currently available have been developed on small samples. It is unclear if these small samples accurately represent the true extent of sexual variation in skeletal morphology, and they may prove unreliable when applied to populations that differ markedly in size and shape from the reference group. Molecular sex determinations for several Cis-Baikal juveniles individuals have been made in prior studies (Mooder, 2006; Thomson, 2007; Moussa, 2015). Unfortunately, there are too few to allow comparison between male and female juveniles prior to adolescence.

Beginning in adolescence, increases in sex hormone concentrations lead to more marked sexual differences in the rate and manner of skeletal growth (Humphrey, 1998). Dr. A. Lieverse provided sex estimations for adolescents and young adults, and these were based on pelvic and cranial morphology (Lieverse, personal comm., 2013). She scored them in five classes: indeterminate sex, probable female/male, and female/male. Some further comment on the accuracy of these estimations proves appropriate to address potential ambiguities. The sex of adolescent remains can be estimated only if the relevant parts of the skeleton, the pelvis and cranium, have sufficiently matured. All reviews of sex estimation from skeletal remains consider pelvic morphology the most reliable indicator of sex. As sexual differences develop throughout adolescence, primarily during the growth spurt, it is possible that estimates will prove less reliable for young adolescents than adults (La Velle, 1995; Rogers, 2009). Arguably, if sex estimates are tentative, one should therefore eschew inclusion of sex data in the analysis. However, of the individuals with estimated sex included in this study, only three adolescents, two aged 17.5, one 18-year-old, and one young adult were classified as probable males or females. All other sex estimates were firmly established. As these are older adolescents, the chance of misclassification due to underdevelopment of sexual characteristics is minimal.

## 4.4 Body Mass Estimation: Theoretical Foundations and Methods

Body size has a large influence on skeletal robusticity, because it applies a mechanical load to the skeleton throughout life (Ruff, 2000; Ruff, 2008; Ruff and Larsen, 2014). Consequently, reconstructions of behavior require that biomechanical properties be standardized by an accurate estimate of body mass to account for variation related to body size. Given the importance of body mass as a determinant of robusticity, this section provides an overview of how body mass is estimated from skeletal remains, focusing mainly on the methods applied to juvenile remains. The specific techniques employed for the Cis-Baikal sample are then described.

# 4.4.1 Theoretical Foundations of Body Mass Estimation

Two types of body mass estimation methods are commonly used, morphological and mechanical. Morphological methods reconstruct body size and shape, the two main determinants of body mass, by modeling the body as a cylinder (Ruff, 1991; Ruff et al., 1997). Stature serves as a measure of the cylinder's height, and it is estimated through anatomical reconstruction or from a highly-correlated measure such as femoral length (Auerbach and Ruff, 2004; Ruff et al., 2012). Body breadth serves as a measure of the cylinder's width, and bi-iliac breadth constitutes the best approximation of this measurement that can be taken on skeletal remains (Ruff, 1991; Ruff et al., 1997). These measurements are placed into equations to produce estimates of body mass. The accuracy of these equations has been verified on samples from diverse ecogeographic contexts (Auerbach and Ruff, 2004; Ruff, 2004).

Although the morphometric method is recommended for well-preserved adult skeletons, it cannot be applied to juveniles, since the immaturity of the pelvis and sacrum makes pelvic dimensions an unsuitable proxy for body breadth (Ruff, 2007). For this reason, studies of juvenile skeletal remains use mechanical methods for body mass estimation. These operate on the precept that, because the skeleton's primary mechanical function is supporting the weight of the body, a relationship exists between the dimensions of weight supporting joint surfaces and the body mass of an individual (Auerbach and Ruff, 2004; Ruff et al., 2012). The existence of this relationship has been experimentally verified in humans and animals, and numerous studies have produced regression equations for human adults that allow for the reliable estimation of body mass from the dimensions of weight bearing epiphyses (*e.g.* McHenry, 1992; Grine et al., 1995; Auerbach and Ruff, 2004; Ruff et al., 2012; Squyres and Ruff, 2015). However, the relationship between joint size and body mass is not equivalent across a wide range of body sizes and shapes, and for this reason mechanical estimation formulae prove less accurate when applied to individuals who fall outside the range of body shapes and size included in the reference sample (Ruff et al., 1997; Auerbach and Ruff, 2004; Kurki et al., 2010).

While many mechanical standards exist for adult populations, Ruff (2007) has developed the only equations widely employed in current publications to estimate juvenile body mass from joint dimensions. The equations were constructed using radiographs and body mass measurements from the Denver Growth Study (Maresh, 1943, 1955; McCammon, 1970; Ruff, 2007). The individuals that took part in the growth study were from middle to upper-middle class families of European ancestry. Radiographs of limb bones and anthropometric measurements were taken every 6 months beginning at 2 months after birth until mid to late adolescence from 1941 to 1967. To produce body mass estimation equations, Ruff (2007) regressed radiographic measurements of the superior- inferior diameter of the femoral head epiphysis and distal femoral mediolateral metaphysis breadth on body mass. Equations were constructed for one-year intervals from birth to age 17, "because body proportions vary significantly throughout growth," (Ruff, 2007, 700). Each equation applies to individuals within a half year of the given age. For example, the equation for six-year old individuals would be used to predict body mass for individuals older than 5.5 and less than or equal to 6.5 years of age. Prior to age seven, reliable measurements of the femoral head were not possible, so only distal metaphysis equations could be constructed. Additionally, after age 14, only equations using femoral head diameter were calculated due to overlap of the distal femoral metaphysis by its epiphysis on radiographic images (Ruff, 2007). In the age range in which both measurements can be taken, years 7-13, the femoral head provided the most accurate estimates. The equations for each age cohort are reproduced in Table 4.7.

	Femoral Metaphyseal Breadth						Femora	al Head	Breadth	
Age (years)	Slope	Int.	CF <sup>a</sup>	%SEE	SEE	Slope	Int.	CF <sup>a</sup>	%SEE	SEE
1	0.751	-0.45	1.003	7.1	0.64					
2	0.994	-1.28	1.001	4.8	0.56					
3	0.899	-0.86	1.002	4.8	0.65					
4	1.048	-1.35	1.002	6.5	1.02					
5	1.096	-1.47	1.002	6.2	1.09					
6	1.034	-1.16	1.002	6.6	1.32					
7	1.095	1.33	1.002	6.3	1.43	0.65	0.92	1.002	6.2	1.41
8	1.01	-0.9	1.004	9.2	2.32	0.749	0.64	1.003	7.9	2.01
9	1.524	-2.89	1.01	14.4	4.13	1.286	1.12	1.006	11.3	3.24
10	1.939	-4.55	1.012	15.8	5.02	1.374	1.41	1.009	13.9	4.42
11	1.690b	-3.46	1.016	18	6.45	1.582	2.11	1.011	14.7	5.28
12	2.263	-5.82	1.015	17.6	6.97	1.725	2.62	1.009	13.5	5.31
13	1.766b	-3.67	1.019	19.7	8.74	1.666	-2.35	1.014	16.7	7.41
14						1.226	-0.68	1.011	14.9	7.44
15						c	_	_	_	_
16						0.842 <sup>b</sup>	0.88	1.009	13.6	6.03
17						1.327	-0.94	1.006	11.4	7.01

*Table 4.7: Ruff (2007) equations for body mass prediction (all measurements natural log transformed prior to calculation)* 

<sup>*a*</sup> correction factor by which to multiply detransformed (raw) estimate

<sup>b</sup> regression near significant (.05<p<0.10)

<sup>c</sup> p>0.10; no equation given

The equations appear to perform reasonably well across development, but the method has several limitations. Estimates for the Denver sample were most accurate early in life, with percent standard error of the estimate (%SEE) ranging from 5 to 7% between years 1-7 (Table 4.7). Prediction errors increased thereafter, and, in individuals older than 10.5, the average prediction error exceeded 13%. Problematically, the relationship between femoral head circumference and body mass was non-significant for the 15 and 16-year-old cohorts (14.5-16.5 years). The trend of increasing prediction error from age eight onwards reversed itself in the 17-year-old cohort, indicating "smaller and more stable patterns of weight change" (Ruff, 2007, 704). The generally poorer performance of equations during adolescence likely reflects the volatile nature of weight changes during this period, a result of increasing idiosyncratic variation in activity levels and diet. Sciulli and Blatt (2008) tested the equations created by Ruff (2007) on a morgue sample of mixed ancestry and varied socio-economic status. Only the distal femur was available, so equations could only be tested up to the 12<sup>th</sup> year. Still estimation errors were

similar in magnitude and followed the same pattern as in the Denver sample, increasing markedly in individuals older than eight years.

Overall the body mass estimation equations developed by Ruff perform well, but several limitations should be kept in mind. Estimate errors increase in later childhood and adolescence. Furthermore, the estimates could be skewed if age is estimated incorrectly. While these equations perform well on modern samples, they may not completely control for differences in body mass within past populations. Cowgill (2010) and Osipov et al. (2016) found that patterning in the size-standardized robusticity of juveniles from past populations seemed to correspond as much with expected differences in weight as activity. The Ruff (2007) formulae overestimated the mass of low body size populations and underestimated the weight of larger populations. The detection of such patterning is not entirely surprising, because the equations were devised using a single modern urban population. Past groups may show a different relationship between growth in joint dimensions and body size. This is exacerbated by the fact that diaphyseal breadths appear more sensitive to mechanical loading, including that introduced by body mass as well as activity, than joint dimensions (Lieberman et al., 2001; Cowgill, 2010). Therefore, while joint dimensions may provide good indications of inter-species differences in body size, diaphyseal architecture may be a more sensitive indicator of differences in both activity and body size in intra-species comparisons (Lieberman et al., 2001). For the study of Cis-Baikal juveniles this raises the possibility that differences between groups in sizestandardized CSG will still reflect variance in body size as well as activity. To assess if this was the case, both size-standardized and size-unstandardized CSG values regressed on age were compared. This is discussed in greater detail in Section 4.7.

# 4.4.2 Body Mass Estimation for Cis-Baikal Individuals <17.5 years old

For the Cis-Baikal sample the Ruff (2007) distal femoral metaphysis equations were used for individuals 6.5 years of age or younger, and the femoral head equations were used for older individuals. The body mass estimates produced using log transformed measures were multiplied by an equation specific correction factor calculated by Ruff (2007) (Table 4.7). This accounts for the bias introduced by detransforming a logarithm. Twenty body mass predictions were made from the distal femoral metaphysis and 25 body mass predictions were made from the femoral head.

# 4.4.3 Body Mass Estimation in Cases for which Ruff (2007) Equations could not be used for individuals <17.5 years old

Three additional methods of producing a body mass estimate had to be used in 35 cases in which the Ruff (2007) equations could not be applied. Six individuals fell into the 15 and 16year-old cohorts (14.5-16.5 years of age), for which no statistically significant equations to predict body mass exist. Another 19 individuals did not have preserved femoral joint surfaces, but the dimensions of other joint surfaces or long bone lengths could be measured. Lastly, eight individuals, the majority less than a year old, were represented by diaphyses with damaged metaphyseal surfaces or they were represented only by an element for which measures of joint dimensions were not collected (ulna midshaft and clavicle midshaft).

For the six individuals between 14.5-16.5 years old, the relationship between body mass and femoral head dimensions for this age class of the Cis-Baikal sample was modelled using interpolation. OLS regression of femoral head breadth on body mass estimates for individuals on either side of this age cohort was used to create equations for body mass estimation. Individuals aged 13.5-14.5 years old were the youngest individuals included in this regression. Adolescents older than 17.5 years old and young adults served as the upper range for interpolation. The inclusion of young adults is appropriate, because Ruff (2007) found that, by the age of 17 years, body mass estimates produced using adult body mass equations were only three percent larger than those produced by the 17-year-old equation, and this difference was not statistically significant. The regression equation and statistical measures of accuracy are provided in Table 4.8.

*Table 4.8: Regression equation used to predict body mass in individuals between 14.5-16.5 years old using the femoral head* 

Ν	Equation	R <sup>2</sup>	SEE
23	2.236*(femoral head SI breadth)-39.921	0.927	1.997

The femoral joint surface required for mass estimation was not preserved in 19 individuals for which an age cohort equation was available. Following Cowgill (2010) and Harrington (2010), femoral joint dimensions were estimated from the size of other joint surfaces and diaphyseal lengths using OLS regressions. These estimation equations were calculated over the age range for which each skeletal dimension could be used to generate a body mass estimate in Ruff (2007), 0.5-13.5 years of age for the distal femur metaphysis and 6.5 to 17.5 years of age

for the femoral head epiphysis. The equations,  $R^2$  values, and SEE are given in Table 4.9 for the distal femur metaphysis and for the femoral head in Table 4.10. The equation with the lowest SEE was used when multiple measures were available, and the number of predictions made from each equation is given in Table 4.11.

*Table 4.9: Equations for predicting distal femur metaphysis mediolateral breadth (individuals aged 0.5-13.5) (ordered by SEE values)* 

Measurement <sup>a</sup>	Ν	Equation	R <sup>2</sup>	SEE
Tibia proximal metaphysis ML breadth	29	1.062x+4.222	0.918	2.94
Femur distal epiphysis ML breadth	21	.646x+15.553	0.859	3.305
Humerus head AP diameter	10	1.104x+19.968	0.774	3.554
Femur diaphysis length	31	.140x+12.494	0.863	3.762
Femur proximal metaphysis SI diameter	33	1.587x+4.193	0.821	3.897
Ulna diaphysis length	17	.256x+7.520	0.843	4.028
Clavicle maximum length	25	.472x+4.570	0.799	4.064
Humerus diaphyseal length	28	.188x+12.750	0.809	4.097
Tibia proximal epiphysis ML breadth	21	.620x+20.624	0.752	4.122
Tibia diaphyseal length	32	.175x+11.959	0.833	4.156
Tibia distal epiphysis ML breadth	21	1.015x+17.945	0.558	4.512
Femur proximal epiphysis SI diameter	22	.911x+21.691	0.581	4.559
Tibia distal metaphysis ML breadth	19	1.397x+9.868	0.741	4.665

<sup>a</sup>SI= Superioinferior; AP=Anteroposterior, ML= Mediolateral

*Table 4.10: Equations for predicting femoral head superior-inferior breadth (individuals aged 7.5-17.5) (ordered by SEE values)* 

<b>Measurement</b> <sup>a</sup>	Ν	Equation	$\mathbb{R}^2$	SEE
Tibia proximal epiphysis ML breadth	23	.542x+5.080	0.907	1.702
Femur proximal metaphysis SI diameter	25	1.071x+1.506	0.822	2.408
Tibia distal metaphysis ML breadth	12	.987x+4.188	0.779	2.423
Femur distal epiphysis ML breadth	22	.528x+3.161	0.839	2.566
Femur diaphysis length	23	.096x+6.556	0.761	2.629
Tibia diaphysis length	23	.118x+6.615	0.738	2.695
Tibia distal epiphysis ML breadth	25	.913x+3.999	0.731	2.941
Humerus diaphysis length	23	.137x+5.465	0.715	3.103
Tibia proximal metaphysis ML breadth	20	.600x+6.838	0.693	3.154
Femur distal metaphysis	25	.627x+1.250	0.744	3.175
Ulna diaphysis length	17	.157x+6.890	0.746	3.242
Humerus head AP diameter	12	.702x+13.551	0.755	3.252
Clavicle maximum length	20	.286x+5.898	0.625	3.793

<sup>a</sup>SI= Superioinferior; AP=Anteroposterior, ML= Mediolateral

Distal Femur Metaphysis			
Measure	Number Estimated		
Distal femur epiphysis breadth	1		
Clavicle maximum length	3		
Femur proximal metaphysis breadth	5		
Ulna diaphyseal length	1		
Tibia proximal metaphysis breadth	4		
Femur diaphysis length	1		
Total Estimated	15		
Femur Head Superior-Infe	rior Breadth		
Femur proximal metaphysis breadth	2		
Tibia proximal epiphysis breadth	1		
Clavicle maximum length	1		
Total Estimated	4		

Table 4.11: Number of individuals for which femoral joint dimensions were estimated from other skeletal measures

Finally, only diaphyses missing metaphyseal ends were available for eight individuals, and this prevented measurement of either length or metaphyseal dimensions. Five of the individuals are less than a year old. The two other individuals were older than 1 year, one 2.5 and the other 3.5 years old respectively. Cowgill (2008) proposed that, in the absence of joint dimensions, one can fit a curve to a bivariate plot of age and estimated body mass to approximate the body mass individuals should attain at a given age. Problematically, in the Cis-Baikal sample, archaeological period specific regressions did not provide a good fit for perinates, they actually made them appear heavier than older individuals in each archaeological period. This likely reflects extrapolation beyond the age range for which independent body mass from age. The way in which the potential problems of homogenization between archaeological periods created by this approach are addressed is given following the description of the curve fitting.

Separate regressions were constructed for different age ranges. Figure 4.1. shows the results of locally weighted (LOESS) regression of body mass on age, which approximates localized trends in the data. This demonstrates an inflection point after five years. After this

point, the slope of the line increases, suggesting that body mass accrues at a faster rate. To account for this potential change in growth rates two regression equations were constructed for separate age ranges. The age of 6.5 years was specifically chosen as a cut-off point, because different femoral dimensions were used to produce body mass estimates in younger and older individuals.

For individuals aged less than 6.5 years, linear, quadratic, and cubic polynomial curves were fit to the data. A quadratic curve had the lowest Standard Estimate of the Error, so body mass estimates from this equation were used. A scatterplot of body mass estimates for individuals aged 0.0-6.5 years old with the quadratic curve used for body mass estimation fit to the data is given in Figure 4.2. A single individual with a dental age of 10.5 years did not have a preserved joint dimension. Body mass was calculated from a curve fit to individuals aged between 7.5-18.0 years old. As with the regression for younger individuals, a quadratic polynomial provided the best fit. A plot of body mass against age for individuals aged 7.5-18.0 years is given in Figure 4.3 with the quadratic curve used for body mass estimation fit to the data. The polynomial regressions used to predict body mass from age for both portions of the sample are given in Table 4.12 along with sample size and R<sup>2</sup> coefficients.

Using a regression equation based on a pooled sample to predict body mass may understate differentiation in body mass between EN and LN individuals. However, most individuals for which this method was used are a year old or younger. In this age range, the Ruff (2007) equations exhibit more error than subsequent age cohorts, because the femur does not play a major weight bearing role prior to the onset of bipedal locomotion (Table 4.7). Thus, it is unclear that a regression of body mass on age would prove any less accurate than one that uses joint surfaces. Also, most of errors introduced by this approach would be confined to this age range. Secondly, as discussed in Section 4.7, the results of analysis of size-standardized biomechanical properties are compared to results obtained from regression of sizeunstandardized properties on age. This comparison explicitly considers how limitations in juvenile body mass estimation techniques affect sample comparisons.

Table 4.12: Equations for interpolating body mass from age

Age Cohort	N	Equation	$\mathbb{R}^2$
<6.5	18	Body Mass= 0.065*(age)2+1.08*(age)+6.65	0.909
>6.5	27	Body Mass= -0.06*(age) <sup>2+5.17*(age)-15.49</sup>	0.826

Figure 4.1: Body mass estimates against age for individuals 0.0-18.0 years old with LOESS curve and visually assessed inflection point marked.







Figure 4.3: Body mass estimates against age for individuals 6.6-18.0 years old with OLS regression curve (Equation: Body Mass= -0.06\*(age)<sup>2</sup>+5.17\*(age)-15.49, R<sup>2</sup>=.826)



## 4.4.4 Young Adult Body Mass Estimation

Body mass estimates for individuals 18.5 years old or older were derived using adult formulae. One 17.5-year-old did not have a preserved femoral head, so body mass was estimated using a young adult formula for the proximal tibia (Squyres and Ruff, 2015). This should result in a sufficiently accurate estimate. Ruff (2007) noted that, in the 17-year-old cohort of the Denver Growth Study sample, adult body mass estimation formulae produced estimates that were only three percent lower than those calculated using the cohort specific equation.

For this study, the body mass of young adults was primarily estimated using the sex appropriate formulae for adult femoral head breadth in Ruff et al. (2012). These standards were derived from a chronologically and eco-geographically diverse sample of skeletons from Holocene European contexts. Most of this sample consists of archaeological specimens, so true body mass was not known. Body mass calculated using the morphological method thus served as a proxy. This is appropriate given the stronger relationship between true body mass and morphological body mass estimates than mechanical estimates. The Ruff et al. (2012) standards are preferred over other mechanical methods due to the large size and diverse origins of the reference sample. Importantly, a substantial number of the individuals come from high latitude northern European populations. This means the Cis-Baikal individuals should fall within the range of body sizes and shapes represented in the reference sample. Older standards are based on smaller samples, and studies have found that their accuracy decreases when applied to populations that differ in terms of average body size and shape (Auerbach and Ruff, 2004).

In cases where the femoral head could not be measured, the equations for knee joint dimensions created by Squyres and Ruff were used (2015). These equations were based on radiographic data from individuals participating in the ongoing Baltimore Longitudinal Study of Ageing. Most individuals followed for this study are of European ancestry, but a substantial number of people from other ethnic backgrounds also participate. This standard should provide comparable estimates to the femoral head, because the knee joint plays a considerable role in supporting the weight of the body (Squyres and Ruff, 2015).

# 4.5 Long Bone Cross-Sectional Geometry

## 4.5.1 Cross-Section Locations

Cross-section locations for each limb element studied are given in Table 4.13 along with the abbreviations used for them. By convention, percentages of bone length are calculated from the distal end. Midshaft sections were taken at 50% of diaphyseal length. The only exception is the juvenile femur. Following Ruff (2003 a, 2003b), the equivalent of the adult midshaft location is 45.5% of diaphyseal length, because the distal epiphysis makes a greater contribution to total length than the proximal one. Other sections are taken either adjacent to landmarks on each element or at set percentages of diaphyseal length.

Table 4.13 List of cross-sections included in the study (all percentages of bone length calculated from distal end)

Abbreviation	Description		
Upper Limb			
R/L/Avg Clav Mid	Midshaft (50%) Clavicle Right, Left, and Average		
R/L/Avg Hum Mid	Midshaft (50%) Humerus Right, Left, and Average		
R/L/Avg Hum Dist	Distal Humerus (35%) Right, Left and Average		
R/L/Avg Ulna Mid	Midshaft (50%) Ulna Right, Left, and Average		
Lower Limb			
Fem ST	Femoral Subtrochanteric. Taken inferior to the lesser trochanter on the best-preserved femur.		
Fem Mid	Femoral Midshaft (50%) taken on the best-preserved femur at 45.5 % when distal metaphysis unfused, 50% for bones in which distal end has fused.		
Tib NF	Tibia Nutrient Foramen. Taken inferior to the nutrient foramen on the best-preserved tibia.		
Tib Mid	Tibia Midshaft (50%) taken on the best-preserved tibia.		

The section locations were selected to ensure compatibility with prior biomechanical studies of both juveniles and adults (Stock and Pfeiffer, 2004; Stock, 2006; Cowgill, 2008; Cowgill, 2010; Harrington, 2010; Gosman et al., 2013; Cowgill, 2014; Davies and Stock, 2014; Shaw et al., 2014). Additionally, use of multiple locations within each limb allows comparisons of variation in mechanical environment between limb segments. The use of two sections in the femur, tibia, and humerus further quantifies intra-diaphyseal mechanical variation within the largest elements (Ruff, 2003 a,b; Cowgill, 2008; Harrington, 2010; Cowgill, 2014). As previous

investigations found low levels of asymmetry in lower limb robusticity, the best-preserved femur and tibia from either side were selected for cross-section extraction (Auerbach and Ruff, 2004; Harrington, 2010). Upper-limb cross-sections from both sides of the body were analyzed whenever possible to account for bilateral asymmetry (Trinkaus et al., 1994). The average of upper limb cross-sectional properties for both sides was also reported. If only one section was available, this value was reported as the average.

Several bones were missing either the proximal or distal end due to taphonomic damage. This did not prevent the identification of sections defined by the position of osteometric landmarks (*e.g.* femur subtrochanteric, tibia nutrient foramen). To define sections taken at set percentages of bone length, the length of the element from the other side was used if possible. If the element from the opposite side was missing or also incomplete, total length was estimated provided the diaphysis only showed limited damage. Specifically, the presence of metaphyseal flare was used as an indication that the diaphysis was complete enough to estimate percentages of bone length with an acceptable degree of accuracy. When section locations could not be determined with a high degree of confidence, the element was excluded from analysis.

## 4.5.2: Cross-Sectional Geometry (CSG) Variables

It has been customary to model long bones as beams, cylindrical structures with "fairly straight long axes whose length is several times greater than their width and depth" (Lieberman et al., 2004, p. 157). When subjected to loading, limb bones behave much like structural beams (Ruff and Hayes, 1983a,b; Ruff et al., 1993; Ruff, 2008). Thus, beam theory, the theoretical framework applied to the assessment of structural integrity in engineering allows the quantification of mechanical competence in diaphyseal cross-sections. In these models, calculation of CSG quantifies the rigidity of the cross-section, its ability to withstand deformation when subjected to mechanical loading. Beam theory recognizes several distinct types of loading, which correlate well with the loadings experienced by elements of the appendicular skeleton during movement (Carter and Beaupre, 2001; Pearson and Lieberman, 2004). Axial strain results from compression, the application of load parallel to the long axis of the element. The most common source of compressive loading is the weight of the body pressing down on the element. Movement of the limb bones results in bending of the diaphysis, the

generation of force perpendicular to the long axis of the bone. Movement also engenders torsion, the application of force in a twisting motion, as in the rotation of the arm.

Analysis of Cross-Sectional Geometry (CSG) quantifies bone size and its resistance to compression, bending and torsion. This section describes the variables employed for analysis. Section 4.6 describes how models of cross-sections were created and analyzed to obtain CSG values for each individual. A list of variables used to quantify robusticity and the abbreviations used for them in tables is given in Table 4.14.

Property	Abbreviation	Definition
	Area	Measurements
Total Subperiosteal Area	ТА	Total area within bone cross-section (mm <sup>2</sup> )
Cortical Area	CA	Area of cross-section occupied by cortical bone (mm <sup>2</sup> )
Medullary Area	MA	Area of the medullary cavity (mm <sup>2</sup> )
Percent Cortical Area	%CA	(CA/TA)*100
	Second Mo	ments of Area (SMAs)
Second moment of area about the mediolateral axis	I <sub>x</sub>	Anteroposterior bending rigidity (mm <sup>4</sup> ) (superioinferior bending rigidity in the clavicle)
Second moment of area about the anteroposterior axis	I <sub>y</sub>	Mediolateral bending rigidity (mm <sup>4</sup> ) (anteroposterior bending rigidity in the clavicle)
Maximum second moment of area	I <sub>max</sub>	Maximum bending rigidity (mm <sup>4</sup> )
Minimum second moment of area	I <sub>min</sub>	Minimum bending rigidity (mm <sup>4</sup> )
Polar second moment of area	J	Torsional and (twice) average bending rigidity (mm <sup>4</sup> )
	S	shape Ratios
Anteroposterior versus mediolateral second moments of area	$I_x/I_y$	Shape as described by ratio of anteroposterior bending rigidity to mediolateral bending rigidity
Maximum second moment of area versus minimum second moment of area	$I_{max} / I_{min}$	Shape as described by ratio of maximum to minimum bending rigidity
	Limb l	Robusticity Ratios
Femoral to Humeral Midshaft Robusticity Ratio	Fem/Hum	The ratio of Femur 50% to Humerus 50% for any CSG property. Calculated for TA, CA, MA, Percent CA, and J.
Tibial to Humeral Midshaft Robusticity Ratio	Tib/Hum	The ratio of Tibia 50% to Humerus 50% for any CSG property. Calculated for TA, CA, MA, Percent CA, and J.
		Asymmetry
Absolute Percent Asymmetry	ABS %ASYM	The absolute values of the difference between the left humerus and right paired upper limb sections divided by the average* 100. Asymmetry is calculated for all upper limb area measurements, second moments of area, and shape ratios.
Directional Percent Asymmetry	DA %ASYM	The difference between the left and right paired upper limb sections divided by the average*100. Negative values indicate right arm dominance, positive values indicate left are

dominance. Calculated for all upper limb area measurements, second moments of area, and shape ratios.

Table 4.14: List of cross-sectional properties analyzed for this dissertation (Adapted from Ruff, 2008)

# 4.5.2.1 Diaphyseal Areas and Second Moments of Area (SMAs)

To calculate area measurements, software programs for biomechanical analyses of crosssections, discussed in Section 4.6, divide the image into small squares, count the number of pixels that fall within the relevant portion of the cross-section, and report the results in millimeters squared (Ruff, 2008). The areal measurements employed are total area, cortical area, and medullary area. Total Area (TA) measures the entire area encapsulated by the cross-section's sub-periosteal border. Cortical Area (CA) measures the amount of cortical bone, and Medullary Area (MA) indicates the size of the medullary cavity. Percent CA (%CA) represents the proportion of the diaphysis occupied by cortical bone.

With regards to the mechanical relevance of these properties, TA provides a basic measure of bone size perpendicular to the long axis. This shows a strong correlation with resistance to torsion and bending (Stock and Shaw, 2007). As a measure of the amount of bone in a section, CA is most directly indicative of a cross-section's resistance to axial loads, compressive forces that run parallel to the long axis of the bone (Ruff, 2008). As MA quantifies empty space, it has no direct biomechanical relevance. However, comparing changes in TA, CA, and MA allows for an understanding of rates of periosteal and endosteal bone deposition and resorption during growth. %CA indicates the amount of the cross-section taken up by cortical bone. As a ratio, this variable is size free, meaning it does not have to be standardized for differences in body size.

Loading of long bones predominantly engenders bending and torsion of the diaphysis rather than direct compression (Ruff, 2008). Bending rigidity is calculated about an axis, a line running in any direction that passes through the section's center point, referred to as the centroid (Ruff and Hayes, 1983a; Biewener, 1992). In biomechanics, the term "about" means that bending is engendered at a right angle to the axis in question. In other words, bending involves the application of force perpendicular to a specified axis. Resistance to bending about an axis is measured using Second Moments of Area (SMAs). By convention SMAs are referred to with the letter "I." Software for the biomechanical analysis of cross-sections quantifies Second Moments of Area (SMAs) by dividing cross-sections into small squares, counting the number occupied by cortical bone, and multiplying these by their squared distance from the axis of interest (Lieberman et al., 2004). As the product of an area measurement times square distance, SMAs are reported in millimeters to the fourth power.

SMAs are commonly measured relative to four standardized axes. Bending in the anteroposterior plane or front to back occurs about the mediolateral axis (x). Therefore, anteroposterior bending rigidity is termed  $I_x$ . Bending in the mediolateral plane occurs about the anteroposterior axis and is referred to as  $I_y$ . One can also calculate the maximum and minimum bending rigidity of a cross-section. These variables are referred to as  $I_{max}$  and  $I_{min}$  respectively. Programs that calculate CSG automatically identify and measure bending rigidity about the axis in which a section is most reinforced ( $I_{max}$ ), and where it is weakest ( $I_{min}$ ). Unlike all other elements, the clavicle's long axis runs mediolateral instead of superioinferior. For this reason,  $I_x$  measures superioinferior bending rigidity and  $I_y$  measures anteroposterior bending rigidity in this element.

The last SMA calculated for biomechanical analysis is the polar second moment of area. By convention this is referred to as J (Ruff, 2008). This measures the cross-section's resistance to torsion, and it is also proportional to average bending resistance of the cross-section. This is so, because in a roughly elliptical section, the sum of two perpendicular bending moments is approximately twice the average bending rigidity experienced about all axes (Beweiner, 1992; Ruff, 2008). Thus, J commonly serves as a measure of overall robusticity. J can be calculated by summing the bending rigidity about any two perpendicular axes, either  $I_x$  and  $I_y$  or  $I_{max}$  and  $I_{min}$ . In this study, the sum of  $I_{max}$  and  $I_{min}$  was used unless biomechanical properties were calculated using the Ellipse Model Method, in which case  $I_x$  and  $I_y$  are summed for J (see Section 4.7.2).

SMAs directly measure bone rigidity, which refers specifically to "the internal resistance of a structure to an externally applied mechanical loading" (Ruff and Hayes, 1983a, 359). Strictly speaking, rigidity is not the same as bone "strength", which in biomechanics refers to the maximum stress that the material furthest from the center along a specific axis can withstand prior to failure (Ruff and Hayes, 1983a, 1983b). These types of measurement are referred to as section moduli. However, patterns of variation in bone strength correspond closely to those observed for bone rigidity. Therefore, the literature often uses the terms rigidity and strength interchangeably (Ruff and Hayes, 1983a; Beweiner, 1992).

#### 4.5.2.2 Shape

An analysis of shape is informative, because the consistent application of greater bending loads in a certain direction will lead to greater deposition of cortical bone about axes that experience the greatest bending loads (Ruff et al, 2006). Shape has traditionally been quantified using ratios of perpendicular bending moments either  $I_x$  and  $I_y$  or  $I_{max}$  and  $I_{min}$  (Ruff, 2008). Equivalent bending of a diaphysis about perpendicular axes will produce a circular cross-section and an SMA ratio close to one. Uneven bending engenders greater deposition about one axis, which results in a more oval diaphysis, and an SMA ratio markedly lower or greater than one. Shape ratios ( $I_x/I_y$  and  $I_{max}/I_{min}$ ) were calculated for all cross-section locations.

## 4.5.2.3 Interlimb Robusticity Ratios

Ratios of limb robusticity compare CSG from different limbs. The chief heuristic value of such ratios is that they compare the structural rigidity of weight bearing to non-weight bearing elements. Following previous biomechanical studies of interlimb robusticity ratios, this study compares CSG of the femur and humerus midshaft or the tibia and humerus midshaft (Ruff, 2003b, 2009; Shaw and Stock, 2013). The midshaft locations were selected, because they allow comparison of external and internal dimensions. Ratios of TA, CA, MA, and J were calculated. Of the SMAs, the second polar moment of area (J) is selected, because it represents both torsional and average bending rigidity (Ruff, 2008). Therefore, it provides a good overall approximation of bone rigidity.

## 4.5.2.4 Asymmetry

Asymmetry is evaluated for paired left and right upper limb cross-sections from the same individuals. This demonstrates differences in limb loading that can arise from behavior or use of tools that lead to a differential loading of the dominant and non-dominant limb (Trinkaus et al., 1994). Asymmetry was calculated in two ways. Absolute asymmetry is the absolute value of the percent difference between the left and right section divided by the average of both sections. This shows the absolute magnitude of the difference between sides. Directional asymmetry is the same calculation, but the absolute value of percent difference is not taken. This variable allows the evaluation of side dominance throughout ontogeny, because right dominant individuals will produce negative values and left dominant individuals will produce positive values. Asymmetry is analyzed for all upper limb area, SMA, and shape ratio measurements.

## 4.5.3 Limitations of CSG Analysis of Bone Loading

The reconstruction of loading histories from CSG must acknowledge several limitations. First, experiments on animal models have shown that the neutral axis of a cross-section, the axis about which maximum bending loads are experienced, does not lie in the same plane as the experimentally measured axis about which bending occurs during normal movement (Demes et al., 1998, 2001; Lieberman et al., 2004). This means that cross-sections are not necessarily reinforced in the regions that experience the highest strains during movement (Ruff et al., 2006a). This issue would particularly affect reconstructions of shape from SMA ratios, as the strain gauge studies would suggest that greater bending rigidity about one plane does not necessarily mean bone experienced the greatest strains about that axis *in-vivo*. Another important limitation is that the neutral axis passes through the section center or centroid, but the actual bending axis does not. This occurs due to bones simultaneously experiencing both bending and compression as well as changes in ground reaction forces, stance, and muscle contractions during movement (Lieberman et al., 2004). As a result, SMAs calculated about the neutral axis can differ from SMAs calculated about the true axis by as much as 55% (Lieberman et al., 2004).

Ruff and colleagues (2006a) dispute that these findings preclude reconstruction of loading history from CSG for several reasons. First, the strain gauge studies have mostly measured strains during normal behavior, *e.g.* walking. CSG may respond primarily to high magnitude loads engendered during more strenuous activity. Studies of exercising animals have shown that the experimentally measured bending axis moves closer towards the neutral axis during exercise bouts, which suggests that "bone structure is correlated with activity, and primarily vigorous activity" (Ruff et al., 2006a, p. 488). Furthermore, strain gauge studies have been conducted on adult animals that have already adapted to their mechanical environment. For that reason, they no longer experience maximum strains along the neutral axis except perhaps during periods of vigorous loading (Ruff et al., 2006a). Interestingly, the same would not be true of juveniles, whose skeletons undergo functional adaptation to considerable changes in behavior and body size. This implies that ontogenetic study of CSG may reliably track how loading changed during growth, because the skeleton continuously reacts to novel changes in its mechanical environment.

Also, while the true bending axis does not pass through the section centroid, bending moments calculated about the neutral and true bending axes are highly correlated (Lieberman et al., 2004). Furthermore, comparing individuals of the same or closely related species largely controls for differences in ground reaction forces, stance, and muscle contraction (Ruff et al., 2006a). Consequently, the high correlation between in-vivo bending rigidity and those calculated about the neutral axis mean that relative differences between groups can still be considered a meaningful indicator of relative differences in how bones were loaded.

This discussion of potential limitations in CSG based reconstructions of bone loading emphasizes that caution should be used in using CSG to reconstruct behavior or test for behavioral differences between groups. CSG may not be as reliable an indicator of habitual loading repertoires as once thought. Indeed, CSG may be most closely correlated with strain environment during particularly vigorous bouts of loading. In that context, one can make the subtle, but important, distinction that CSG analyses may not capture habitual differences in loading as much as habitual differences in the most osteogenic types of loading. Still, keeping these limitations in mind, using CSG as a general indicator of age related changes in load magnitude allows for reconstruction of how bone adapts to its mechanical environment during life and how this process differed between populations.

## 4.6: Techniques for Calculating CSG Properties

Measurement of CSG was done non-invasively using three different methods, with the choice of method depending on the availability of periosteal contours and radiographs. First, this section discusses how radiographs and periosteal contours were collected. Second it provides an overview of the three techniques employed to create cross-section models and calculate CSG. Visual depictions of the three methods employed and a cross-section image obtained through direct imaging of both external and internal morphology through computed tomography (CT) scanning are given in Figure 4.4.

Figure 4.4: Methods for modelling cross-sections with a computed tomography (CT) cross-section image for reference. Adapted from O'Neill and Ruff (2004) and Davies et al. (2012)



## 4.6.1 Acquisition of Periosteal Contours and Radiographic Measurements

In this study, periosteal contours, outlines of the external cross-section surface, were available for all section locations (Table 4.13). Biplanar x-rays were collected in anteroposterior and mediolateral views at the humerus midshaft, femur midshaft, and tibia midshaft for individuals younger than 16 years old. Only periosteal contours were available for adolescents and young adults older than 16 years. This was due to the limited size of the radiographic sensor, which prohibited the visualization of the entire diaphysis in individuals older than 16 years.

Periosteal contours were primarily extracted from 3D surface scans of long bones. 3D scans were obtained using a Konica Minolta Virtuoso 3D Scanner and the Tributary software program (Three Rivers 3D). Three or four rotary scans were taken of each element, with bones repositioned 90 degrees between rotations to ensure the entire element was scanned. Each rotary scan consisted of six automatically aligned scans taken at 60-degree increments using an automated rotary table. Scan sets from each rotation were then fused into a 3D mesh and aligned to anatomical axes in the Geomagic Design X software program. Anatomical alignments were made using the methodology of Ruff (2002), following a protocol developed by Davies and Macintosh (personal comm., 2013). New protocols had to be created for aligning the ulna and clavicle as no available methodology details the alignment of 3D scans for these elements. Ruff (2002) aligned the ulna in articulation with the radius, but 3D scanning prohibits this approach in

isolated elements. Instead, the ulna was aligned in isolation from the radius, using landmarks of the proximal joint surface to define the anteroposterior and mediolateral planes. The ulna was aligned so that the olecranon and coronoid processes were facing anterior, and the radial notch was facing laterally. Also, as no methodology exists for the anatomical alignment of the clavicle from 3D scans, this was done by defining the mediolateral axis as the plane created between the most medial and lateral projections of the element. The anteroposterior plane was aligned so that it ran parallel to the anteroposterior axis of the acromial surface.

Periosteal contours were extracted at the location of interest using the AsciiSection program (Davies et al., 2012) or the measure section tool in Geomagic Design and saved as TIFF images. AsciiSection was used to extract sections taken at set percentages of bone length. Geomagic Design was preferred for extraction of the femur subtrochanteric and tibia nutrient foramen sections, because the landmark of interest could be directly visualized. AsciiSection images were exported with a known scale (20 pixels/mm). Geomagic Design images included a scale bar for calibration. The scale was then calculated in the ImageJ software package (Schneider et al., 2012) using the set scale function.

Latex molds of humerus, femur, and tibia midshaft sections were previously collected by Dr. D. Temple for the femur, humerus, and tibia midshaft. He provided these for analysis of additional specimens. Molds were taken using Cuttersill putty following Churchill (1994). Anterior, posterior, lateral, and medial surfaces were marked on the cast. These were digitized by placing them on a flatbed scanner with a grid of known size to allow scaling in ImageJ as described above. To preserve anatomical alignment, the anterior surface was placed facing the top of the scan bed, and the medial surface was identified with a marker placed adjacent to the cast. Digitized images were saved as TIFF files and imported into ImageJ. The image was then scaled, and the internal outline of the cast was traced to create a periosteal contour.

For several of the young adults in the sample, femora were too large to fit on the rotary table. Drs. J. Stock and A. Macintosh provided previously collected CSG properties of the femoral midshaft for these individuals (personal comm, 2016). Femur subtrochanteric sections were not collected for these individuals.

To reconstruct the endosteal dimensions, radiographs were taken in the anteroposterior (AP) and mediolateral (ML) orientations using the Nomad GoPro X-Ray machine and a SuniRay sensor at the humerus, femur, and tibia midshaft in individuals younger than 16 years old. Due to the limited size of the radiograph sensor, the entire diaphyseal diameter could not be visualized in individuals older than sixteen. Radiographs were provided by Dr. D. Temple, and I carried out the measurements. As the whole diaphysis does not fit on the sensor, the exact position of the cross-section location was marked with a radio-opaque object of known size. This was placed either on the anterior or medial side of the diaphysis. Prior to measurement, the image of known size was also used to correct for radiographic parallax, a form of image distortion created by the distance between the x-ray sensor and the x-ray emitter. This was done using the calibrate measurement tool in the Dr. Suni software. Measurement of the anterior, posterior, medial, and lateral cortical breadths were then taken using the measure tool in the Dr. Suni software.

As diagenetic degradation of cortical bone can make measurements inaccurate, this was controlled for in the following manner. Following Ives and Brickley (2004), the external surface was examined for post-depositional erosion. Elements for which the cortex showed extensive erosion such that the periosteum was mostly removed were excluded from the sample. At the endosteal surface, the internal cortical bone border had to be clearly distinguishable from any foreign material such as soil, which had entered the medullary cavity through holes in the diaphysis. Also, the presence of broken spurs of cortical bone was dealt with by measuring adjacent to the broken border, where the edge was smooth (Ives and Brickley, 2004). If internal cortical bone boundaries could not be clearly defined, the section was excluded from the analysis.

## 4.6.2 Latex Cast Method (LCM)

Radiographs were only available for the humerus, femur, and tibia midshaft sections of individuals younger than 16 years old. For these sections the LCM method was employed to reconstruct the cross-section. This method directly models the periosteal contour. The medullary cavity is approximated as an ellipse using measures of anterior, posterior, medial, and lateral cortical breadth to approximate its offset from the section's central point, the centroid. Studies evaluating the accuracy of this method found that approximating the endosteal contour as an ellipse did not lead to significant errors (O'Neill and Ruff, 2004). When compared to
photographs of direct sections, the percent standard error for LCM derived CSG ranged between 5-9%. Average percent error for medullary area was greater, approximately 16%. The cross-section produced using this method is illustrated in Figure 4.4.

To construct LCM models, this study followed the method developed by Churchill (1994). Radiographic measurements of anterior, posterior, medial, and lateral cortical thickness were plotted in the digitized periosteal contour obtained from 3D scans or moulds as shown in Figure 4.4. These served as a guide for tracing out an elliptical approximation of the medullary cavity. Calculation of CSG was then performed using the Moment Macro (Ruff, n.d.) plugin for ImageJ.

#### 4.6.3 Ellipse Model Method (EMM)

Due to the small size of several of the youngest individuals in the sample, humerus, femur and tibia midshaft periosteal contours could not be cast or scanned. The 3D scanner did not focus on the element, and the alignment of scans failed. Small size also precluded the placement of periosteal moulds. Following O'Neill and Ruff (2004), the cross-sectional properties of these elements were derived from radiographs only using the Ellipse Model Method (EMM). This method operates under the simplifying assumption that the endosteal and periosteal contour are shaped approximately like ellipses (Figure 4.4). No model of the periosteal surface was employed. Instead measurements of total and endosteal width in the AP and ML planes were taken directly from radiographs, as described in section in 4.6.1. Formulae for deriving the mechanical properties of an elliptical cross-section were then used to calculate CSG, and these are given in Table 4.15. The other methods discussed allow quantification of bone rigidity about the axes of maximum and minimum bending rigidity. However, EMM analyses can only quantify anteroposterior and mediolateral bending rigidity, because periosteal and endosteal dimensions are only measured along these axes (Figure 4.4). These were summed to obtain the second polar moment of area (J). More detail description of these variables is given in Section 4.5 and Table 4.14.

Stock (2002) and O'Neill and Ruff (2004) evaluated the accuracy of the EMM. When applied to adults, this technique produces higher percent error than the LCM method, between 7-16 percent (O'Neill and Ruff, 2004). However, studies of juvenile cross-sections do not attempt

to correct CSG calculated with this method, because juvenile diaphyses, especially those of infants and young children, more closely resemble an ellipse (Cowgill, 2010).

Table 4.15 Ellipse model method equations for calculating biomechanical properties from biplanar radiographs (Adapted from O'Neill and Ruff, 2004)

Cross-Sectional Property	Formula <sup>1</sup>
Total Area	$TA = \pi * [(AP*ML)/4]$
Cortical Area	$CA=\pi/4*[(AP*ML) - (ap*ml)]$
Medullary Area	MA= $\pi^*$ [(ap*ml)/4]
Second Moment of Area about the mediolateral axis (I <sub>x</sub> )	$I_x = \pi / 64*[(AP^3*ML) - (ap^3*ml)]$
Second Moment of Area about the anteroposterior axis (Iy)	$I_y = \pi / 64*[(AP*ML^3) - (ap*ml^3)]$
Polar Second Moment of Area (J)	$J = I_x + I_y$

 $\overline{}^{1}$  AP, ML= external measures; ap, ml= internal measures. AP, ap = anteroposterior dimensions; ML, ml = mediolateral dimensions

#### 4.6.4 Solid Cast Method (SCM)

The solid cast method (SCM) calculates CSG solely from periosteal dimensions. An example of the cross-section model analyzed in this method is given in Figure 4.4. This method was applied in two cases. First, radiographs were not available for any clavicle midshaft, distal humerus, ulna midshaft, femur subtrochanteric, and tibia nutrient foramen sections. In addition, radiographs were not available for individuals older than 16 years for the humerus midshaft, femur midshaft, and tibia midshaft. As discussed, this problem arose because the X-ray sensor was too small to image diaphyseal breadth at the pertinent section locations. CSG properties for solid sections extracted from 3D scans were calculated using the MomentMacro plugin for ImageJ.

SCM measures can serve as accurate proxies for LCM measures. The bony tissue furthest from the section's central point makes the greatest contribution to bone strength (Shaw and Stock, 2007; Sparacello and Pearson, 2010). Thus, periosteal contours alone can approximate differences in SMAs between different groups, and differences in endosteal dimensions would have to be quite large to affect the results (Sparacello and Pearson, 2010). The accuracy of this method in comparison to LCM has been evaluated in several studies of adult bones (Shaw and Stock, 2007; Sparacello and Pearson, 2010; Davies et al., 2012; Macintosh et al., 2013). These have generally shown a high correlation between SCM and LCM or CT scan derived SMA,

though accuracy varies throughout the diaphysis. SCM derived SMA measures show higher errors relative to LCM in locations where bone cortices are especially thin, such as the proximal end of the femur or tibia (Macintosh et al., 2013). A recent study has also shown high correlations between LCM and SCM derived properties in ontogenetic series (Harrington et al., 2017).

In the current study, the potential that SCM produced less accurate estimations of CSG than LCM sections were controlled for in two ways. First, for the analysis of juveniles younger than 16 years, LCM analysis of humerus, femur, and tibia midshaft is used as the "gold standard" for analyzing growth. The results for comparisons using these sections are prioritized if they show a different pattern than sections modeled using only the SCM. This does not apply if SCM analysis detects difference in Total Area, which it models as accurately as the LCM or EMM. Thus, the detection of such a difference could not reflect methodological error. Furthermore, there is value in determining whether SCM sections show the same growth patterns as growth series that utilize periosteal and endosteal dimensions. Access to radiographic equipment is often limited or prohibitively expensive (Davies et al., 2012). Thus, this study can contribute to an understanding of if SCM sections can accurately capture ontogenetic change in bone robusticity, and whether this method can be used to detect growth differences in CSG.

The further use of SCM for individuals older than 16 years does not present major obstacles to the study for three reasons. First, prior studies of adults have shown that the average percent error of SCM compared to true CSG values does not exceed 5% for the femur and tibia midshaft, as well as both the humerus midshaft and distal sections (Macintosh et al., 2013). Second, the percentage of a cross-section filled with cortical bone increases with age. Consequently, SCM for adolescents and adults is calculated in the age-range when errors are likely smallest. Third, prior studies of Cis-Baikal adult robusticity have estimated CSG using the SCM, so this study will model the robusticity of older adolescents and young adults with comparable accuracy (Stock and Macintosh, 2016).

#### 4.7 Analysis of Growth Trends and Sample Comparisons: Outline of Results Section

This section provides a general outline of the structure of the results section, explaining the rationale for the analyses, as well as the methodology employed for detecting general ontogenetic trends and for making comparisons between different groups. All statistical tests were carried out in the R statistical program (R Core Team, 2013). The results are broken into three sections by data type. Area and SMA measures are presented in chapter 5, shape ratios  $(I_x/I_y \text{ and } I_{max}/I_{min})$  in chapter 6, and interlimb robusticity ratios in chapter 7. Asymmetry in upper limb area and SMAs is analyzed in chapter 5, and asymmetry in shape is investigated in chapter 6. In each chapter, the visual and statistical analysis of Cis-Baikal juvenile bone robusticity focuses first on the detection of general ontogenetic trends and how CSG properties change with age. Subsequently, chronological and geographic variation in bone development is assessed by comparing individuals from different archaeological periods and cemeteries.

Unlike the other chapters, chapter 5 treats the data in two different ways. First, groups are compared using area and SMA measures standardized for differences in body size. As discussed in Section 4.4 and the preceding literature review in Ch. 2, prior studies strongly suggest that available size-standardization techniques for juvenile skeletal material may not completely remove the effects of body mass (Cowgill, 2010; Osipov et al., 2016). Therefore, to assess how size-standardization affects comparisons, size-unstandardized measures of area and SMA are also used to compare different groups. Given the strong correlation between areas, SMAs, and body mass, this may also allow new insights on differences in body size within Middle Holocene Cis-Baikal populations. As discussed below, %CA, % asymmetry, limb shape, and interlimb robusticity, do not require standardization for body size, so differentiation between groups for these variables is examined without standardization for body size.

#### 4.7.1 Analysis of General Ontogenetic Trends

Prior to comparisons of individuals from different archaeological periods and cemeteries, CSG properties for the whole Cis-Baikal sample against age were analyzed to describe general ontogenetic patterns in all three chapters. To assist in detecting relationships between CSG and age, LOESS curves were fit to the data. The LOESS procedure fits polynomial curves to consecutive sections of the plot. This type of curve fitting is ideal for visualizing growth patterns in cases where rates of change are likely to vary over time. The local value of the curve is defined only by points within a localized vicinity, and the width of this localized vicinity is determined by a smoothing factor (Cleveland, 1979; Cleveland and Develin, 1988). Following the recommendation of Cleveland (1979) for aiding visual perception of patterns in a data plot, a smoothing factor of .5 was employed.

## 4.7.2 Cohorts and Groupings for Comparisons

In each chapter, the sample was divided into two cohorts:

Cohort 1: Juveniles aged 0-16 years old of indeterminate sex, and

Cohort 2: Adolescent and young adult females and males

One female in the second cohort was 14, and another was 15 years old. These are included to maximize the age range over which analysis of sex-related differences can be conducted. Otherwise, all males and females were at least 16 years old.

These cohorts are a useful division, because the first covers the majority of ontogeny, and sex estimation from skeletal remains is not feasible in this age range except in isolated cases of early maturing adolescents. The second cohort allows for consideration of sexual differences, which should generate increasing variation in bone robusticity during adolescence. Thus, when sex can be estimated with a high degree of confidence, one should account for it in comparisons of adolescents and young adults.

To analyze chronological and geographic variation within the sample, the individuals within both cohorts are subdivided in two different ways. First, both cohorts are subdivided according to archaeological period. Thus, indeterminate sex juveniles younger than 16 years were divided into an Early Neolithic (EN) and a Late Neolithic (LN) group. The second cohort of adolescents and young adults was divided into four subgroups: EN Females, EN Males, Late Neolithic and Early Bronze Age (LN/EBA) Females, and LN/EBA Males. As discussed in Section 4.1, the larger proportion of EBA individuals with sex estimates favors the combination of LN and EBA individuals. If this were not done, there would only be four LN males and one LN female to compare to the more numerous EN older adolescent/ young adult females and males. Furthermore, past studies of adult robusticity have always amalgamated the LN and EBA individuals (Stock et al., 2010; Lieverse et al., 2011; Stock and Macintosh, 2015). Therefore, amalgamation of the sample allows assessment of if previously observed adult differences are established by the end of adolescence.

In addition, individuals from different cemeteries were compared. Essentially, this differs from the archaeological period analysis in the two EN cemetery samples, Shamanka and Lokomotiv are compared separately to LN Ust-Ida individuals. This was only done for the first cohort, individuals younger than 16 years old of indeterminate sex. Subdividing the adolescent/ young adult females and males by cemetery produced very small groups, which limits the utility of such analysis in the second cohort.

### 4.7.3 Generation of Standardized Residuals for Group Comparisons

In each chapter, individuals from different archaeological periods and cemeteries are compared using standardized residuals. The same technique for detecting differences has been applied in multiple growth studies (*e.g.* Mays et al., 2009; Temple et al., 2014). Standardized residuals measure differences in how some dependent variable relates to an independent variable in different groups. Fitting a polynomial curve to a combined sample containing all groups of interest creates a mathematical approximation of the general relationship (Mays et al., 2009). This serves as "a datum for the population under study, from which departure associated with various factors can be evaluated statistically" (Mays et al., 2009, p.411). The standardized residual, the distance of the individual from the curve divided by the pooled standard deviation, expresses the extent of this departure in terms of standard deviation (Mays et al., 2009; Temple et al., 2014). In other words, standardized residuals quantify the distance of each individual data point above or below this mathematical curve in terms of the variation exhibited within the combined sample. Consequently, if after a curve is fit to the combined Cis-Baikal sample, groups show differing distributions of standardized residuals, this would indicate a difference between them.

Two types of relationships were evaluated using standardized residuals. In Chapter 5, area and SMA measures of different groups were compared using measures of bone robusticity regressed on body size to partition the variation in area and SMAs attributable to body size from that related to other factors. Secondly, age-related change in size-unstandardized area and SMA measures, shape, and interlimb robusticity ratios was assessed by regressing variables of interest on age. The following section discusses how standardized residuals were generated to remove the effects of body size and to model relationships with age.

### 4.7.3.1: Size Standardization of Areas and SMAs

Ruff (2000) investigated the allometric relationships between body size and CSG properties for the lower and upper limbs. He found that cross-sectional areas scale with body mass, and SMAs scale with the product of body mass and bone length squared. Areas scale with

body mass, because they predominantly respond to compressive loading, which cause axial strain. By convention, areas are standardized by body mass estimates. To standardize SMAs for differences in body size one must additionally account for bone length. While body mass contributes to the magnitude of bending and torsion, the force of such loading also increases in conjunction with the length of the lever or moment arm along which force travels. Bone length squared serves as an adequate proxy for this measurement (Ruff, 2000). The only exception is sections of the femur close to the hip joint. Here CSG increases in tandem with hip breadth rather than bone length, because mediolateral strains predominate over anteroposterior strains close to the hip joint. However, since the immaturity of the pelvic girdle prevents quantification of pelvic dimensions, it is standardized to bone length in this dissertation. Ruff (2000) and Cowgill (2008, 2010) also found that, although the lower limb plays a larger role in supporting body weight than the upper limb, the scaling relationships between CSG and body size are very similar for both limbs. Therefore, the same standardization process applies to the CSG of lower and upper limb elements.

To maintain consistency with prior work of Osipov et al. (2016), log<sub>10</sub> of area measurements was regressed against the log<sub>10</sub> of body mass to remove the effect of body size on cross-sectional areas (TA, CA, MA). The log<sub>10</sub> of SMAs values were regressed on the log<sub>10</sub> of (body mass \* bone length<sup>2</sup>). Log transformation produces a linear relationship between the two variables. Statistical comparisons of individuals were then performed on the standardized residuals generated from these regressions. Size standardization was carried out only for area and SMA measures. Past studies of both adults and juveniles have predominantly treated %CA, limb shape, interlimb robusticity ratios, and % asymmetry as largely unaffected by differences in body mass (Stock and Pfeiffer, 2004; Ruff, 2008; Cowgill, 2008; Shaw and Stock, 2011; Osipov et al., 2016). In these cases, the use of intra-individual ratios largely controls for differences in body size. Therefore, these variables were not standardized by body size measures prior to analysis.

# 4.7.3.2: Generation of Standardized Residuals to Assess Change in CSG with Age

The second type of relationship evaluated using standardized residuals was between CSG and age. In chapter 5 the effect of size standardization on area and SMA comparisons was quantified by evaluating age related change in size-unstandardized values of these properties. This also allows consideration of how differences in CSG might reflect differences in body size growth between groups. Body size is also not standardized for in analyses of percent CA, asymmetry, shape ratios, and interlimb robusticity ratios. Curves modeling the relationship of these variables to age were used to generate standardized residuals for the analysis of growth differences.

To select the curve or equation that best fits the data, the forward selection methodology of Zar (2010) was used. Polynomials of consecutively higher orders were fit to bivariate plots of CSG data against age until additional terms no longer significantly improved the fit. Standardized residuals were then calculated from this curve. If no curve fitting showed a significant relationship between the dependent variable and age, true values were used.

# 4.7.4: Visual and Statistical Comparisons of Individuals from Different Archaeological periods and Cemeteries

Comparisons of individuals from different archaeological periods and cemeteries utilized a combination of visual and statistical analysis. In the first cohort, which consists of individuals aged 0-16 years of indeterminate sex, boxplots of standardized residuals or true values were visually compared for individuals grouped by archaeological period and cemetery of burial. In the second cohort, female and male adolescents and young adults, individuals were grouped by sex and archaeological period for visual comparison of boxplots. Given the small sample sizes, statistical analysis was conducted using Mann-Whitney's U tests, the non-parametric version of the t-test (Mays, 2008; Cowgill, 2010).

Some studies that compare multiple groups and variables make post-hoc adjustments to p-values. This represents an attempt to control for the fact that preforming an increased number of statistical tests increases the probability of achieving at least one statistically significant result by chance alone (Rice, 1989). One of the most common post-hoc adjustments is the Bonferroni correction, which divides the p-value below which results are considered statistically significant by the number of comparisons. This new, reduced p-value serves as the cut off for statistical significance. However, this approach has been criticized as overly restrictive, markedly reducing statistical power. Moran (2003) considers this especially problematic in ecological studies where the ability to replicate the experiment are limited, samples sizes are small, and individuals within groups show a high degree of inter-individual variation. All these factors may lead to the production of p-values close to the cut-off for statistical significance, and the same

considerations apply to an archaeological study (Cowgill, 2008, 2010). Post-hoc correction also penalizes complex analyses, since comparisons of more groups leads to a marked reduction in the *p*-value cut off for statistical significance (Moran, 2003; Cowgill, 2010). Lastly, correction for multiple comparisons is further complicated by the fact that it remains unclear what constitutes a multiple comparison. Some researchers apply a correction to a single table or type of variable, others apply it to all comparisons that test the same null hypothesis (Cabin and Mitchell, 2000). These different approaches would markedly change the significance threshold. For instance, in the current investigation, *p*-values thresholds for statistical significance would be lower for comparisons of unsexed juveniles younger than 16 years when they are divided by cemetery than when they are divided by archaeological period. This could create a situation in which nuanced differentiation between groups would be dismissed as a statistical artifact.

Following the suggestions of Moran (2003), post-hoc corrections are not made. The most important consideration is whether results of statistical tests can "satisfy rules of logic and reason," (Moran, 2003, p. 405). Acknowledging the potential for multiple analyses to produce at least one significant result by chance, the achievement of significance for one or two variables is treated with caution. However, the detection of several statistically significant or nearly significant results at the same cross-section location are more likely to represent an important differentiation between groups. Even though one comparison may reach statistical significance by chance, the achievement of significance for multiple tests is much less probable (Moran, 2003). This investigation does not focus exclusively on statistical testing. The results of these procedures are contextualized by visual comparisons, which describe the extent to which samples from different archaeological periods and cemeteries show overlap or differentiation in ranges of biomechanical properties.

To determine at what ages differences between groups compared arise during growth, scatterplots of standardized residuals or raw values against age were generated when statistical comparisons detected differences between groups. Visual inspection of these plots was then used to assess when during development groups began to differ. Ruff et al. (2013) and Temple et al. (2014) previously employed a similar approach. In this respect, the current investigation differs slightly from that of previous growth studies of bone robusticity with larger sample sizes (e.g. Cowgill, 2010; Osipov et al., 2016). These determined the age at which differences emerged by

subdividing samples into multiple narrower age cohorts and making statistical comparisons. This approach is eschewed here, because such division of the available Cis-Baikal assemblage severely reduces statistical power. Multiple divisions of a small sample would make cohort specific sample sizes so small as to render comparisons statistically meaningless, and group differences in age distribution might introduce further errors (Cowgill, 2014a; Temple et al., 2014). Therefore, it is preferable to critically examine the whole sample distribution to identify when developmental differences emerge.

# **Chapter 5: Results Part 1- Development of Area and Second Moments of Area** (SMAs): **Ontogenetic Patterning and Sample Comparisons**

# 5.1 Ontogenetic Trends in Area and Second Moments of Area (SMAs)

This section explores general growth trends in area and SMA measures. Skeletal Growth Profiles (SGPs) (*sensu* Hoppa, 1992) for size-unstandardized area and SMA measures track changes in cross-section area as well as resistance to bending and torsion with age. The same general relationship between variables and age is seen at all section locations. Scatterplots are only presented for average humerus midshaft, femur midshaft, and tibia midshaft sections, because both periosteal and medullary contours were measured for these sections.

SGPs of total area (TA), cortical area (CA), and medullary area (MA) against age for each section are given in Figures 5.1.1-5.1.3 for the humerus, femur, and tibia midshaft. Both TA and CA increase with age at a roughly equivalent rate up to the age of 16 years, beyond which a lack of radiographs precludes analysis of CA. Inter-individual variation also increases in both variables as individuals get older. An uptick in the LOESS lines just before the age of ten years indicates that the rate of accrual increases in older children and young adolescents. After the age of 15 years, TA increases less rapidly, though some young adults produce the highest values, implying that periosteal bone accrual continues into late adolescence. The similar growth of TA and CA until 15 years of age indicates that periosteal apposition increases diaphyseal crosssection size from birth to adolescence. It should also be noted that the growth curves resemble those seen in a plot of body mass against age presented in Figure 5.1.4.

The LOESS lines fit to scatterplots of MA against age in Figures 5.1.1-5.1.3 show that MA increases at a slower rate than TA or CA. However, the MA LOESS line plateaus after the age of ten years. Individuals older than this display substantial variation. Some adolescents older than this produce values equivalent to individuals younger than ten years. Other adolescents exhibit higher values. Recall that previous studies have shown than bone is resorbed at the endosteal surface from birth until middle to late adolescence (Ruff et al., 1994). Subsequently, the endosteal surface transitions to a state of bone formation Therefore, the plateau in MA LOESS lines after the tenth year may indicate some adolescents have begun to experience endosteal deposition while others have not.





Area Measure --- Total Area --- Cortical Area · • · Medullary Area



Figure 5.1.2: Scatterplots of size unstandardized femur midshaft total area, cortical area, and medullary Area against Age

Figure 5.1.3: Scatterplots of size unstandardized tibia midshaft total area, cortical area, and medullary area against age



Area Measure -- Total Area -- Cortical Area · • Medullary Area



Figure 5.1.4: Scatterplot of body mass estimates against age

As illustrated in Figure 5.1.5, Percent Cortical Area (%CA) increases with age in both the upper and lower limb as the diaphyses become more "filled in" with age. The humerus exhibits a markedly lower range than the femur and tibia midshaft from shortly after birth. However, the difference between the humerus and lower limb elements appears to decrease in adolescence. The general increase in %CA with age is also consistent with the rate of periosteal apposition outpacing the rate of endosteal resorption throughout ontogeny in both the upper and lower limb.



Figure 5.1.5: Scatterplots of percent cortical area against age for humerus, femur, and tibia midshaft

Growth profiles for Second Moments of Area (SMAs) are represented by plots of the second polar moment of area (J) against age in Figure 5.1.6. As was the case for TA and CA, J increases more rapidly after the age of ten years, and the rate of accrual begins to decrease after the age of 15 years. However, some young adults produce higher values than adolescents, demonstrating that the accrual of bending and torsional strength continues, albeit at a decreased rate, after the end of adolescence.



Figure 5.1.6: Scatterplots of size unstandardized second polar moment of area (J) for humerus, femur, and tibia midshaft against age

Boxplots for TA and J of female and male adolescents and young adults in Figures 5.1.7 and 5.1.8 demonstrate that males produce higher values of TA and J than females for both limbs. What proportion of this sexual dimorphism is attributable to body size and differences in activity will be the subject of analyses in subsequent sections.



Figure 5.1.7: Sexual dimorphism in size unstandardized total area (TA) for the humerus, femur, and tibia midshaft: adolescents and young adults





5.1.1 Relationships of Cross-Sectional Geometric Properties to Body Size and Age

Prior to the comparison of size-standardized area and SMA measures for individuals from different units of analysis (archaeological periods and cemeteries) in Sections 5.2 and 5.3, it proves important to report the relationship of CSG variables to appropriate body size proxies

(body mass for area measures and product of body mass and bone length for SMAs). Correlation coefficients ( $R^2$ ) for each variable are given in Table 5.1. In general correlations are high. Body size explains most of the variation in TA, CA, and SMA measures. The exception is MA, which has markedly lower correlation coefficients, implying a much weaker relationship to body size.

Section	TA	CA	MA	Ix	Iy	Imax	Imin	J
Fem ST	0.86	_	_	0.89	0.92	0.91	0.91	0.91
Fem Mid	0.86	0.86	0.43	0.96	0.96	0.96	0.97	0.96
Tib NF	0.92	_	_	0.95	0.93	0.96	0.93	0.95
Tib Mid	0.92	0.89	0.47	0.96	0.93	0.96	0.94	0.96
L Clav Mid	0.89	_	_	0.90	0.91	0.91	0.91	0.91
R Clav Mid	0.87	_	_	0.88	0.88	0.88	0.89	0.89
Avg Clav Mid	0.89	_	_	0.91	0.91	0.92	0.92	0.92
L Hum Mid	0.89	0.92	0.28	0.94	0.92	0.93	0.92	0.93
R Hum Mid	0.90	0.9	0.4	0.94	0.91	0.93	0.92	0.93
Avg Hum Mid	0.90	0.92	0.36	0.94	0.92	0.94	0.92	0.94
L Hum Dist	0.88	_	_	0.91	0.86	0.89	0.89	0.89
R Hum Dist	0.89	_	_	0.92	0.89	0.92	0.92	0.91
Avg Hum Dist	0.89	_	_	0.93	0.89	0.91	0.91	0.91
L Ulna Mid	0.87	_	_	0.91	0.90	0.91	0.90	0.91
R Ulna Mid	0.9	_		0.9	0.90	0.92	0.88	0.92
Avg Ulna Mid	0.89	_		0.92	0.92	0.92	0.90	0.93
<ul> <li>data for en</li> </ul>	dostec	ıl dime	nsions	not av	vailabl	е		

Table 5.1: Correlation coefficients ( $R^2$ ) for area and SMA measures regressed on body size

As discussed in Ch.4, existing methods for juvenile body mass estimation have limitations, and, for this reason, growth in size-unstandardized CSG is also compared in Section 5.4. Standardized residuals for these comparisons were generated by regressing CSG on age. For the sake of brevity, Table 5.2 presents correlation coefficients only for the humerus, femur, and tibia midshaft, as these sections were constructed using both periosteal and endosteal dimensions. In general, R<sup>2</sup> values are similar though slightly lower compared to regressions of CSG on body mass (Table 5.1). %CA is regressed only on age as it is a size free variable. R<sup>2</sup>

values for this variable are similar to those seen for MA.

Section	ТА	CA	%CA	MA	Ix	Iy	Imax	Imin	J
L Hum Mid	0.86	0.90*	0.35	0.18	0.77	0.74	0.76	0.74	0.79
R Hum Mid	0.88	0.85*	0.46	0.31	0.81	0.75	0.78	0.79	0.80
Avg Hum Mid	0.88	0.83	0.39	0.30	0.81	0.75	0.78	0.78	0.80
Fem Mid	0.92	0.91*	0.27	0.39	0.81	0.86	0.83	0.88	0.86
Tib Mid	0.84	0.90*	0.3	0.43	0.74	0.71	0.73	0.76	0.75

Table 5.2: Correlation coefficients ( $R^2$ ) for area and SMA measures regressed on age

\*Quadratic polynomial provides the best fit, all other regressions linear.

# 5.2 Comparisons of Size-Standardized Lower Limb Area and SMAs

Boxplots of TA, J, CA, MA, and %CA are given in Figures 5.2.1-5.2.5 for lower limb comparisons of indeterminate sex individuals younger than 16 years from different archaeological periods. Visual comparison of femur subtrochanteric TA and J show no difference between EN and LN juveniles (Figure 5.2.1, 5.2.2). From the femur midshaft to the tibia midshaft, LN individuals younger than sixteen exhibit a higher range of size-standardized residuals than their EN predecessors for TA, CA, MA, and J, though there is considerable overlap (Figures 5.2.1-5.2.4). Boxplots of %CA presented in Figure 5.2.5 do not show a clear difference between archaeological periods. LN individuals fall in the upper portion of the EN range for the femur midshaft, but there is less differentiation between samples for the tibia midshaft.



Figure 5.2.1: Boxplots of standardized residuals for lower limb total area (TA) by archaeological period: indeterminate sex individuals 0-16 years old

Figure 5.2.2: Boxplots of standardized residuals for lower limb polar second moment of area (J) by archaeological period: indeterminate sex individuals 0-16 years old







Figure 5.2.3: Boxplots of standardized residuals femur midshaft and tibia midshaft cortical area



Figure 5.2.5: Boxplots of standardized residuals for femur midshaft and tibia midshaft percent cortical area (%CA) by archaeological period: indeterminate sex individuals 0-16 years old



Results of statistical tests are given in Table 5.3. As expected based on boxplots, there are no significant differences at the femur subtrochanteric section. At the femur midshaft and the two tibia sections, the LN individuals demonstrate significantly greater size-standardized TA and SMAs at p<0.05. Additional variables differ significantly at P<0.1 (see table for p-values). The differentiation appears stronger at the tibia sections, since comparisons of more SMAs reach significance. Of the SMAs, only I<sub>x</sub>, which measures anteroposterior reinforcement, does not differ significantly at any section, indicating that individuals from different archaeological periods do not show a clear difference in bending rigidity in this plane. CA comparisons are significant at the femur midshaft (<p<0.1) but not the tibia midshaft. The comparison of MA is significant at the tibia midshaft (p<0.1). %CA does not show any differentiation. The weaker differentiation in CA and MA than TA indicates that greater bone accrual at the periosteal envelope is primarily responsible for elevated levels of bending and torsional rigidity in the LN lower limb. The lower EN medullary area observed using boxplots is consistent with slower rates of endosteal resorption in this group (Figure 5.2.4).

Table 5.3: Statistical comparisons of size-standardized lower limb areas and SMAs by archaeological period: indeterminate sex individuals 0-16 years old

Section	TA	CA	MA	%CA	Ix	Iy	Imax	Imin	J
Fem ST	0.779	—	—	—	0.552	0.977	0.858	0.515	0.770
Fem Mid	0.044**	0.066*	0.465	0.742	0.167	0.044**	0.188	0.059*	0.092*
Tib NF	0.004**	_	_	_	0.404	0.0007**	0.022**	0.005**	0.008**
Tib Mid	0.029**	0.231	0.067*	0.547	0.165	0.032**	0.015**	0.021**	0.032**

\*significant at 0.05< p<0.1

\*\* significant at p<0.05

endosteal dimensions not available

Boxplots for indeterminate sex individuals younger than 16 years grouped by cemetery are presented in Figures 5.2.6-5.2.10. Visual comparison of femur subtrochanteric TA and J indicate no difference between cemeteries (Figures 5.2.6, 5.2.7). At the femur midshaft and both tibia sections Ust-Ida individuals produce the highest range of residuals for all variables except %CA (Figures 5.2.6-5.2.10). The two EN samples have a very similar range of residuals, but Shamanka individuals generally produce a slightly lower range of size-standardized residuals than Lokomotiv for TA, MA and SMAs at tibia sections. CA and Percent CA do not show any difference between these two cemeteries (Figure 5.2.6-5.2.10).





Figure 5.2.7: Boxplots of standardized residuals for second polar moment of area (J) by cemetery: indeterminate sex individuals 0-16 years old







Figure 5.2.8: Boxplots of standardized residuals for femur and tibia midshaft cortical area (CA) by



Figure 5.2.10: Boxplots of standardized residuals for femur and tibia midshaft percent cortical area (%CA) by cemetery: indeterminate sex individuals 0-16 years old



Results of statistical comparisons for individuals from different cemeteries are presented in Table 5.4. As suggested by boxplots, there are no statistically significant differences between Lokomotiv and Shamanka at p<0.05, but comparison on I<sub>y</sub> of the tibia nutrient foramen is nearly significant at p<0.1. Ust-Ida differs significantly from Lokomotiv, which is in the same microregion, for only two femoral midshaft variables (CA and Iy) at p<0.05. Two additional variables  $I_{min}$  and J are significant at p<0.1. In the two tibia sections, only the comparison of tibia nutrient foramen  $I_y$  is significant at p<0.1. By contrast, EN Shamanka juveniles do not show as much differentiation in femoral robusticity compared to Ust-Ida, but they have more gracile tibiae. In this element, significant differences are detected for TA, MA, and all SMAs except  $I_x$ , the measure of anteroposterior bending rigidity.

Comparison	Section	ТА	СА	MA	% CA	Ix	Iy	Imax	Imin	J
	Fem ST	0.721	_	_	_	0.429	0.804	0.377	0.875	0.668
	Fem Mid	0.699	0.494	0.120	0.120	0.963	0.643	0.645	0.645	0.853
EN Lokomotiv- EN Shamanka	Tib NF	0.153	—	_	_	0.279	0.054*	0.145	0.103	0.103
	Tib Mid	0.525	0.874	0.287	0.491	0.792	0.367	0.487	0.207	0.458
	Fem ST	0.903	_	_	_	0.219	0.952	0.434	0.646	0.483
	Fem Mid	0.128	0.011**	0.830	0.237	0.194	0.034**	0.197	0.087*	0.081*
EN LOKOMOTIV- LN UST-Ida	Tib NF	0.142	—	_	_	1.000	0.091*	0.424	0.363	0.243
	Tib Mid	0.136	0.329	0.388	0.890	0.446	0.215	0.138	0.263	0.238
EN Shamanka – LN Ust-Ida	Fem ST	0.769	_	_	_	0.990	0.928	0.806	0.560	0.969
	Fem Mid	0.074*	0.385	0.228	0.744	0.308	0.179	0.352	0.149	0.256
	Tib NF	0.002**	—	—	_	0.250	0.0003**	0.007**	0.0007**	0.003**
	Tib Mid	0.041**	0.309	0.049**	0.345	0.153	0.030**	0.015**	0.012**	0.027**

Table 5.4: Statistical comparisons of size-standardized lower limb areas and SMAs by cemetery: indeterminate sex individuals 0-16 years old

\* nearly significant at 0.05<p<0.1

\*\* significant at p<0.05

data for endosteal dimensions not available

Scatterplots of standardized residuals for variables that showed significant differences were analyzed to determine the age at which differences between samples become evident. Plots of the two tibial sections are given in Figure 5.2.11 for TA and 5.2.12 for J. For all four variables, the Shamanka individuals produce the lowest values prior to the age of five years. However, a sizeable number of EN Shamanka individuals younger than five years also produce values as high as LN individuals. The tendency for EN individuals, especially from Shamanka, to produce a clearly lower range of size-standardized properties becomes evident after the fifth year. Still, overlap between individuals from different archaeological periods and cemeteries remains considerable throughout growth. Although there are fewer EN Lokomotiv individuals, their range of residual values is intermediate to that of the other two cemeteries. For the comparison of femur properties in Figure 5.2.13, TA and J were chosen to maintain consistency with tibia comparisons, and these variables also show significant differences in statistical comparisons at p<0.1 (Tables 5.3 and 5.4). As expected, given the detection of fewer statistical differences, the tendency for Ust-Ida individuals to produce a higher range of residuals is not as clearly expressed as at the tibia sections (Figure 5.2.11, 5.2.12). Nevertheless, as in the tibia sections, the Ust-Ida individuals exhibit an elevated range of residuals after the age of five years compared to the two EN samples.

Figure 5.2.11: Scatterplot of standardized residuals for tibia section total area (TA): indeterminate sex individuals 0- 16 years old



Time Period • Early Neolithic • Late Neolithic

Figure 5.2.12: Scatterplot of standardized residuals for tibia section second polar moment of area (J): indeterminate sex individuals 0-16 years old



Time Period • Early Neolithic • Late Neolithic

Figure 5.2.13: Scatterplot of standardized residuals for femur midshaft total area (TA) and second polar moment of area (J): indeterminate sex individuals 0-16 years old



Time Period 

Early Neolithic

Late Neolithic

The only statistically significant differences revealed by examination of internal properties occurred in femur midshaft CA for the Lokomotiv to Ust-Ida comparison and tibia midshaft MA for the Ust-Ida to Shamanka comparison. Figure 5.2.14 gives scatterplots of standardized residuals against age for these variables. Inspection of femur midshaft CA residuals against age demonstrates that Lokomotiv individual produce the lowest range of values after five years, though this may be an artifact of there being very few Lokomotiv individuals younger than this. Just as interesting is the fact that variation in femur midshaft CA appears greatest shortly after birth. Several EN Shamanka perinates produce extremely low size-standardized values. This likely reflects poor accrual of bone tissue in some individuals that died around the time of birth. Tibia midshaft medullary area shows clearer differentiation between groups. Some Shamanka individuals produce the lowest values of medullary area from birth. However, the Shamanka range complete overlaps that of Ust-Ida individuals younger than five years. Only

after this point does the overlap between samples decrease, with Shamanka individuals exhibiting a lower range than Ust-Ida individuals. Thus, the difference appears to become better defined with age.

Figure 5.2.14: Scatterplot of standardized residuals for femur midshaft cortical area (CA) and tibia midshaft medullary area (MA): indeterminate sex individuals 0-16 years old



Time Period • Early Neolithic • Late Neolithic

For the female and male adolescents and young adults, boxplots of TA are given in Figure 5.2.15 and boxplots for J are given in Figure 5.2.16. Statistical comparisons of females and males are given in Table 5.5. For the femur midshaft, visual inspection of boxplots and statistical comparisons show that neither total area nor SMAs show any evidence of sexual dimorphism in either the EN or LN/EBA period. Likewise, there is no evidence of chronological differentiation between individuals of the same sex.

Conversely at the tibia nutrient foramen and midshaft, the boxplots of TA and J grouped by archaeological period and sex show sexual dimorphism in both archaeological periods (Figures 5.2.15 and 5.2.16). Chronological differences are most pronounced for females, with the EN group producing a markedly higher range, though small LN/EBA female sample size (n=2) raises the possibility that this is a sampling artifact. EN males also appear slightly more robust than LN/EBA males. Statistical comparisons of tibia TA and SMAs in Table 5.5 indicate that males have significantly or nearly significantly more robust tibiae than females from the same archaeological period. Males from different archaeological periods do not differ significantly, but EN females are significantly more robust than LN/EBA females at the tibia nutrient foramen section (p<0.1).







Figure 5.2.16: Standardized residuals for lower limb second polar moment of area (J) by archaeological period: female and male adolescents and young adults

Comparison	Section	TA	Ix	Iy	Imax	Imin	J				
Sexual Dimorphism											
	Fem Mid	0.818	1.000	0.699	0.818	0.589	0.818				
EN	Tib NF	0.295	0.181	0.138	0.181	0.731	0.181				
	Tib Mid	0.138	0.008**	0.073*	0.005**	0.731	0.022**				
	Fem Mid	0.533	1.000	1.000	0.800	0.533	1.00				
LN/EBA	Tib NF	0.071*	0.095*	0.095*	0.095*	0.095*	0.095*				
	Tib Mid	0.143	0.095*	0.095*	0.095*	0.095*	0.095*				
		Ch	ronological	Change							
	Fem Mid	0.857	0.642	0.857	0.857	0.857	1.00				
Females	Tib NF	0.071*	0.071*	0.071*	0.071*	0.071*	0.071*				
	Tib Mid	0.286	0.286	0.286	0.286	0.286	0.286				
	Fem Mid	0.762	0.610	0.610	0.914	0.476	0.762				
Males	Tib NF	0.366	0.530	0.530	0.530	0.530	0.639				
	Tib Mid	0.836	0.876	1.000	1.000	0.343	0.530				

Table 5.5: Statistical comparisons of size-standardized lower limb areas and SMAs by archaeological period and sex: female and male adolescents and young adults

\* significant at p<0.1

\*\* significant at p<0.05

### 5.3: Chronological and Regional Comparisons of Upper Limb Robusticity

For the upper limb sections, boxplots of left, right, and average values showed the same general patterns. Therefore, only boxplots of average values, for which sample sizes are largest, are presented. Statistical tests are carried out for both side specific and average values. Asymmetry is discussed further in Sections 5.5 and 5.6.

Boxplots by archaeological period of size-standardized TA and J for indeterminate sex juveniles younger than 16 years old are presented in Figures 5.3.1 and 5.3.2. Visual analysis demonstrates that EN and LN indeterminate sex juveniles younger than 16 years old show heavy overlap at all sections. Still, LN individuals produce a slightly higher range of size-standardized residuals for the clavicle and ulna midshaft but not at the two humerus sections. Statistical comparisons presented in Table 5.6 show that there are no significant differences in TA and SMAs from the clavicle midshaft to the distal humerus. Only for right and average ulna midshaft total area do comparisons of TA and SMAs detect statistically significant differences. The presence of significant differences in only one section location, may be an artifact of sample size. Due to poorer preservation of smaller elements, fewer ulnae were available for analysis than humeri, especially from LN Ust-Ida.







Figure 5.3.2: Boxplots of standardized residuals for average upper limb polar second moment of area (J) by archaeological period: indeterminate sex individuals 0-16 years old

Table 5.6: Statistical comparisons of upper limb size-standardized areas and SMAs by archaeological period: indeterminate sex individuals 0-16 years old

Sections	ТА	CA	МА	% CA	Ix	Iy	Imax	Imin	J
Left									
L Clav Mid	0.244	_	—	—	0.781	0.286	0.523	0.832	0.635
L Hum Mid	0.255	0.553	0.071*	0.050**	0.448	0.822	0.280	0.488	0.822
L Hum Dist	0.667	_	_	—	0.795	0.708	0.751	0.885	0.840
L Ulna Mid	0.583	—	—	—	0.902	0.115	0.286	0.360	0.286
Right									
R Clav Mid	0.245	_	_	—	0.387	0.232	0.207	0.303	0.207
R Hum Mid	0.259	0.973	0.009**	0.011**	0.631	0.845	0.830	0.770	0.763
R Hum Dist	0.494	_	_	—	0.602	0.968	0.718	0.925	0.758
R Ulna Mid	0.028**	_	_	—	0.037**	0.090**	0.053*	0.042**	0.042**
Average									
Avg Clav Mid	0.137	_	_	—	0.372	0.173	0.218	0.430	0.332
Avg Hum Mid	0.215	0.981	0.013**	0.009**	0.668	0.768	0.534	0.387	0.915
Avg Hum Dist	0.347	_	—	_	0.796	0.973	0.991	0.955	0.955
Avg Ulna Mid	0.147	_	—	—	0.118	0.047**	0.033**	0.067*	0.040**

\* significant at p<0.1

\*\* significant at p<0.05

- data for endosteal dimensions not available

The greatest chronological differentiation emerged for comparisons of internal architecture at the humerus midshaft. Boxplots of humeral midshaft CA grouped by archaeological period in Figure 5.3.3 indicate that the EN range is larger, completely overlapping the LN sample, though statistical comparisons find no significant difference (Table 5.6). In contrast, as demonstrated by boxplots of MA and %CA in Figures 5.3.4 and 5.3.5, LN juveniles exhibit a noticeably higher range of size-standardized medullary area and a lower range of %CA. These differences are statistically significant (Table 5.6). The discrepancy is unexpected given homogeneity in TA and CA across archaeological periods (Table 5.6). It is possible to explore the cause of differences in percent cortical area further by plotting size-unstandardized values of area measures against age. Plots for each area measure with archaeological period specific regression lines are given in Figure 5.3.6 for individuals younger than 16 years old. LN individuals exhibit higher values of TA and MA but not CA for age prior to body size standardization. This indicates higher EN %CA results from reduction in both periosteal apposition and endosteal resorption relative to the LN sample during development. As sizestandardized MA differs more between archaeological periods than TA, it appears that reduced EN endosteal resorption compensates for less bone being added on the periosteal surface during growth. This maintains equivalence in cortical area across archaeological periods and results in greater %CA in the EN.





Figure 5.3.4: Boxplots of standardized residuals for average upper limb medullary area (MA) by archaeological period: indeterminate sex individuals 0-16 years old



Figure 5.3.5: Boxplots of standardized residuals for average upper limb percent cortical area (%CA) by archaeological period: indeterminate sex individuals 0-16 years old


Figure 5.3.6: Scatterplots of size-unstandardized average humerus midshaft area measures for age with EN and LN regression lines for individuals 0-16 years old.



Comparison of indeterminate sex individuals younger than 16 years from different cemeteries indicates variability between cemeteries. Boxplots of average TA and J grouped by cemetery are presented in Figures 5.3.7 and 5.3.8. Ust-Ida individuals produce a slightly higher range of size-standardized residuals than individuals from the two EN cemeteries, except at the humerus midshaft and distal sections. As illustrated in Figure 5.3.9, there is little differentiation between samples for humerus midshaft CA, and Shamanka demonstrates the greatest variability in this property. Both EN cemeteries show a lower range of MA and higher %CA than Ust-Ida, and Shamanka produces the lowest and highest ranges respectively for these properties (Figures 5.3.10, 5.3.11).



Figure 5.3.7: Boxplots by cemetery of total area (TA) standardized residuals by cemetery: indeterminate sex individuals 0-16 years old









Figure 5.3.10: Boxplot by cemetery of humerus midshaft medullary area (MA) standardized residuals by cemetery: indeterminate sex individuals 0-16 years old







Statistical comparisons of individuals from different cemeteries are given for the left, right, and average values in Table 5.7-5.9. These indicate that the two EN cemeteries show no significant differences, except for %CA of the right humerus, due to the higher Shamanka range. The two Angara River Valley cemeteries, Lokomotiv and Ust-Ida, differ significantly only for right and average ulna TA and SMAs (Table 5.8 and 5.9), and the visually detected difference in

humeral midshaft internal dimensions does not achieve significance. Instead, significant differences in MA and %CA emerge in comparisons of Shamanka and Ust-Ida, reflecting Shamanka's especially low range of MA and high range of %CA (Figures 5.3.10, 5.3.11). Thus, comparisons of different cemeteries suggest that, as in the lower limb, Shamanka and Ust-Ida show the greatest differentiation. Although several significant differences are detected between Lokomotiv and Ust-Ida, they emerge in a different portion of the upper limb than for the Ust-Ida to Shamanka comparison. The fact that there are fewer ulnae than humeri also raises the possibility that this result is a statistical artifact.

Comparisons	Section	ТА	CA	MA	%CA	Ix	Iy	Imax	Imin	J
	L Clav Mid	1.00	_	_	_	1.00	0.299	0.211	0.536	0.536
	L Hum Mid	0.837	0.967	0.340	0.432	1.00	0.684	0.825	0.504	0.862
EN LOROMOUV- EN Shamanka	L Hum Dist	0.588	_	_	_	0.898	0.579	0.701	0.831	0.765
	L Ulna Mid	0.479	_	_	_	0.591	0.859	0.859	0.677	0.677
	L Clav Mid	0.354	_	_	_	0.651	0.651	0.910	0.693	0.955
EN Lokomotiv- LN Ust-Ida	L Hum Mid	0.224	0.585	0.443	0.255	0.645	1.00	0.382	0.878	0.721
	L Hum Dist	1.00	_	_	_	0.733	0.247	0.437	0.437	0.437
	L Ulna Mid	0.225	_	_	_	0.811	0.161	0.371	0.161	0.217
	L Clav Mid	0.364	_	_	_	1.00	0.243	0.285	1.00	0.530
	L Hum Mid	0.462	0.667	0.047**	0.052*	0.494	0.781	0.402	0.305	0.940
EN Snamanka- LN Ust-Ida	L Hum Dist	0.570	_	_	_	0.910	0.850	0.970	0.791	0.850
	L Ulna Mid	0.817	—	—	—	0.977	0.192	0.371	0.585	0.437

Table 5.7: Statistical comparisons of left size-standardized upper limb areas and SMAs by cemetery: indeterminate sex individuals 0-16 years old

\* significant at p<0.1

\*\* significant at p<0.05

data for endosteal dimensions not available

Comparisons	Section	TA	CA	MA	%CA	Ix	Iy	Imax	Imin	J
	R Clav Mid	0.285	_	_	_	0.961	0.661	0.591	0.733	0.591
	R Hum Mid	1.00	0.574	0.104	0.027**	1.00	0.743	1.00	0.768	0.913
EN LOKOMOTIV- EN Shamanka	R Hum Dist	0.444	_	—	—	0.659	0.547	0.602	0.718	0.718
	R Ulna Mid	0.250	_	_	_	0.146	0.704	0.611	0.439	0.364
	R Clav Mid	0.955	_		_	0.581	0.626	0.494	0.673	0.537
	R Hum Mid	0.319	0.649	0.359	0.543	0.880	0.940	0.660	0.842	0.820
EN LOKOMOTIV- LN UST-IDA	R Hum Dist	0.887	_	_	_	0.533	0.494	0.494	0.657	0.494
	R Ulna Mid	0.004**	_	—	—	0.017**	0.136	0.136	0.018**	0.018**
	R Clav Mid	0.085*	_	—	_	0.438	0.204	0.220	0.276	0.204
EN Shamanka- LN Ust-Ida	R Hum Mid	0.394	0.744	0.004**	0.003**	0.611	0.853	1.00	0.587	0.817
	R Hum Dist	0.434	_	—	—	0.769	0.743	0.959	0.904	1.00
	R Ulna Mid	0.108	_	—	—	0.123	0.168	0.097*	0.137	0.137

*Table 5.8: Statistical comparisons of right size-standardized upper limb areas and SMAs by cemetery: indeterminate sex Individuals 0-16 years Old* 

\* significant at p<0.1

\*\* significant at p<0.05

- data for endosteal dimensions not available

Table 5.9: Statistical comparisons of average size-standardized upper limb area measures and SMAs by cemetery: indeterminate sex Individuals 0-16 years Old

Comparisons	Section	TA	CA	MA	%CA	Ix	Iy	Imax	Imin	J
	Avg Clav Mid	0.512	_	_	_	0.817	0.311	0.485	0.877	0.588
	Avg Hum Mid	0.776	0.636	0.265	0.265	0.754	0.754	1.00	0.661	0.893
EN LOKOMOTIV- EN SNAMANKA	Avg Hum Dist	0.412	_	_	_	0.681	0.392	0.506	0.636	0.591
	Avg Ulna Mid	0.366	_	—	—	0.249	0.682	0.494	0.335	0.437
	Avg Clav Mid	0.564	_	_	_	0.376	0.717	0.796	0.678	0.796
	Avg Hum Mid	0.184	0.615	0.168	0.139	0.486	1.00	0.486	0.950	0.753
EN LOROMOUV- LN USI-IUA	Avg Hum Dist	0.681	_	_	_	0.696	0.393	0.565	0.629	0.696
	Avg Ulna Mid	0.035**	_	_	_	0.045**	0.130	0.032**	0.032**	0.032**
	Avg Clav Mid	0.091*	_	_	_	0.552	0.112	0.138	0.441	0.261
EN Shamanka- LN Ust-Ida	Avg Hum Mid	0.427	0.704	0.013**	0.011**	0.881	0.702	0.725	0.289	0.987
	Avg Hum Dist	0.314	_	—	—	0.939	0.531	0.725	0.680	0.725
	Avg Ulna Mid	0.339	_	—	—	0.288	0.083*	0.092*	0.184	0.110

\* nearly significant, 0.05<p<0.1

\*\* significant at p<0.05

— data for endosteal dimensions not available

Given the results of visual and statistical comparisons, analysis of the age at which significant differences emerge focuses on the MA and %CA of the humerus midshaft and TA and J of the ulna midshaft. Scatterplots of standardized residuals for humerus midshaft MA and %CA against age are provided in Figure 5.3.12. As seen in the lower limb for Tibia MA, several Shamanka individuals younger than five years produce the lowest values of MA and the highest

values of %CA. However, the rest of the Shamanka perinates/infants overlap the Ust-Ida range. After the age of five years, the overlap between the two groups decreases.

Figure 5.3.12: Scatterplots of humerus medullary area (MA) and percent ca (%CA) standardized residuals against age: indeterminate sex individuals 0-16 years old Humerus Midshaft MA Average



Time Period • Early Neolithic • Late Neolithic

Examination of ulna midshaft TA and J standardized residuals plotted against age in Figure 5.3.13 reveals that a very weak trend for EN juveniles to produce a lower range of residuals emerges after age five years. Interestingly, although only the Lokomotiv-Ust-Ida comparisons is significant, several Shamanka individuals produce the lowest values after the fifth year. Thus, the statistical comparisons may be compromised by very small sample size, particularly for the Lokomotiv group.



Figure 5.3.13: Scatterplots of ulna midshaft total area (TA) and second polar moment of area (J) standardized residuals against age: indeterminate sex individuals 0-16 years old

By the end of ontogeny, females and males exhibit differences in size-standardized measures of upper limb robusticity. Boxplots comparing EN and LN/EBA male and female TA and J in Figures 5.3.14 and 5.3.15 show that males have higher size-standardized robusticity than females from the same archaeological period for all sections. The results of statistical tests given in Tables 5.10-5.12 for left, right, and average values show that the difference between males and females from the same archaeological period is significant for several variables in all sections. As was the case for the lower limb, boxplots and statistical tests indicate that LN/EBA females are also significantly more gracile than EN females (Figures 5.3.14 and 5.3.15; Tables 5.8-5.10). Conversely, no significant reduction occurs in male robusticity between archaeological periods, although EN males exhibit a slightly higher range.



Figure 5.3.14: Boxplots of standardized residuals for average upper limb total area (TA) by archaeological period: female and male adolescents and young adults





Table 5.10:	Statistical	l сотра	risons c	of size-s	tandard	ized left	upper	limb measures of TA and	SMAs by
archaeologi	cal period	l and se	x: fema	le and r	nale ado	olescent	s and y	oung adults	
Comparison	Section	TA	Iv	Iv	Imax	Imin	I	1	

Comparison	Section	ТА	Ix	Iy	Imax	Imin	J
		Sex	kual Dimorp	ohism			
	L Clav Mid	0.022**	0.014**	0.035**	0.022**	0.005**	0.013**
IC N I	L Hum Mid	0.315	0.441	0.074*	0.336	0.036**	0.200
EIN	L Hum Dist	0.027**	0.178	0.034**	0.149	0.034**	0.054*
	L Ulna Mid	0.053*	0.035**	0.064*	0.064*	0.064*	0.035**
	L Clav Mid	0.096*	0.182	0.182	0.182	0.046**	0.096*
I N/ED A	L Hum Mid	0.053*	0.053*	0.053*	0.053*	0.053*	0.053*
LIN/EDA	L Hum Dist	0.053*	0.053*	0.053*	0.053*	0.053*	0.053*
	L Ulna Mid	0.064*	0.064*	0.165	0.165	0.064*	0.064*
		Chro	onological (	Change			
	L Clav Mid	0.222	0.222	0.222	0.056*	0.222	0.056*
Famalas	L Hum Mid	0.089*	0.117	0.089*	0.117	0.089*	0.089*
remates	L Hum Dist	0.192	0.296	0.117	0.296	0.117	0.192
	L Ulna Mid	0.770	0.143	1.00	0.380	0.770	0.380
	L Clav Mid	0.200	0.423	0.200	0.109	0.150	0.337
Malos	L Hum Mid	0.806	0.739	0.841	0.641	0.841	0.947
Maits	L Hum Dist	0.270	0.257	0.739	0.641	0.317	0.317
	L Ulna Mid	0.257	0.257	0.257	0.131	0.257	0.186

\* significant at p<0.1 \*\* significant at p<0.05

Comparison	Section	TA	Ix	Iy	Imax	Imin	J
		Sex	ual Dimor	ohism			
	R Clav Mid	0.042**	0.181	0.022**	0.073*	0.118	0.056*
	R Hum Mid	0.041**	0.149	0.012**	0.124	0.034**	0.074*
EN	R Hum Dist	0.102	0.354	0.077*	0.233	0.063*	0.162
	R Ulna Mid	0.034**	0.074*	0.093*	0.074*	0.036**	0.027**
	R Clav Mid	0.182	0.317	0.182	0.182	0.182	0.182
	R Hum Mid	0.046**	0.182	0.046**	0.046**	0.046**	0.046**
LN/EBA	R Hum Dist	0.046**	0.046**	0.046**	0.046**	0.046**	0.046**
	R Ulna Mid	0.165	0.064*	0.165	0.064*	0.064*	0.64
		Chro	onological (	Change			
	R Clav Mid	0.273	0.364	0.364	0.273	0.485	0.485
	R Hum Mid	0.117	0.044**	0.044**	0.044**	0.044**	0.044**
Females	R Hum Dist	0.036**	0.036**	0.036**	0.036**	0.036**	0.036**
	R Ulna Mid	0.581	0.218	0.581	0.581	0.327	0.436
	R Clav Mid	0.109	0.109	0.200	0.15	0.109	0.15
	R Hum Mid	0.664	0.637	0.906	1.00	0.195	0.814
Males	R Hum Dist	0.664	0.637	0.814	0.724	0.556	0.724
	R Ulna Mid	0.308	0.61	0.396	0.126	0.497	0.308

Table 5.11: Statistical comparisons of size-standardized right upper limb measures of TA and SMAs by archaeological period and sex: female and male adolescents and young adults

\* significant at p<0.1

\*\* significant at p<0.05

Table 5.12: Statistical comparisons of average size-standardized upper limb measures of TA and SMAs by archaeological period and sex: female and male adolescents and young adults

Comparison	Section	IA	IX	Iy	Imax	Imin	J
		Sexu	al Dimorp	hism			
	Avg Clav Mid	0.056*	0.118	0.022**	0.022**	0.031**	0.031**
T NI	Avg Hum Mid	0.131	0.288	0.053*	0.165	0.053*	0.078*
EIN	Avg Hum Dist	0.063*	0.211	0.035**	0.182	0.043**	0.078*
	Avg Ulna Mid	0.046**	0.046**	0.074*	0.074*	0.046**	0.015**
	Avg Clav Mid	0.182	0.317	0.182	0.096*	0.182	0.182
LNICDA	Avg Hum Mid	0.046**	0.046**	0.046**	0.046**	0.046**	0.046**
LN/EBA	Avg Hum Dist	0.046**	0.046**	0.046**	0.046**	0.046**	0.046**
	Avg Ulna Mid	0.121	0.053*	0.053*	0.053*	0.053*	0.053*
		Chro	nological C	hange			
	Avg Clav Mid	0.197	0.197	0.133	0.143	0.133	0.390
	Avg Hum Mid	0.121	0.121	0.030**	0.061*	0.030**	0.030**
Females	Avg Hum Dist	0.133	0.133	0.061*	0.133	0.061*	0.197
	Avg Ulna Mid	0.814	0.346	0.637	0.239	0.814	0.346
	Avg Clav Mid	0.109	0.423	0.078*	0.109	0.150	0.200
Malaa	Avg Hum Mid	0.828	0.724	0.637	0.556	0.556	1.00
Males	Avg Hum Dist	0.515	0.556	0.814	0.637	0.724	0.814
	Avg Ulna Mid	0.558	0.242	0.464	0.242	0.380	0.380
1							

\* significant at p<0.1

\*\* significant at p<0.05

# 5.4: Chronological and Regional Comparisons of Body Size Unstandardized Lower and Upper Limb Robusticity

As discussed in the methods section, juvenile body mass estimation is subject to considerable limitations. These limitations combined with evidence that CSG is more sensitive to differences in body mass than joint dimensions, from which body mass estimates are derived, raise the possibility that variation detected using size-standardized CSG reflects uncontrolled for differences in body mass as well as activity (Ruff et al., 1991; Lieberman et al., 2001; Cowgill, 2010). To explore this possibility, patterns detected in the previous two sections are compared to size-unstandardized measures of CSG regressed on age. Analysis was limited to three section locations, humerus midshaft, femur midshaft, and tibia midshaft, because both external and internal dimensions can be evaluated. Additionally, size-standardized analysis detected differences between archaeological periods and cemeteries at these locations. Comparisons are

only made here for individuals younger than 16 years old, because body mass estimates from joint dimensions are more accurate for older adolescents and young adults (Ruff, 2007; Chapter 4, this dissertation).

Boxplots of standardized residuals for TA, CA, MA and J grouped by archaeological period for the three sections are presented in Figure 5.4.1-5.4.4. In general, EN juveniles produce a lower range of residuals for TA and CA in all sections, except the humerus midshaft, where CA does not differ between archaeological periods (Figures 5.4.1 and 5.4.2). MA is also lower in EN individuals, though differences are more apparent at the humerus and tibia than at the femur midshaft (Figure 5.4.3). Boxplots of J show less differentiation between archaeological periods than seen for TA and CA at all three sections (Figure 5.4.4).







Figure 5.4.2: Boxplots of standardized residuals for cortical area (CA) regressed on age by archaeological period: indeterminate sex individuals 0-16 years old

Figure 5.4.3: Boxplots of standardized residuals for medullary area (MA) regressed on age by archaeological period: indeterminate sex individuals 0-16 years old







Statistical comparisons of size-unstandardized upper limb area and SMA measures by archaeological period in Table 5.13 show similar patterns to size-standardized comparisons reported in the preceding sections. At the humerus midshaft, only size-unstandardized MA differs significantly between EN and LN individuals. Size-standardized comparisons also detect differences in MA but not TA or SMAs. Size-unstandardized comparisons produce a slightly different result for chronological comparisons of the lower limb. Only femur and tibia midshaft TA as well as femur CA and tibia MA still prove significantly higher in the LN sample when CSG are regressed on age rather than body mass (Table 5.9). Differences in tibia and femur midshaft SMAs are not detected without body size standardization. Thus, controlling for body size makes EN lower limbs appear more gracile relative to the LN sample in terms of bending and torsional rigidity, but not area measures.

3								
Section	ТА	CA	MA	Ix	Iy	Imax	Imin	J
L Hum Mid	0.303	0.760	0.065*	0.287	0.732	0.193	0.240	0.397
R Hum Mid	0.1812	0.610	0.004**	0.610	0.892	0.770	0.770	0.812
Avg Hum Mid	0.100	1.00	0.004**	0.576	0.871	0.421	0.486	0.762
Fem Mid	0.017**	0.009**	0.257	0.968	0.315	0.931	0.375	0.659
Tib Mid	0.027**	0.434	0.044**	0.404	0.672	0.643	0.419	0.730
* significant at	p<0.1							

Table 5.13: Statistical comparisons of body size unstandardized area and SMA measures by archaeological period: indeterminate sex individuals 0-16 years old

\*\* significant at p<0.05

Boxplots for variables with indeterminate sex juveniles grouped by cemetery are given in Figures 5.4.5-5.4.8, and these plots reveal some additional differentiation in the data. For TA there is no clear differentiation between EN cemeteries, and, as was the case in size-standardized comparisons, both EN groups show a lower range of standardized residuals than LN Ust-Ida individuals (Figure 5.4.5). For CA and J, Lokomotiv individuals generally produce the lowest range of standardized residuals, while Shamanka and Ust-Ida display a more similar range of values (Figure 5.4.6, 5.4.7). Shamanka exhibits the lowest values of MA of any cemetery, and this was also the case for size-standardized comparisons (Figure 5.4.8).

Figure 5.4.5: Boxplots of standardized residuals for total area (TA) regressed on age by cemetery: indeterminate sex individuals 0-16 years old







Figure 5.4.7: Boxplots of standardized residuals for second polar moment of area (J) regressed on age by cemetery: indeterminate sex individuals 0-16 years old







Results of statistical comparisons for the three cemeteries are given in Table 5.14. Lokomotiv individuals show significantly lower values at either p<0.05 or p<0.1 than the other two cemeteries for several variables in all sections. Importantly, this group shows just as many differences compared to Shamanka as to Ust-Ida. Shamanka and Ust-Ida primarily differ with regards to endosteal dimensions and tibia total area, which also differed in size-standardized comparisons. Comparisons of femur midshaft TA, CA, and MA are also significant at p<0.1. The increased gracility of the Lokomotiv sample revealed in boxplots and statistical tests constitutes the greatest departure from size-standardized analysis, which found fewer differences between Lokomotiv and other cemeteries.

Comparison	Section	ТА	CA	MA	Ix	Iy	Imax	Imin	J
	L Hum Mid	0.711	1.00	0.261	0.120	0.045**	0.142	0.408	0.069*
	R Hum Mid	0.959	0.383	0.064*	0.328	0.082*	0.165	0.371	0.130
EN Lokomotiv-EN Shamanka	Avg Hum Mid	0.506	0.149	0.190	0.056*	0.016**	0.051*	0.238	0.023**
	Fem Mid	0.782	0.069*	0.088*	0.104	0.089*	0.152	0.141	0.089*
	Tib Mid	0.916	0.039**	0.458	0.051*	0.075*	0.075*	0.075*	0.045**
	L Hum Mid	0.255	0.913	0.488	0.171	0.110	0.067*	0.172	0.129
	R Hum Mid	0.319	0.248	0.401	0.283	0.218	0.240	0.354	0.189
EN Lokomotiv-LN Ust Ida	Avg Hum Mid	0.126	0.429	0.126	0.168	0.114	0.083*	0.237	0.103
	Fem Mid	0.062*	0.004**	0.830	0.166	0.048**	0.207	0.067*	0.083*
	Tib Mid	0.108	0.108	0.251	0.387	0.108	0.357	0.057*	0.258
	L Hum Mid	0.504	0.572	0.035**	0.572	0.537	0.659	0.529	0.877
	R Hum Mid	0.267	1.00	0.002**	0.983	0.267	0.693	0.554	0.572
EN Shamanka-LN Ust-Ida	Avg Hum Mid	0.312	0.574	0.005**	0.668	0.118	0.736	0.736	0.342
	Fem Mid	0.040**	0.082*	0.078*	0.495	0.856	0.587	0.909	0.682
	Tib Mid	0.044**	0.943	0.040**	0.081*	0.666	0.187	0.91	0.221

Table 5.14: Statistical comparisons of body size unstandardized area and SMA measures by cemetery: indeterminate sex individuals 0-16 years old

\* significant at p<0.1

\*\* significant at p<0.05

Given the potentially closer linkage between body mass and CSG than joint dimensions, the results of cemetery comparisons are consistent with Lokomotiv individuals exhibiting the lowest range of body mass during growth. To further ascertain how well body mass standardization controls for differences in body mass within the Cis-Baikal sample, it is important to see how inter-sample patterning in body mass estimates compares to that seen in raw CSG values. Both should show similar inter-group patterns if body mass is the primary determinant of variation in CSG. Boxplots of standardized residuals for body mass against age grouped by archaeological period and by cemetery are given in Figure 5.4.9. These plots show the same general relationship between groups as seen for size-unstandardized CSG variables regressed on age. EN individuals have lower residuals of body mass for age than Ust-Ida individuals, and Lokomotiv produces the lowest range of the three cemeteries. This mirrors the results for comparisons of size-unstandardized CSG.





To determine when differences in body mass arise, a scatterplot of body mass against age with cemetery specific LOESS lines for individuals younger than 16 years old is given in Figure 5.4.10. Visual comparison confirms that Lokomotiv produces the lowest range of body mass during growth. Compared to the other two cemeteries, Shamanka shows an intermediate range of values. Since overlap of points makes it difficult to see if cemetery samples are differentiated prior to the age of five years, a plot of the data for individuals aged 0.0-6.0 years old is given in Figure 5.4.11. Lokomotiv produces a lower range of body mass compared to Ust-Ida after the age of two years. However, given the lack of LN Ust-Ida individuals younger than two years, the analysis cannot determine if the difference exists prior to this age.



Figure 5.4.10: Scatterplot of body mass against age for indeterminate sex individuals 0-16 years old

Cemetery 🛥 EN Lokomotiv 🔺 EN Shamanka 📲 LN Ust-Ida

Figure 5.4.11: Scatterplot of body mass against age for indeterminate sex individuals 0-5.9 years old



Cemetery ---- EN Lokomotiv --- EN Shamanka ---- LN Ust-Ida

Given the patterning detected, it is reasonable to assume that CSG regressed on age can be treated as an indicator of differences in body mass. Furthermore, the similar patterning of size-unstandardized CSG and body mass estimates suggests that size-standardization applied in Sections 5.2 and 5.3 controls for some differences in body mass. Still, interpretations of these results should also consider the potential for body mass to have a greater effect on CSG measures than joint dimensions (Lieberman et al., 2001; Cowgill, 2010). Thus, there are chronological and inter-cemetery differences in body mass, and size-standardization using joint dimensions may not have completely controlled for this. This raises the possibility that EN individuals may be more robust than they appear in comparisons of size-standardized robusticity. Comparisons of size-unstandardized area and SMA values confirm that LN individuals demonstrate higher rates of periosteal deposition and endosteal resorption than EN individuals. The Lokomotiv group is especially gracile, which might indicate that this group has the lowest body mass and grows more slowly overall. However, since the EN Shamanka group exhibits the slowest rate of endosteal resorption, differences in growth rate cannot fully explain the slower endosteal resorption seen among EN groups. Instead, critical contrasts of size-standardized and sizeunstandardized results suggest chronological and inter-cemetery variation in both activity levels and the accrual of body mass.

#### 5.5 Ontogeny of Upper Limb Asymmetry in Area and Second Moments of Area

As discussed in the methods section, growth in asymmetry is measured in two ways. Absolute asymmetry measures the magnitude of asymmetry regardless of which side is stronger. Directional asymmetry allows evaluation of side dominance, also referred to as handedness, with age. Scatterplots of absolute asymmetry in TA and J against age are presented in Figures 5.5.1 and 5.5.2 respectively for all upper limb section locations. Although the oldest individuals show the greatest asymmetry, absolute asymmetry increases weakly with age. Inter-individual variation is substantial at all ages.



Figure 5.5.1: Scatterplots of absolute asymmetry in total area (TA) against age

Figure 5.5.2: Scatterplots of absolute asymmetry in second polar moment of area (J) against age Clavicle Midshaft Humerus Midshaft



Plots of directional asymmetry are presented in Figures 5.5.3 and 5.5.4 for TA and J. Negative values correspond to right side dominant individuals and positive values indicate left side dominance. For TA and J, the clavicle midshaft and ulna show little change in side dominance with age. A weak right-side dominance becomes evident in adolescence at the ulna midshaft and in young adulthood at the clavicle midshaft. However, the clavicle is unique in that, prior to the age of 15 years, most individuals actually appear to show left side dominance. The two humeral sections show clear development of right side dominance with age, and this emerges earlier than in other sections. Most individuals have more robust right humeri after the age of five years.



Figure 5.5.3: Scatterplots of directional asymmetry in total area (TA) against age



Figure 5.5.4: Scatterplots of directional asymmetry for second polar moment of area (J) against age

Plots of absolute and directional asymmetry for humeral midshaft CA, presented in Figure 5.5.5, show that, as for TA, absolute asymmetry increases with age, and right arm dominance emerges after the age of five years. As seen in Figure 5.5.6, the absolute magnitude of asymmetry in MA initially decreases from birth until the fifth year. Subsequently, the medullary cavity again becomes more asymmetric with age. Right dominance in MA initially decreases with age. However, after the age of ten years, the right medullary cavity is larger in most individuals.



Figure 5.5.5: Scatterplots of absolute and directional asymmetry in cortical area (CA) against age Absolute Asymmetry Directional Asymmetry



Figure 5.5.6: Scatterplots of absolute and directional asymmetry in medullary area (MA) against age

## 5.6: Chronological and Regional Variation in Absolute Asymmetry of Upper Limb Robusticity

Group comparisons employ absolute asymmetry, which ignores whether the left or right arm was dominant. As seen in the preceding section, only weak increases occurred in absolute asymmetry, and curve fitting did not produce a significant fit for most sections. Therefore, true values of absolute asymmetry values rather than standardized residuals are used for sample comparisons. EN and LN indeterminate sex juveniles younger than 16 years do not show clear chronological differentiation in asymmetry. Boxplots of absolute percent asymmetry in TA and J shows heavy overlap between EN and LN groups (Figures 5.6.1 and 5.6.2). Only at the ulna midshaft does the LN sample produce a clearly higher range. Comparison of boxplots for CA and MA in Figure 5.6.3 also demonstrate little chronological change in the magnitude of asymmetry. Results of statistical comparisons given in Table 5.15 confirm that there is almost no significant chronological difference in upper limb asymmetry for area and SMA measures prior to the age of 16 years. Only at the ulna midshaft do two SMAs show significant differentiation.



Figure 5.6.1: Absolute percent asymmetry in total area (TA) by archaeological period: indeterminate sex individuals 0-16 years old

Figure 5.6.2: Absolute percent asymmetry in second polar moment of area (J) by archaeological period: indeterminate sex individuals 0-16 years old







Table 5.15: Statistical comparisons of absolute asymmetry in upper limb area and SMA measures by archaeological period: indeterminate sex individuals 0-16 years old

Section	ТА	CA	MA	Ix	Iy	Imax	Imin	J
Clav Mid	0.77	_	_	0.572	0.68	0.51	0.93	0.91
Hum Mid	0.83	0.23	0.65	0.682	0.907	0.92	0.217	0.78
Hum Dist	0.34	_	_	0.113	0.488	0.262	0.248	0.40
Ulna Mid	0.20	_	_	0.407	0.283	0.079*	0.807	0.036**

\* significant at p<0.1

\*\* significant at p<0.05

data for endosteal dimensions not available

Further division of the indeterminate sex juveniles by cemetery also does not produce clear evidence of differences between groups. A visual analysis of boxplots in Figures 5.6.4-5.6.6 shows heavy overlap between cemetery samples for TA and J, as well as humerus midshaft CA and MA. The most notable differences are that Shamanka produces the highest asymmetry in clavicle TA and J, while Ust-Ida demonstrates the greatest asymmetry in these properties at the ulna midshaft (Figures 5.6.4 and 5.6.5). For humerus midshaft CA and MA, Shamanka again demonstrates the highest range of asymmetry values (Figure 5.6.6).



Figure 5.6.4: Absolute percent asymmetry in total area (TA) by cemetery: indeterminate sex individuals 0-16 years old

Figure 5.6.5: Absolute percent asymmetry in second polar moment of area (J) by cemetery: indeterminate sex individuals 0-16 years old





Statistical tests comparing the three cemeteries given in Table 5.16 confirm that asymmetry does not differ markedly between cemeteries. Significant differences for multiple properties in a section only emerge when comparing Lokomotiv and Shamanka clavicle midshaft TA and SMAs. The boxplots show that this reflects the high Shamanka values for these properties (Figures 5.6.4 and 5.6.5). LN Ust-Ida and EN Lokomotiv only differ with regards to ulna midshaft J.

Figure 5.6.6: Absolute percent asymmetry in cortical area (CA) and medullary area (MA) by

Comparison	Section	ТА	CA	MA	Ix	Iy	Imax	Imin	J
	Clav Mid	0.022**	_	_	0.668	0.032**	0.032**	0.046**	0.015**
EN Laboration EN Chamarka	Hum Mid	0.257	0.280	0.440	0.463	0.463	0.661	0.770	0.549
EN LOKOMOTIV- EN SNAMANKA	Hum Dist	0.808	—	—	0.808	0.544	1.00	0.903	0.808
	Ulna Mid	0.234	_	_	0.497	0.396	0.734	0.865	0.308
	Clav Mid	0.234	_	_	0.529	0.263	0.03**	0.234	0.234
	Hum Mid	0.462	0.671	0.203	0.54	0.540	0.947	0.739	1.00
EN LOKOMOTIV- LN UST-Ida	Hum Dist	0.370	_	_	0.282	0.929	0.420	0.420	0.370
	Ulna Mid	0.086	_	_	0.667	0.133	0.283	0.519	0.032**
EN Shamanka- LN Ust-Ida	Clav Mid	0.120	_	_	0.775	0.092	0.357	0.216	0.193
	Hum Mid	0.683	0.165	0.935	0.87	0.806	0.923	0.124	1.00
	Hum Dist	0.452	—	—	0.215	0.479	0.376	0.400	0.535
	Ulna Mid	0.321	—	—	0.352	0.352	0.082*	0.620	0.082*

*Table 5.16: Statistical comparisons of absolute asymmetry in upper limb area and SMA measures by cemetery: indeterminate sex individuals 0-16 years old* 

\* significant at p<0.1

\*\* significant at p<0.05

data for endosteal dimensions not available

Scatterplots of clavicle midshaft TA and J against age are presented in Figure 5.6.7 to evaluate the age at which Lokomotiv and Shamanka begin to differ. The age at which differences emerge proves difficult to evaluate as only one Lokomotiv individual younger than five years is

present. Nevertheless, after this point, the Shamanka sample produces a higher range of absolute asymmetry. It should not escape notice that Shamanka clavicles are also more asymmetric compared to Ust-Ida after this age. The small Lokomotiv sample size raises the possibility that detection of significance could be a statistical error. The scatterplot of asymmetry in ulna midshaft J provided in Figure 5.6.8 again suggests that significant differences between Lokomotiv and Ust-Ida result from small Lokomotiv sample size (n=2). However, Ust-Ida individuals produce the highest range through most of ontogeny. Overall, the asymmetry comparisons do not provide conclusive evidence of differentiation in asymmetry prior to the age of 16 years. Differences are seen only in isolated sections, and these may be artifacts of very small sample sizes.









In the comparisons of females and males older than sixteen from different archaeological periods, boxplots of TA and J provided in Figures 5.6.11 and 5.6.12 show that EN males produce the highest values of clavicular asymmetry and lowest range of ulna asymmetry. Statistical tests presented in Table 5.17 detect significant differences at p<0.05 across multiple variables only in comparisons of EN males and females at the clavicle and ulna midshaft. The tendency for EN males to appear more asymmetric than LN/EBA males is significant at p<0.1 for several clavicle and humerus midshaft variables, and significant at p<0.05 for humerus midshaft I<sub>v</sub>.



Figure 5.6.9: Absolute asymmetry in total area (TA) by archaeological period: female and male adolescents and young adults

Figure 5.6.10: Absolute asymmetry in second polar moment of area (J) by archaeological period: female and male adolescents and young adults



	Section	TA	Ix	Iy	Imax	Imin	J
			Sexual Di	morphism			
	Clav Mid	0.01**	0.046**	0.199	0.046**	0.022**	0.022**
EN	Hum Mid	0.495	0.558	0.435	0.495	0.626	0.626
EN	Hum Dist	0.929	0.722	0.534	0.424	0.657	0.929
	Ulna Mid	0.021**	0.064*	0.015**	0.011**	0.298	0.028**
	Clav Mid	0.317	0.317	1.00	0.505	0.739	0.317
I N/ED A	Hum Mid	0.699	1.00	1.00	0.439	0.699	0.699
LIN/EBA	Hum Dist	0.699	0.439	0.699	0.245	0.439	0.699
	Ulna Mid	0.564	0.564	1.00	0.564	0.564	0.564
			Chronologi	ical Change			
	Clav Mid	1.00	0.38	0.143	0.558	0.558	1.00
Esselar	Hum Mid	1.00	0.77	0.558	0.77	0.77	1.00
remates	Hum Dist	0.192	0.602	0.117	0.602	0.296	0.602
	Ulna Mid	0.433	1.00	0.117	0.794	0.602	0.794
	Clav Mid	0.055*	0.109	0.109	0.262	0.055*	0.078*
Malas	Hum Mid	0.221	0.713	0.027**	0.903	0.086*	0.27
wales	Hum Dist	0.54	1.00	0.086	0.713	0.713	0.54
	Ulna Mid	0.569	0.21	0.425	0.305	0.909	0.425

Table 5.17: Statistical comparisons of absolute asymmetry in upper limb area and SMAs by archaeological period and sex: female and male adolescents and young adults

\* significant at p<0.1 \*\* significant at p<0.05

# 5.7: Summary of Variation Detected in the Ontogeny of Limb Robusticity within Cis-Baikal Populations

Within the Cis-Baikal sample, area and SMA measures increased with age. TA and CA demonstrated a more similar growth trajectory than MA. Young adult ranges of TA and SMAs are achieved by late adolescence. Study of upper limb asymmetry demonstrates a weak increase in absolute percent difference with age in all sections. However, right arm dominance emerges earlier in the humerus than the clavicle or ulna.

Comparisons of size-standardized area and SMAs detect differences between juveniles younger than 16 years from different archaeological periods and cemeteries. Overall, sizestandardized comparisons detect a general trend towards greater robusticity in LN juveniles, and this appears most pronounced in the lower limb. Upper limb comparisons identify slower endosteal resorption during growth in the EN sample, especially among Shamanka individuals, which results in lower MA and higher %CA. Conversely, there are few statistical differences in upper limb TA and SMAs. LN individuals may have significantly more robust ulna midshafts than EN individuals, but the result could also reflect reduced sample size compared to other sections. In the lower limb, LN individuals have more robust lower limbs once body size has been accounted for, though this difference is not evident at the femur subtrochanteric section. More significant differences in total area and SMAs are detected in comparisons of the two tibia sections than the femur midshaft, implying that differentiation between archaeological periods is more pronounced in the distal limb segment. In both the upper and lower limb, chronological differences in size-standardized area and SMAs are primarily the result of differentiation between Shamanka and Ust-Ida individuals. Differences between archaeological periods and cemeteries are visible by the age of five years. By the end of adolescence, sexual dimorphism emerges in both upper and lower limb robusticity. Decreases in robusticity from the EN to the LN/EBA appear more pronounced in females than males.

Unlike size-standardized analysis, the additional comparison of size-unstandardized area and SMAs regressed on age emphasize the gracility of Lokomotiv individuals. It is also important that size unstandardized CSG for individuals from different archaeological periods and cemeteries show similar patterning to body mass estimates, and Lokomotiv individuals younger than 16 years of age produce the lowest range of size-unstandardized CSG values. While potentially an artifact of sample size, this may reflect poorer accrual of body mass in juveniles buried at this cemetery. The results of size-unstandardized analysis have methodological implications. Prior studies have proposed that raw measures of area and SMAs may be more sensitive to differences in body mass than joint dimensions, which grow under heavier genetic constraint (Cowgill, 2010; Osipov et al., 2016). Therefore, indications of lower body mass in EN juveniles raises the possibility that size-standardized comparisons may underestimate the robusticity of EN juveniles, especially those buried at the Lokomotiv cemetery.

Comparisons of asymmetry detected no clear differentiation in the indeterminate sex juvenile sample. The greatest differentiation is apparent at the clavicle Thus, Cis-Baikal juveniles from different archaeological periods and cemeteries loaded the left and right upper limb in a similar manner.

# **Chapter 6: Results Part 2- Development of Limb Shape: Ontogenetic Patterning and Sample Comparisons**

### 6.1 Ontogeny of Diaphyseal Shape

Limb shape is quantified using ratios of SMAs calculated about perpendicular axes. The upper and lower limb sections show distinct relationships between shape and age, so age related changes are described separately for each limb.

Several lower limb sections show more pronounced age-related change in shape than the upper limb. Plots of lower limb  $I_x/I_y$  against age are given in Figure 6.1.1 and correlation coefficients ( $R^2$ ) for curve fittings of  $I_x/I_y$  on age are given in Table 6.1. At the femur subtrochanteric section,  $I_x/I_y$  values decrease with age, particularly after the age of ten years, as the section becomes more mediolaterally reinforced. From the femur midshaft to tibia midshaft,  $I_x/I_y$  increases with age, indicating more rapid anteroposterior than mediolateral expansion of the lower limb throughout this region during growth (Figure 6.1.1). As seen in Table 6.1,  $R^2$  values for curve fittings indicate that the correlation between  $I_x/I_y$  and age is stronger at the femur midshaft and tibia nutrient foramen sections than the femur subtrochanteric and tibia midshaft sections.



Figure 6.1.1: Scatterplots of lower limb I<sub>x</sub>/I<sub>y</sub> against age

Table 6.1: Correlation coefficients ( $R^2$ ) for Lower Limb  $I_x/I_y$  regressed on age\*

Variable	R <sup>2</sup>
Fem ST	0.12
Fem Mid	0.46
Tib NF	0.37
Tib Mid	0.15

\*First order (linear) polynomials provide the best fit in all cases

Scatterplots of  $I_{max}/I_{min}$  against age are given in Figure 6.1.2, and correlation coefficients (R<sup>2</sup>) for curve fitting are given in Table 6.2. At the femur subtrochanteric section, this ratio does not change markedly during growth, and curve-fitting does not produce a significant fit. Although both maximum and minimum strains increase with age, they do so at an equivalent rate. In individuals older than ten years, the LOESS line trends upwards, suggesting increasing disparity between  $I_{max}$  and  $I_{min}$ . Such patterning would match the trend of increasing disparity in  $I_x/I_y$  during this period. However, the lack of older adolescents and young adults for this section location makes the conclusion tentative. At the femoral midshaft, change in  $I_{max}/I_{min}$  with age resembles a U-shaped curve. After birth, the difference between  $I_{max}$  and  $I_{min}$  initially decreases. It then increases in individuals older than ten years. Compared to the femur, tibia  $I_{max}/I_{min}$
evidenced by higher correlation coefficients (Table 6.2). At the femur midshaft, tibia nutrient foramen, and tibia midshaft,  $I_x/I_y$  and  $I_{max}/I_{min}$  values fall within the young adult range after the tenth year (Figures 6.1.1 and 6.1.2).



Figure 6.1.2: Scatterplots of lower limb I<sub>max</sub>/I<sub>min</sub> against age

Table 6.2: Correlation coefficients ( $R^2$ ) for lower Limb  $I_{max}/I_{min}$  regressed on age

Variable	$\mathbb{R}^2$
Fem ST	n.s.
Fem Mid <sup>1</sup>	0.21
Tib NF	0.62
Tib Mid <sup>1</sup>	0.52

1: FM  $I_{max}/I_{min}$  and TM  $I_{max}/I_{min}$  fit to a second-order (quadratic) polynomial. All other ratios fit with a first order function. n.s.: Curve-fitting non-significant

For the upper limb, right and left sections show similar patterns, so only plots of average values are presented. Asymmetry is addressed in Sections 6.4 and 6.5. Scatterplots of upper limb  $I_x/I_y$ , against age with LOESS lines for each section are given in Figure 6.1.3. In all sections, ratio values range from 0.4 to 1.7. Correlation coefficients for curve fittings of  $I_x/I_y$  ratios on age are given in Table 6.3. There is no statistically significant change with age in ratio values at the clavicle or humerus midshaft. At the distal humerus,  $I_x/I_y$  increases with age, and the correlation is significant, an indication that the diaphysis becomes more anteroposteriorly reinforced during

growth. Visual inspection of the plot indicates that the increase appears most noticeable after the age of five years (Figure 6.1.3). Conversely, values decrease slightly with age at the ulna midshaft as the shaft becomes more reinforced along the mediolateral axis. Both visual inspection of the plots and the low correlation coefficients indicate that the age-related trends detected at the distal humerus and ulna midshaft are extremely weak (Figure 6.1.3 and Table 6.3).





Variable	R <sup>2</sup>
L Clav Mid	n.s.
R Clav Mid	n.s.
Avg Clav Mid	n.s.
L Hum Mid	n.s.
R Hum Mid	n.s.
Avg Hum Mid	n.s.
L Hum Dist	n.s.
R Hum Dist	0.23
Avg Hum Dist	0.28
L Ulna Mid	0.05
R Ulna Mid	0.007
Avg Ulna Mid	0.07

Table 6.3: Correlation coefficients ( $R^2$ ) for upper limb  $I_x/I_y$  regressed on age\*

\*First order (linear) polynomials provide the best fit in all cases where age and ratio values show a significant correlation. n.s.: Curve- fitting non-significant

Plots of  $I_{max}/I_{min}$  ratios against age for each section are given in Figure 6.1.4. Ratios of  $I_{max}$  and  $I_{min}$  show a greater deviation from circularity than  $I_x$  and  $I_y$ . Values range from just above 1.0 to just below 3.0. The plots indicate the clavicle midshaft becomes more circular, and the humerus and ulna midshaft sections become less evenly reinforced with age. Only the distal humerus shows no discernible change during development. Correlation coefficients for curve fittings, given in Table 6.4, show that significant relationships exist between ratio values and age for the clavicle and ulna midshaft section. At the humerus midshaft, only average values show a statistically significant relationship to age. Regardless the low correlation coefficients suggest very weak change with age for all sections.



Figure 6.1.4: Scatterplots of upper limb I<sub>max</sub>/I<sub>min</sub> against age

Variable	R <sup>2</sup>
L Clav Mid	0.05
R Clav Mid	0.21
Avg Clav Mid	0.17
L Hum Mid	n.s.
R Hum Mid	n.s.
Avg Hum Mid	0.03
L Hum Dist	n.s.
R Hum Dist	n.s.
Avg Hum Dist	n.s.
L Ulna Mid	0.06
R Ulna Mid	0.05
Avg Ulna Mid	0.10

Table 6.4: Correlation coefficients (R<sup>2</sup>) for upper limb I<sub>max</sub>/I<sub>min</sub> against age\*

\*First order (linear) polynomials provide the best fit in all cases where age and ratio values show a significant correlation n.s.: Curve- fitting non-significant

#### 6.2: Chronological and Regional Variation in the Ontogeny of Lower Limb Shape.

To compare individuals from different archaeological periods and cemeteries, standardized residuals from regression of lower limb shape ratios on age were compared for all variables except femur subtrochanteric  $I_{max}/I_{min}$ . Given the lack of significant relationship to age for this variable, true ratio values were used instead of standardized residuals (Table 6.2). Boxplots for comparisons of EN and LN indeterminate sex juveniles younger than 16 years are given in Figures 6.2.1 and 6.2.2 for  $I_x/I_y$  and  $I_{max}/I_{min}$  respectively. Visual analysis of both femur subtrochanteric ratios indicates no difference between EN and LN juveniles. At the femur midshaft, tibia nutrient foramen, and tibia midshaft sections, the EN sample produces a higher range of residuals for  $I_x/I_y$  and  $I_{max}/I_{min}$  than the LN sample. Results for statistical comparisons of juveniles from the two archaeological periods are provided in Table 6.5. EN individuals younger than sixteen show significantly higher ratios of  $I_x/I_y$  for the femur midshaft and tibia nutrient foramen sections at p<0.05, and the tibia midshaft comparison for this ratio is significant at p<0.1. There are no significant differences in  $I_{max}/I_{min}$  between archaeological periods.





Figure 6.2.2: Boxplots of standardized residuals for lower limb  $I_{max}/I_{min}$  by archaeological period: indeterminate sex individuals 0-16 years old (true ratio values used for the femur subtrochanteric section due to non-significant curve fit)



Table 6.5: Statistical comparisons of lower limb shape ratios by archaeological period: indeterminate sex individuals 0-16 years old

Section	Ix/Iy	Imax/Imin
Fem ST	0.930	0.417
Fem Mid	0.027**	0.185
Tib NF	0.004**	0.173
Tib Mid	0.076*	0.106

\*\* significant at p<0.05

Boxplots of the indeterminate sex juveniles grouped by cemetery are given in Figures 6.2.3 and 6.2.4 for  $I_x/I_y$  and  $I_{max}/I_{min}$  respectively. Both EN groups, Lokomotiv and Shamanka, produce a higher range of  $I_x/I_y$  and  $I_{max}/I_{min}$  than LN Ust-Ida individuals. The exception to this rule is the femur subtrochanteric section, where the three groups demonstrate more homogeneous values. The results for statistical comparisons are provided in Table 6.6. The two EN groups do not differ significantly for either ratio, and Lokomotiv exhibits no significant differences when compared to Ust-Ida. The Shamanka individuals produce a significantly higher range of  $I_x/I_y$  than

LN Ust-Ida at the femur midshaft and tibia nutrient foramen sections (Table 6.6). There are no significant differences in  $I_{max}/I_{min}$ .





Figure 6.2.4: Boxplots of standardized residuals of lower limb  $I_{max}/I_{min}$  (true ratio values used for the femur subtrochanteric section due to non-significant curve fit) by cemetery: indeterminate sex individuals 0-16 years old



Table 6.6: Statistical comparisons of lower limb shape ratios by cemetery: indeterminate sex individuals 0-16 years old

Comparison	Section	Ix/Iy	Imax/Imin
	Fem ST	0.510	0.693
EN Lokomotiv- EN Shamanka	Fem Mid	0.726	0.857
	Tib NF	0.308	0.424
	Tib Mid	0.958	0.121
	Fem ST	0.687	0.903
	Fem Mid	0.176	0.234
EN LOKOMOTIV-LIN UST-Ida	Tib NF	0.152	0.451
	Tib Mid	0.187	0.889
	Fem ST	0.905	0.310
	Fem Mid	0.029**	0.304
EN Shamanka- LN Ust-Ida	Tib NF	0.0031**	0.171
	Tib Mid	0.110	0.407

\*\* significant at p<0.05

Scatterplots of standardized residuals for femur midshaft and tibia nutrient foramen  $I_x/I_y$  are presented in Figure 6.2.5 to determine the age at which differences between archaeological periods and cemeteries become apparent. The overlap between Shamanka and Ust-Ida is heaviest between birth and five years for both sections, although several EN Shamanka individuals already produce the highest values. The tendency for Shamanka individuals to exhibit higher ratios than the Ust-Ida sample becomes more apparent after the age of five years. Lokomotiv individuals occupy an intermediate position, though values are generally elevated relative to Ust-Ida.





Comparisons of adolescent and young adult females and males do not consider the femur subtrochanteric section due to a lack of periosteal contours for this section (see Chapter 4). Visual analysis of adolescent and young adult  $I_x/I_y$  ratios in Figure 6.2.6 shows sexual dimorphism at the femur midshaft in both the EN and LN/EBA samples. Males have more anteroposteriorly expanded femoral midshafts compared to females from the same

archaeological period. The same pattern is not detected in either tibia section. The boxplots of  $I_{max}/I_{min}$  in Figure 6.2.7 demonstrate sexual dimorphism in both the femur midshaft and both tibia sections for EN individuals, with males producing higher values. LN/EBA individuals show sexual dimorphism at the femur midshaft and tibia midshaft. Results of statistical comparisons in Table 6.7 detect only one significant difference between females and males from the same archaeological period, EN males have significantly higher ranges of tibia midshaft Imax/Imin than EN females. There is also no statistically significant difference in shape between individuals of the same sex from different archaeological periods. These results may well be an artifact of sample size, especially since only two LN/EBA females are included in the sample.

Figure 6.2.6: Boxplots of standardized residuals by archaeological period for lower limb I<sub>x</sub>/I<sub>y</sub>: female and male adolescents and young adults





Figure 6.2.7: Boxplots of standardized residuals by archaeological period for lower limb  $I_{max}/I_{min}$ : female and male adolescents and young adults

Table 6.7: Statistical comparisons of lower limb shape ratios by archaeological period and sex: female and male adolescents and young adults

Comparison	Fem Mid Ix/Iy	Fem Mid Imax/Imin	Tib NF Ix/Iy	Tib NF Imax/Imin	Tib Mid Ix/Iy	Tib Mid Imax/Imin
			Sexual Dimorpl	nism		
EN	0.310	0.132	0.775	0.116	0.391	0.01**
LN/EBA	1.00	0.130	0.739	0.739	0.739	1.00
			Chronological Cl	hange		
Females	0.857	0.857	0.505	0.505	0.739	0.182
Males	0.610	0.910	0.199	0.886	0.317	0.116

\*\* significant at p<0.05

## 6.3: Chronological and Regional Variation in the Ontogeny of Upper Limb Shape

As demonstrated in Section 6.1, a considerable number of upper limb shape variables do not show a statistically significant relationship to age. Even when curve fittings are significant,  $R^2$  values are very low. For this reason, true ratio values are employed for both boxplots and statistical comparisons rather than standardized residuals generated through curve fitting. Boxplots of average values are presented for the sake of brevity. Asymmetry in upper limb shape ratios is discussed in Section 6.4 and 6.5. Boxplots of average  $I_x/I_y$  and  $I_{max}/I_{min}$  for EN and LN indeterminate sex juveniles younger than 16 years old are given in Figures 6.3.1 and 6.3.2 respectively. Unlike the lower limb, neither group consistently produces a higher range of residuals across the upper limb for either ratio. Results of statistical tests given in Table 6.8 only show significant differences for  $I_x/I_y$  at the left ulna midshaft at p<0.05. However,  $I_x/I_y$  comparisons are significant at p<0.1 for the left humerus midshaft and distal humerus. Thus, while one cannot exclude the possibility of chronological differences in upper limb shape, differences are less pronounced than those detected in the lower limb.







Figure 6.3.2: Boxplots of ratio values for average upper limb I<sub>max</sub>/I<sub>min</sub> by archaeological period: indeterminate sex individuals 0-16 years old

Table 6.8: Statistical comparisons of upper limb shape ratios by archaeological period: indeterminate sex individuals aged 0-16 years

Section	Left Ix/Iy	Left Imax/Imin	Right Ix/Iy	Right Imax/Imin	Average Ix/Iy	Average Imax/Imin
Clav Mid	0.26	0.89	0.39	0.19	0.19	0.4
Hum Mid	0.07*	0.75	0.84	0.32	0.29	0.35
Hum Dist	0.09*	0.57	0.85	0.24	0.4	0.47
Ulna Mid	0.02**	0.18	0.54	0.71	0.2	0.39

\*\* significant at p<0.05

As for archaeological period comparisons, boxplots for ratios grouped by cemetery given in Figures 6.3.3 and 6.3.4 show heavy overlap between the three cemeteries and no consistent patterning across adjacent sections. The statistical comparisons of these three groups in Table 6.9 detect significant differences only at the clavicle and ulna midshaft. EN Lokomotiv and Shamanka differ significantly for left clavicle  $I_{max}/I_{min}$ . EN Shamanka and LN Ust-Ida differ significantly for left clavicle, average clavicle and left ulna midshaft  $I_x/I_y$  at p<0.05. The failure to detect significant differences in the same sections as when the EN combined sample was compared to the LN group raises the possibility that differences between groups are detected either due to chance or represent artifacts of sample size.



Figure 6.3.3: Boxplots of raw values of upper limb  $I_x/I_y$  by cemetery: indeterminate sex individuals 0-16 years old





Comparison	Section	Left Ix/Iy	Left Imax/Imin	Right Ix/Iy	<b>Right Imax/Imin</b>	Average Ix/Iy	Average Imax/Imin
	Clav Mid	0.124	0.021**	0.618	0.618	0.151	0.483
EN Lokomotiv- EN	Hum Mid	0.933	0.153	0.882	0.157	0.951	0.105
Shamanka	Hum Dist	0.362	0.606	0.938	0.312	0.213	0.91
	Ulna Mid	0.763	0.159	0.11	0.26	0.215	0.188
	Clav Mid	0.839	0.104	0.977	0.435	0.896	0.128
EN Laboration IN 11-4 Lis	Hum Mid	0.156	0.371	0.784	0.869	0.242	0.845
EN LOKOMOTIV- LN UST-10a	Hum Dist	0.053*	0.47	0.953	0.953	0.249	0.63
	Ulna Mid	0.243	0.697	0.459	0.459	0.832	0.671
	Clav Mid	0.048**	0.081*	0.204	0.189	0.044**	0.891
EN Shamanka- LN Ust-Ida	Hum Mid	0.111	0.801	0.722	0.256	0.374	0.203
	Hum Dist	0.291	0.744	0.962	0.136	0.909	0.493
	Ulna Mid	0.035**	0.065*	0.322	0.475	0.151	0.172

Table 6.9: Statistical comparisons of upper limb shape ratios by cemetery: indeterminate sex individuals 0-16 years old

\*\* significant at p<0.05

Scatterplots of left clavicle  $I_x/I_y$  and  $I_{max}/I_{min}$  against age are given in Figure 6.3.5, and scatterplots of left ulna midshaft  $I_x/I_y$  and distal humerus  $I_x/I_y$  values against age are presented in Figure 6.3.6. These variables were employed to evaluate the age at which difference become apparent, because they show significant differences in either archaeological period or cemetery comparisons. At the clavicle midshaft, both ratios exhibit decreasing separation between the samples with age (Figure 6.3.5). The three cemeteries show the most differentiation shortly after birth, primarily due to outliers in the Shamanka and Lokomotiv groups. Similarly, as seen in Figure 6.3.6, at the ulna midshaft, the tendency for EN Shamanka to produce higher values than LN Ust-Ida is clearest at birth, and overlap between samples increases with age, though this may also reflect the fact that most Shamanka individuals are younger than five years old. The detection of the greatest differentiation early in development suggests that differences in upper limb shape do not correlate with behavioral variation. One would expect differences attributable to behavior become more pronounced with age.

As show in Figure 6.3.6, for left distal humerus  $I_x/I_y$ , there is a weak tendency for EN individuals to show lower values of  $I_x/I_y$  relative to the LN sample between the age of five years and ten years, although two Shamanka individuals produce the highest values in this age range. After the age of 15 years, overlap between archaeological periods increases, though this may reflect small sample size.



Figure 6.3.5: Scatterplots of clavicle midshaft shape ratios for indeterminate sex individuals 0-16 years old

Time Period • Early Neolithic • Late Neolithic





Time Period • Early Neolithic • Late Neolithic

While comparisons of indeterminate sex juveniles do not show clear differences between individuals from different archaeological periods and cemeteries, sexual differentiation appears in adolescence and young adulthood. Figures 6.3.7 and 6.3.8 show boxplots of shape ratios for EN and LN/EBA females and males. In both archaeological periods, males produce lower ranges of  $I_x/I_y$  and  $I_{max}/I_{min}$  than females at both humeral cross-section locations, but not the clavicle or ulna midshaft. Females have more anteroposteriorly reinforced humeri than males. In addition, EN males have more anteroposteriorly reinforced humeri than LN/EBA males, but LN/EBA males have higher ratios of  $I_{max}/I_{min}$ , which suggests that the humeri of these individuals are less circular. LN/EBA females exhibit higher values for both ratios compared to EN females at both humeral sections.

Statistical comparisons of the females and males are presented in Table 6.10. There are significant differences either at p<0.05 or p<0.1 in humeral  $I_x/I_y$  and  $I_{max}/I_{min}$  between females and males in both archaeological periods. There is also tentative evidence for change between

archaeological periods. Females and males show several significant chronological differences in humerus midshaft shape at p<0.1. However, only the comparison of right humerus midshaft  $I_{max}/I_{min}$  in males reaches significance at p<0.05. Sexual dimorphism is apparent in both humeral sections, and humeral shape may also differentiate individuals of the same sex from different archaeological periods.



Figure 6.3.7: Boxplots of upper limb  $I_x/I_y$  by archaeological period: female and male adolescents and young adults



Figure 6.3.8: Boxplots of upper limb  $I_{\text{max}}/I_{\text{min}}$  by cemetery: female and male adolescents and young adults

Comparison	Section	Left Ix/Iy	Left Imax/Imin	Right Ix/Iy	<b>Right Imax/Imin</b>	Average Ix/Iy	Average Imax/Imin
			Se	xual Dimorphi	sm		
	Clav Mid	0.475	0.775	0.269	0.615	0.191	0.615
EN	Hum Mid	0.072*	0.034**	0.027**	0.072*	0.041**	0.029**
EN	Hum Dist	0.06*	0.05**	0.005**	0.008**	0.009**	0.017**
	Ulna Mid	0.487	0.817	0.657	0.477	0.657	0.534
	Clav Mid	1.00	0.505	0.739	0.739	1.00	0.505
I N/ED A	Hum Mid	0.053*	0.121	0.096*	0.505	0.046**	0.182
LIN/EBA	Hum Dist	0.121	1.00	0.096*	0.096*	0.096*	0.182
	Ulna Mid	0.643	0.355	0.165	0.165	0.439	0.439
			Chr	onological Cha	inge		
	Clav Mid	0.38	0.38	0.554	0.693	0.43	0.844
Famalas	Hum Mid	0.157	0.099*	0.099*	0.059*	0.076*	0.076*
remates	Hum Dist	1.00	0.814	0.667	0.283	0.554	0.554
	Ulna Mid	0.602	0.602	0.519	0.283	0.197	1.00
	Clav Mid	0.631	0.337	0.631	0.522	0.522	0.423
Malas	Hum Mid	0.111	0.391	0.233	0.017**	0.083*	0.065*
wiates	Hum Dist	0.221	0.178	0.588	0.745	0.448	0.329
	Ulna Mid	1.00	1.00	0.308	0.497	0.77	1.00

Table 6.10: Statistical comparisons of upper limb shape ratios by archaeological period and sex: female and male adolescents and young adults

\* significant at p<0.1 \*\* significant at p<0.05

#### 6.4: Ontogeny of Asymmetry in Upper Limb Shape

Absolute percent asymmetry and directional asymmetry values were calculated for upper limb  $I_x/I_y$  and  $I_{max}/I_{min}$ . Scatterplots of absolute asymmetry in  $I_x/I_y$  and  $I_{max}/I_{min}$ , given in Figures 6.4.1 and 6.4.2 respectively, show no clear change in the range of values with age, though adolescents and young adults produce the greatest range in the humeral sections. Likewise, scatterplots of directional asymmetry against age, provided in Figures 6.4.3 and 6.4.4 reveal that, a nearly equal number of individuals are left or right-side dominant at all ages. The only exceptions are consistent left side dominance in clavicle  $I_x/I_y$  and consistent right-side dominance in humerus midshaft  $I_{max}/I_{min}$  throughout the age range under examination. As these tendencies are present from birth, it is improbable that they relate to differences in activity.



Figure 6.4.1: Scatterplots of absolute asymmetry in upper limb I<sub>x</sub>/I<sub>y</sub> against age

Figure 6.4.2: Scatterplots of absolute asymmetry of upper limb  $I_{\text{max}}/I_{\text{min}}$  against age





Figure 6.4.3: Scatterplots of directional asymmetry in upper limb  $I_x/I_y$  against age

Figure 6.4.4: Scatterplots of directional asymmetry in upper limb I<sub>max</sub>/I<sub>min</sub> against age Clavicle Midshaft Humerus Midshaft



## 6.5 Chronological and Regional Variation in Upper Limb Shape Asymmetry

The true values of absolute asymmetry rather than standardized residuals are used for sample comparisons due to a lack of a significant relationship between variables and age. Boxplots of the absolute values of asymmetry in  $I_x/I_y$  and  $I_{max}/I_{min}$  for EN and LN indeterminate sex juveniles younger than 16 years old are given in Figures 6.5.1 and 6.5.2. The two archaeological periods show heavy overlap for both ratios, and statistical comparisons of these groups in Table 6.11 detect no significant differences at any section location. Splitting the indeterminate sex sample by cemetery does not reveal additional differentiation. Boxplots of cemetery samples presented in Figures 6.5.3 and 6.5.4 do not show consistent differences, except that Lokomotiv shows a high range for ulna midshaft shape ratios. As was the case for archaeological period comparisons, results of statistical comparisons in Table 6.12 indicate no significant differences in shape asymmetry between the three cemetery groups. Only three comparisons are significant at p<0.1. The fact that only isolated variables reach significance is consistent with spurious detection of statistical differentiation by chance, perhaps due to sample size. All comparisons where p-values are below 0.1 involve the Lokomotiv group where n=4.







Figure 6.5.2: Boxplots of absolute asymmetry for upper limb  $I_{max}/I_{min}$  by archaeological period: indeterminate sex individuals 0-16 years old

Table 6.11: Statistical comparisons of absolute percent asymmetry in shape ratios by archaeological period: indeterminate sex individuals 0-16 years old

Section	Ix/Iy	Imax/Imin
Clav Mid	0.902	0.621
Hum Mid	0.605	0.345
Hum Dist	0.444	0.444
Ulna Mid	0.723	0.849

\*\* significant at p<0.05



Figure 6.5.3: Boxplots of absolute asymmetry for upper limb  $I_x/I_y$  by cemetery: indeterminate sex individuals 0-16 years old

Figure 6.5.4: Boxplots of absolute percent asymmetry for upper limb  $I_{max}/I_{min}$  by cemetery: indeterminate sex individuals 0-16 years old



*Table 6.12: Statistical comparisons of absolute percent asymmetry in shape ratios by cemetery: indeterminate sex individuals 0-16 years old* 

Comparison	Section	Ix/Iy	Imax/Imin
	Clav Mid	0.568	0.886
EN Laboration EN Chamanha	Hum Mid	0.454	0.851
EN LOKOMOUV- EN SNAMANKA	Hum Dist	0.365	0.069*
	Ulna Mid	0.396	0.089*
	Clav Mid	0.575	0.889
EN Laborativ, I.N.Uat Ida	Hum Mid	0.768	0.768
EN LOROMOUV- EN UST-IUA	Hum Dist	0.733	0.654
	Ulna Mid	0.390	0.053*
	Clav Mid	0.775	0.505
EN Shamanka I N Hat Ida	Hum Mid	0.744	0.248
En Shamanka- En Ust-Ida	Hum Dist	0.289	0.232
	Ulna Mid	0.495	0.420

\*\* significant at p<0.05

The homogeneity between archaeological periods seen in indeterminate sex juveniles is also evident in adolescent/young adult females and males. Boxplots comparing individuals from different archaeological periods presented in Figures 6.5.5-6.5.6 do not show consistent differences between males and females from different archaeological periods across sections. Statistical comparisons of females and males in Table 6.13 reveal only two significant differences between females and males from the same archaeological period. EN females have higher asymmetry for humerus distal I<sub>max</sub>/I<sub>min</sub> than EN Males, and LN/EBA females show less asymmetry in clavicle midshaft I<sub>max</sub>/I<sub>min</sub> than LN/EBA males. The sporadic detection of differences in only some sections suggests that dimorphism, if it exists, is quite weak, affecting only isolated portions of the upper limb.



Figure 6.5.5: Boxplots for absolute percent asymmetry for upper limb  $I_x/I_y$  by archaeological period: female and male adolescents and young adults

Figure 6.5.6: Boxplots for absolute percent asymmetry for upper limb  $I_{max}/I_{min}$  by archaeological period: female and male adolescents and young adults



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*Table 6.13: Statistical comparisons of absolute asymmetry in shape ratios by archaeological period and sex: female and male adolescents and young adults* 

Comparison	Section	Ix/Iy	Imax/Imin		
Sexual Dimorphism					
	Clav Mid	0.568	0.886		
EN	Hum Mid	0.922	0.495		
EN	Hum Dist	0.158	0.041**		
	Ulna Mid	0.247	0.247		
	Clav Mid	0.317	0.046**		
LN/EBA	Hum Mid	0.439	0.699		
	Hum Dist	0.505	0.699		
	Ulna Mid	0.564	0.083*		
Ú	Chronological	Change			
	Clav Mid	0.558	0.38		
Formalas	Hum Mid	0.558	0.77		
remates	Hum Dist	0.427	0.192		
	Ulna Mid	0.602	0.068*		
	Clav Mid	0.873	0.15		
Malas	Hum Mid	0.221	0.086*		
iviaies	Hum Dist	0.278	0.327		
	Ulna Mid	0.425	0.909		

\*\* significant at p<0.05

## 6.6: Summary of Limb Shape Analysis

Scatterplots of limb shape against age showed that shape ratios did not undergo strong changes with age in upper limb sections, though several significant patterns emerge. The clavicle becomes more rounded with age, while other sections become less circular with age. The distal humerus also becomes more reinforced in the anteroposterior plane while the ulna undergoes mediolateral buttressing during growth. At the subtrochanteric section of the femur, the lower limb becomes more mediolaterally reinforced with age. In contrast, the femur midshaft, tibia nutrient foramen, and tibia midshaft sections undergo anteroposterior reinforcement during growth. I<sub>max</sub>/I<sub>min</sub> also increases with age from the femur midshaft to tibia midshaft. However, this ratio exhibits a unique relationship with age at the femur midshaft, initially decreasing after birth and then increasing in individuals older than ten years.

Comparisons of shape ratios in indeterminate sex juveniles younger than 16 years old find that EN juveniles produce higher values of femur midshaft and tibia section shape ratios than LN juveniles. This patterning is most strongly expressed at the femur midshaft and tibia nutrient foramen section, suggesting that certain regions of the lower limb may be more sensitive to differences in strain distribution. It is intriguing that further subdivision of this cohort by cemetery showed the greatest differentiation between Ust-Ida and Shamanka juveniles, because these cemeteries also showed the greatest differences in measures of area and SMAs. If not entirely an artifact of sample size, the finding reinforces the idea that there is significant variation in bone functional adaptation between individuals from different cemeteries as well as archaeological periods. While lower limb shape provides strong evidence of differentiation prior to 16 years of age, upper limb shape ratios do not show clear differences. Different upper limb variables show statistical differences in archaeological period and cemetery comparisons, and the same differences are not seen in adjacent limb sections. These results raise the possibility that isolated comparisons reach statistical significance by chance. Ranges of upper limb shape asymmetry show almost no change with age, though young adults produce the highest values, implying increased heterogeneity towards the end of development. Thus, it is unsurprising that no differences in upper limb shape asymmetry emerge during ontogeny. Sexual dimorphism in bone shape appears by young adulthood in both the upper and lower limbs.

Overall, shape ratios show weaker relationships to age than measures of area and SMAs. Comparisons of juveniles younger than 16 years from different archaeological periods and cemeteries indicate both chronological and regional differentiation in lower limb shape, but no clear difference in the upper limb. By the end of the growth period, bone shape variation in both limbs is consistent with the emergence of sexual differences in cross-section shape. In the upper limb dimorphism is restricted to the humerus, whereas in the lower limb it is apparent in both the femur and tibia.

# **Chapter 7: Results Part 3- Development of Interlimb Robusticity Ratios: Ontogenetic Patterning and Sample Comparisons**

#### 7.1: Ontogeny of Interlimb Robusticity Ratios

Interlimb robusticity ratios allow analysis of how individuals accrue bony tissue and strength in the weight bearing lower limb relative to the non-weight bearing upper limb. Ratios were constructed by dividing either femur or tibia midshaft CSG by humerus midshaft CSG. Using these ratios allows evaluation of age related change in ratios of both external and internal dimensions. Ratios are constructed for TA, CA, MA, and J. Plots for ratios using average humeral values are presented, because general growth patterns followed the same trajectory for ratios that employed the left and right humerus.

Scatterplots of TA and J ratios against age are presented in Figures 7.1.1 and 7.1.2 respectively. Both ratios exhibit a similar ontogenetic pattern. At birth, the femur is slightly stronger than the humerus and the tibia is about as strong. Subsequently, as evidenced by the sharp increase in the LOESS lines, lower limb sections accrue TA and, as evidenced by plots of J, bending and torsional strength faster than the humerus midshaft. Between years 10-15, trend lines plateau, signifying that the limbs accrue cortical tissue and strength at a similar rate. After the age of 15 years, values become more variable. A decrease occurs in the tibia/humerus ratio LOESS line, suggesting that the external diameter of the upper limb expands slightly faster than that of the lower limb for some individuals in this age range. Other older adolescents and young adults exhibit values as high as individuals between the age of 10-15 years. The femur/humerus ratio exhibits a less pronounced decrease in ratio values after the age of 15 years. Scatterplots of CA ratios against age, given in Figure 7.1.3, show the same growth pattern from birth to the age of 16 years as TA and J. Ratio values increase rapidly after birth and then plateau after the age of ten years. However, a lack of older adolescent and young adult individuals makes it impossible to determine if inter-individual variation in upper limb CA ratios increases in later adolescence and young adulthood. The similarities in ontogenetic patterns for TA and CA ratios between years 0-16 suggests that both primarily reflect the effects of periosteal apposition.

Figure 7.1.1: Scatterplots of femur/humerus and tibia/humerus midshaft total area (TA) against age











By contrast, scatterplots for MA ratios in Figure 7.1.4 exhibit little age-related change. However, one must note that several outlying values skew the LOESS line for individuals younger than ten years, especially for the femur/humerus ratio. If one were to exclude these individuals, MA ratio values would increase slightly for the first five years, suggesting that, on average, the medullary cavity of the lower limb expands slightly faster than that of the upper limb. Still, this trend is markedly weaker than that seen for other variables (Figure 7.1.4). Correlation coefficients for curve fitting are presented in Table 7.1. A significant relationship exists between variables and age, except for MA ratios.





Table 7.1: Correlation coefficients (R<sup>2</sup>) for interlimb robusticity ratios

Section	TA	CA	MA	J
L Fem/Hum	0.49	0.44	n.s.	0.84
R Fem/Hum	0.36	0.28	n.s.	0.32
Avg Fem/Hum	0.5	0.44	n.s.	0.43
L Tib/Hum	0.57 <sup>1</sup>	0.62	n.s.	0.49
R Tib/Hum	0.39 <sup>1</sup>	0.61 <sup>1</sup>	n.s.	0.39 <sup>1</sup>
Avg Tib/Hum	0.54 <sup>1</sup>	0.56	n.s.	0.5 <sup>1</sup>

<sup>1</sup> Cubic polynomial produces best fit. Otherwise quadratic polynomial produces best fit. n.s.: Curve fitting non-significant.

### 7.2: Chronological and Regional Variation in Interlimb Robusticity Ratios

Comparisons of TA, CA, and J use standardized residuals from curve fittings of ratios to age. Comparisons of MA utilize true ratio values as no curve fit proved significant (Table 7.1). Boxplots for ratios using average humeral values are presented in text, because plots of left and right humerus ratios showed the same general patterns of differentiation between groups. Results of statistical tests are presented for left, right, and average values. Boxplots of TA, J, and CA for EN and LN indeterminate sex juveniles younger than 16 years old are given in Figure 7.2.1-

7.2.3. LN individuals consistently produce a higher range of values for these properties. Conversely, Figure 7.2.4 demonstrates that LN individuals produce lower values of MA interlimb ratios for the femur/humerus, but not the tibia/humerus comparison, indicating that EN individuals have relatively larger medullary cavities in the femur than the humerus.

Figure 7.2.1: Boxplots of standardized residuals of interlimb total area (TA) ratios by archaeological period: indeterminate sex individuals 0-16 years old







Figure 7.2.3: Boxplots of standardized residuals of interlimb cortical area (CA) ratios by archaeological period: indeterminate sex individuals 0-16 years old







Results for statistical comparisons of EN and LN indeterminate sex juveniles younger than 16 years are given in Table 7.2. The results highlight significant differences between individuals from different archaeological periods in femur/humerus CA at p<0.05 and differences in tibia/humerus CA ratios at p<0.1. A significant difference is also detected in second polar moment of area (J) ratios for the right and average femur to humerus ratio comparisons and average femur/humerus MA ratio at p<0.1. There are no statistically significant differences in TA ratio comparisons. Overall the patterns detected are concordant with two possibilities. Either EN individuals experience relatively greater upper limb loading or LN lower limb loadings are greater during ontogeny. Regardless, the difference is most pronounced for CA ratios.

Table 7.2: Statistical comparisons of interlimb robusticity ratios by archaeological period: Indeterminate sex individuals 0-16 years old

Ratio	ТА	CA	MA	J
L Fem/Hum	0.488	0.034**	0.251	0.319
R Fem/Hum	0.204	0.005**	0.146	0.068*
Avg Fem/Hum	0.389	0.003**	0.085*	0.089*
L Tib/Hum	0.262	0.057*	0.440	0.140
R Tib/Hum	0.330	0.059*	0.616	0.402
Avg Tib/Hum	0.239	0.064*	0.745	0.326

\* significant at p<0.1

\*\* significant at p<0.05

Boxplots for comparisons of indeterminate sex juveniles from different cemeteries are given in Figures 7.2.5-7.2.8. Comparisons of TA, J, and CA in Figures 7.2.5-7.2.7 show that Ust-Ida exhibits the highest range of values. The Lokomotiv group produces the lowest range of

values, while Shamanka exhibits an intermediate range compared to the other two cemeteries. Figure 7.2.8 demonstrates that the opposite pattern prevails for MA ratios, LN Ust-Ida produces the lowest values and EN Lokomotiv produces the highest, and this trend appears especially pronounced when the femur represents the lower limb.

Figure 7.2.5: Boxplots of standardized residuals of interlimb total area (TA) ratios by cemetery: indeterminate sex individuals 0-16 years old



Figure 7.2.6: Boxplots of standardized residuals of interlimb second polar moment of area (J) ratios by cemetery: indeterminate sex individuals 0-16 years old










Results of statistical comparisons for indeterminate sex juveniles younger than 16 years old divided by cemetery are given in Table 7.3. As was the case for size-standardized robusticity and limb shape, the EN Lokomotiv and Shamanka individuals do not differ significantly at p<0.05 for any variable. However, CA ratio comparisons are significant at p<0.1 when left and average humeral values are used for ratios. Comparisons of these two EN groups to the Ust-Ida sample also detect only one significant differences in TA ratios at p<0.1. For J ratios, only the tibia/ left humerus comparison for EN Lokomotiv to LN Ust-Ida is statistically significant at p<0.05. However, two other J ratios are significant at p<0.1 when these cemeteries are compared. Clearer differentiation between the EN cemeteries and Ust-Ida emerges in comparisons of CA. Lokomotiv CA ratios are significantly lower compared to Ust-Ida at p<0.05. By contrast, comparisons of EN Shamanka to LN Ust-Ida only detect a difference in CA for the femur/right humerus ratio at p<0.05, though the comparison of average values is also significant at p<0.1. Interestingly, the greater differentiation of Lokomotiv than Shamanka from Ust-Ida is the opposite of the results of size-standardized comparisons of limb robusticity, where Shamanka differed most from Ust-Ida (Chapter 5). Instead, the patterning in interlimb ratios resembles that seen in size-unstandardized comparisons of robusticity, for which Lokomotiv differed significantly from the other cemeteries. This finding suggests that patterning in inter-limb robusticity ratios may reflect differences in body size.

Comparison	Ratio	ТА	CA	MA	J
EN Lokomotiv- EN Shamanka	L Fem/Hum	0.189	0.063*	0.298	0.298
	R Fem/Hum	0.598	0.343	0.461	0.461
	Avg Fem/Hum	0.246	0.065*	0.246	0.116
	L Tib/Hum	0.132	0.088*	0.482	0.269
	R Tib/Hum	0.396	0.322	1.000	0.48
	Avg Tib/Hum	0.191	0.075*	0.438	0.122
EN Lokomotiv - LN Ust-Ida	L Fem/Hum	0.205	0.011**	0.136	0.156
	R Fem/Hum	0.248	0.01**	0.137	0.117
	Avg Fem/Hum	0.154	0.002**	0.025**	0.075*
	L Tib/Hum	0.121	0.039**	0.366	0.039**
	R Tib/Hum	0.174	0.062*	0.497	0.308
	Avg Tib/Hum	0.063*	0.028**	0.800	0.063*
EN Shamanka - LN Ust-Ida	L Fem/Hum	1.00	0.228	0.547	0.702
	R Fem/Hum	0.265	0.033**	0.286	0.15
	Avg Fem/Hum	0.806	0.064*	0.382	0.263
	L Tib/Hum	0.509	0.160	0.563	0.409
	R Tib/Hum	0.534	0.131	0.722	0.534
	Avg Tib/Hum	0.624	0.231	0.514	0.828

Table 7.3: Statistical comparisons of interlimb robusticity ratios by cemetery: indeterminate sex individuals 0-16 years old

\* significant at p<0.1

\*\* significant at p<0.05

To determine the age at which differences arise, a scatterplot of standardized residuals against age for femur/humerus average CA is presented in Figure 7.2.9. This variable was selected as it shows significant differences in both archaeological period and cemetery comparisons. Prior to the age of five years, three Shamanka individuals produce the lowest values, but the other three Shamanka individuals in this age range produce similar values to Ust-Ida individuals. The LN Ust-Ida individuals produce a more clearly elevated range of residuals beginning just before the fifth year. A lack of Lokomotiv individuals younger than five years precludes analysis of when differences emerge between this group and Ust-Ida, but, after the fifth year, Lokomotiv produces the lowest range. However, the narrow Lokomotiv range relative to Shamanka may be a byproduct of small sample size (n = 8).







Examination of female and male individuals older than 16 years shows limited evidence of dimorphism. Boxplots of the femur/humerus ratios for females and males grouped by archaeological period and sex estimate in Figures 7.2.10 show sexual dimorphism. Females producing a higher range than males. This indicates they have more gracile humeri compared to femora than males. This is especially the case for the two LN/EBA females, which also produce a markedly higher range than the EN females. Males from different archaeological periods do not exhibit differences in femur/humerus ratio values. Tibia/humerus ratios do not show the same sexual dimorphism as femur/ humerus ratios, and LN/EBA females do not produce elevated values compared to EN females. Regardless of which lower limb element is used, statistical comparisons in Table 7.3 detect no significant differences in either TA or J ratios between males and females from the same archaeological period or between individuals of the same sex from different archaeological periods at p<0.05. Only the right femur/humerus comparisons is significant at p<0.1 when EN females are compared to EN males and LN/EBA females.





Table 7.4: Mann-Whitney U comparisons of interlimb robusticity ratios by archaeological period and sex: female and male adolescents and young adults

Comparison	Ratio	TA	J			
Sexual Dimorphism						
EN	L Fem/Hum	0.69	0.55			
	R Fem/Hum	0.06*	0.10			
	Avg Fem/Hum	0.66	0.43			
	L Tib/Hum	0.131	0.131			
	R Tib/Hum	0.909	0.569			
	Avg Tib/Hum	0.685	0.291			
	L Fem/Hum	0.13	0.13			
LN/EBA	R Fem/Hum	0.13	0.13			
	Avg Fem/Hum	0.13	0.13			
	L Tib/Hum	0.643	0.355			
	R Tib/Hum	0.439	0.439			
	Avg Tib/Hum	0.439	0.439			
Chronological Change						
Females	L Fem/Hum	0.69	0.54			
	R Fem/Hum	0.06*	0.10			
	Avg Fem/Hum	0.66	0.43			
	L Tib/Hum	0.355	0.643			
	R Tib/Hum	1.00	0.564			
	Avg Tib/Hum	0.439	0.439			
Males	L Fem/Hum	0.56	0.56			
	R Fem/Hum	0.41	0.56			
	Avg Fem/Hum	0.73	0.73			
	L Tib/Hum	0.257	0.705			
	R Tib/Hum	0.167	0.167			
	Avg Tib/Hum	0.167	0.372			

\* significant at p<0.1

\*\* significant at p<0.05

## 7.3: Summary of Interlimb Ratio Analysis

TA, CA, and J ratios increase from birth to the tenth year of life as the lower limb grows in cross-sectional size and strength at a faster rate than the upper limb. Between years 10-16, the two limbs accrue bone at a similar rate, and there is evidence for a late adolescent spurt in humeral robusticity accrual, which results in a decrease in the range of ratio values. Conversely, the ratio of endosteal dimensions, MA, undergoes much smaller age-related changes. A slight increase in the first five years of life suggests smore rapid endosteal expansion in the lower limb, but considerable inter-individual variation makes this trend extremely weak.

Comparisons of the indeterminate sex juveniles less than 16 years old show that EN individuals generally exhibit lower values for TA, CA, and J ratios than LN juveniles but higher ranges of MA ratios. This indicates that either the lower limb of juveniles becomes relatively more robust or the upper limb relatively more gracile from the EN to the LN period. While differences in TA, J, and MA are consistent but usually non-significant, CA ratios show statistically significant differences across archaeological periods and between samples from different cemeteries. As for measures of limb robusticity and limb shape, the two EN cemeteries show few significant differences from each other. However, in comparisons of the two EN cemeteries to Ust-Ida, it is Lokomotiv that demonstrates the most significant differences in CA. Conversely, Shamanka individuals showed the greatest differentiation from Ust-Ida for comparisons of size-standardized CSG (Chapter 5). The greater differentiation of Lokomotiv could reflect small sample size and the restricted age distribution of this sample. However, the result also mirrors comparison of size-unstandardized area and SMA measures. When body size was not controlled for, EN Lokomotiv individuals showed the lowest ranges of cross-sectional size and strength. Similar inter-cemetery patterning in interlimb robusticity ratios suggests that body mass may affect ratio values. Examination of when differences in ratios emerge suggest that small differences may be present shortly after birth, but differences between samples become more pronounced with age. Whether this reflects increased differentiation in relative limb loading due to behavior or growing disparity in body mass will receive further discussion in Chapter 9.

Comparisons of female and male adolescents and young adults primary highlight that females have relatively more robust femora, which implies decreased loading of the upper limb relative to males, especially in the LN/EBA. Otherwise, there is no evidence of dimorphism in the tibia ratios or differentiation in ratio values between males from different archaeological periods.

# **Chapter 8: Discussion Part 1- General Ontogenetic Trends**

#### 8.1: Structure of Discussion

Analysis of Cis-Baikal juvenile Cross-Sectional Geometry (CSG) demonstrated agerelated change in the accrual of robusticity, bone shape, and interlimb robusticity ratios. Bone robusticity and shape exhibit distinct rates of age related change in individuals from different archaeological periods and cemeteries, and sexual dimorphism in these properties is apparent by young adulthood. Discussion of these results will be split into two chapters. To begin, the discussion first considers how methodological limitations affect the interpretation of general ontogenetic trends and comparisons of individuals from different archaeological periods and cemeteries. The remainder of Chapter 8 analyzes the biological significance of the general ontogenetic trends detected. Chapter 9 presents archaeological interpretations of developmental differences between individuals from different archaeological periods and cemeteries, focusing on the implications for reconstructions of Middle Holocene Cis-Baikal behavior and health.

#### 8.2 Limitations of the Study

Several limitations must be acknowledged prior to a discussion of the results. The crosssectional nature of the sample and the use of "non-survivors" create some uncertainty regarding the accuracy with which growth has been modelled accurately. Pooling of LN and EBA females and males also may have obscured some variation between archaeological periods. Limitations in the methods used to quantify cross-sectional geometry also affect the analysis. The modeling of CSG from sections that do not include endosteal dimensions could have obscured changes in CSG with age and reduced the accuracy of sample comparisons. Also, the use of only several sections within the upper and lower limb limits the resolution of these results. Regions of the elements that were not sampled may show different sensitivity to loading and respond in a unique manner to localized mechanical influences. This section discusses the extent to which these issues may have affected the findings laid out in the subsequent discussion.

Both analyses of ontogenetic trends and sample comparisons are limited by the fact that growth is not directly measured in a cross-sectional sample of individuals, who either died prior to reaching skeletal maturity or did not survive for many years thereafter. Only longitudinal studies that follow individuals throughout development can directly measure growth rates and velocity or identify significant biological events (*e.g.* puberty and the growth spurt) (Saunders, 2008). Bioarchaeological studies of deceased individuals can only infer this information, keeping in mind the following inherent ambiguities of cross-sectional studies. Various age ranges are not equally well represented in bioarchaeological samples, and limitations inherent in methods for estimating age, body mass, and sex in juvenile remains make interpretations of growth patterns approximated from skeletal data tentative. For instance, as discussed below, for several variables differences between indeterminate sex juveniles from different archaeological periods become apparent after five years of age. However, given the error of age estimates and the presence of few individuals younger than five years, the differences may actually emerge slightly before or after this age.

In addition, the study utilizes individuals who did not survive into adulthood. If these individuals experienced more episodes of illness, malnutrition, or other developmental disturbances during life than those that survived, they may have exhibited slower growth, delayed skeletal maturation, or been less active than those that survived into adulthood (Wood et al, 1992). For these reasons the growth patterns extrapolated from those that died prior to reaching adulthood may not be completely representative of the growth of individuals who survived. However, there is no strong reason to think that Cis-Baikal non-survivors differed markedly in terms of developmental stress, diet, and activity levels from survivors. There is little skeletal evidence for chronic illness, evidence that death likely occurred quickly (Lieverse, 2010). Likewise, variation in Middle Holocene diet can mostly be attributed to groups exploiting distinct foraging ranges or practicing different seasonal rounds, rather than differential access to resources within groups based on social status (Weber and Bettinger, 2010; Weber and Goriounova, 2013; Weber et al., 2016b). Even if differences between survivors and nonsurvivors did exist, the magnitude of these differences was likely to have been rather small. For instance, Saunders and Hoppa (1993) review of studies on living populations concluded that nonsurvivors likely experienced more nutritional and disease-related stress than survivors. However, this should only result in minor differences in growth. Indeed, the "actual measurable difference in total femoral length is probably never more than several millimeters" (Saunders, 2008, p. 133). Thus, there is little evidence that the growth and maturation of non-survivors proceeded at a markedly slower pace compared to survivors. Furthermore, comparisons between nonsurvivors from different archaeological periods and cemeteries should still provide meaningful information about variation in behavior and health throughout the Middle Holocene. If nonsurvivors from one group show more signs of developmental stress than those from another, it is reasonable to assume that survivors showed similar differences.

While the use of non-survivors likely does not complicate sample comparisons, the pooling of Late Neolithic (LN) and Early Bronze Age (EBA) female and male adolescents and young adults older than 16 years for comparison to the Early Neolithic (EN) sample could have obscured some variation between archaeological periods. Combining these individuals obscures potential variation between LN and EBA individuals. Indeed, there is an imbalance between chronological units. The EN lasts approximately 475 years while the LN and EBA combined last approximately 1,850 years (Weber et al., 2016a; Table 3.1, this dissertation). Thus, the LN/EBA sample may have exhibited more chronological variation in behavior and health than the EN. However, the decision to pool samples was not merely taken to increase sample size. This grouping was made to examine if sexual and chronological differences in robusticity found in past studies of adults had been established by young adulthood. It may well be the case that LN and EBA individuals differ in important ways in terms of health and behavior (Waters-Rist, 2011; Lieverse et al., 2013). However, evaluating such chronological change would first require reanalysis of larger adult samples, which falls beyond the scope of the current investigation. Otherwise, if differences were detected between LN and EBA adolescents and young adults, it would be unclear whether these reflected biological realities or an artifact of small sample size.

Another limitation for analysis arises from the availability of endosteal contours for only certain locations. LCM sections were only available for the humerus, femur, and tibia midshaft, the sections for which radiographs were available. Comparison of all other sections (clavicle midshaft, distal humerus, ulna midshaft, femur subtrochanteric, tibia nutrient foramen) utilized SCM sections. Since SCM sections do not account for endosteal dimensions, they do not estimate Second Moments of Area (SMAs) as accurately as LCM sections (Shaw and Stock, 2007; Sparacello and Pearson, 2010; Davies et al., 2012; Macintosh et al., 2013). In Chapter 8, the analysis of general ontogenetic trends, this limitation does not affect interpretation of growth in area and SMAs, because sections in which CSG was calculated using the LCM showed the same pattern as SCM sections (chapter 5). For comparisons of asymmetry, measures of Total Area (TA) show the same patterns as SMAs in all upper limb sections (chapter 5). As SCM measures TA as accurately as LCM, methodological error cannot explain variation in the

ontogeny of asymmetry between upper limb elements. Inability to track change at the endosteum poses a greater problem for analyzing age-related change in shape ratios ( $I_x/I_y$  and  $I_{max}/I_{min}$ ), because some sections modeled using SCM show ontogenetic patterns distinct from those seen at adjacent LCM sections (chapter 6). Still, periosteal breadth along a specific axis correlates strongly with bending strength, because the material furthest from the section's center makes the greatest contribution to bending rigidity (Sparacello and Pearson, 2010). Consequently, the pattern detected using SCM should provide a valid approximation of relative loading about different axes (Shaw and Stock, 2007; Davies et al., 2012; Macintosh et al., 2013). Therefore, differences in mechanical environment between sections provide a more convincing explanation for intra-limb variation in ontogenetic patterns than methodological error.

The use of SCM also imposes some limitations on comparisons of individuals from different archaeological periods and cemeteries in Chapter 9. It was not possible to assess intergroup variation in Cortical Area (CA) and Medullary Area (MA) at the clavicle midshaft, ulna midshaft, femur subtrochanteric, and tibia nutrient foramen sections Therefore, if substantial differences exist between groups in CA an MA, SCM sections may not have captured differences in SMAs between groups at these locations (Shaw and Stock, 2007; Sparacello and Pearson, 2010; Davies et al., 2012; Macintosh et al., 2013). Several lines of evidence indicate that this problem did not affect comparisons. First, despite evidence for differences in endosteal dimensions, particularly in the upper limb, visual and statistical comparisons of individuals from different archaeological periods and cemeteries indicate that sections modelled using SCM showed the same variation between groups as adjacent LCM sections. The most notable exception is femur subtrochanteric SMAs. However, as discussed below, the unique patterns seen in this section compared to the rest of the lower limb may well arise from its proximity to the hip joint. Secondly, group comparisons of TA, which SCM estimates as accurately as LCM, showed the same patterning as comparisons of SMAs. Indeed, all the differences between groups discussed below would remain valid if SMAs were only considered for sections modeled using LCM and only TA was used for SCM sections. Lastly, prior studies of adults have only ever employed SCM sections (Stock et al., 2010; Lieverse et al., 2011; Stock and Macintosh, 2016). Therefore, the evaluation of sexual dimorphism and chronological variation in robusticity among adolescents/young adults should be as accurate as prior studies.

It should also be noted that this study only used one or two sections to represent entire elements. This precluded a more refined understanding of how robusticity and shape develop throughout entire diaphyses. Consequently, this study cannot fully account for localized variation in genetics, muscle attachment, phenotypic plasticity, safety factors, and the mechanosensitivity of the periosteum and endosteum. Variation in all of these factors can affect the accrual of cortical tissue (Pearson and Lieberman, 2004; Adams and Ackert-Bicknell, 2015; Nadell and Shaw, 2016). The patterns detected at the sections analyzed are useful indicators of ontogenetic trends and differences between populations. Still, the results are limited in that more fine-grained analyses of general ontogenetic trends and comparisons of individuals from different archaeological periods and cemeteries would be possible if CSG was evaluated across entire elements rather than single sections. However, achieving this level of resolution would require access to CT imaging or the acquisition of more radiographs.

Lastly, comparisons of different groups only serve as indicators of relative differences in body size, workloads, and distance traveled. It is not possible to translate this into more absolute measures of differences in muscle exertion, body size, and distance traveled. Current understanding of the osteogenic potential of different loading modes is limited (Pearson and Lieberman, 2004). The multifactorial etiology of CSG and the fact that SMA measures constitute only approximations of true bending rigidity and bending axes further prohibit more fine-grained interpretations (Demes et al., 1998, 2001; Lieberman et al., 2004; Ruff et al., 2006a). Given these limitations, the magnitude of relative differences in behavior and health indicated by CSG analysis is assessed critically, with interpretations contextualized using other lines of evidence.

#### 8.3: Introduction to Analysis of General Ontogenetic Trends

Different measures of bone robusticity and shape showed distinct developmental patterns. Prior to a discussion of differences in growth between Cis-Baikal juveniles from different archaeological periods and cemeteries, it is necessary to explore the general relationships between different CSG properties and age. Examination of these trends is important for two reasons. First, how individuals achieve adult levels of bone robusticity and skeletal form is a growing research interest (Cowgill, 2010; Cowgill et al., 2010; Gosman et al., 2013; Ruff et al., 2013; Osipov et al., 2016). Adult levels of bone robusticity and morphology emerge during growth, and the skeleton's sensitivity to loading decreases once skeletal development has ended (Ruff et al., 1994; Pearson and Lieberman, 2004; Ruff et al., 2006a). Therefore, it proves important to define and compare the general ontogenetic patterns detected in different regions of the upper and lower limbs. General ontogenetic studies have been carried out for some measures of robusticity and shape, but these have used small samples drawn from a limited number of populations (Sumner and Andriacchi, 1996; Ruff et al., 1994; Ruff, 2003 a, 2003b; Cowgill et al., 2010; Ruff et al., 2013; Cowgill, 2014b). Many of these studies have also employed single cross-section locations to represent entire limbs. Analysis of additional populations, section locations, and variables will improve understanding of how bone size, rigidity, and shape changes throughout different regions of the skeleton during growth.

The second reason for identifying and analyzing general ontogenetic patterns is to create a foundation for discussing differences between groups of Cis-Baikal juveniles from different archaeological periods and cemeteries. Interpretations of group comparisons must rest upon a foundational understanding of how and why bone accrues throughout the skeleton. The bone robusticity and shape of certain section locations may exhibit greater sensitivity to differences in behavior. Other sections may show a closer relationship to body form (shape and size) during growth. Genetic determinants of limb morphology and changes in hormone concentration with age may further modulate the effect that behavior and body form have on load magnitude and distribution (Frisancho et al., 1970; Ruff et al., 1994; Peacock et al., 2005; Cowgill, 2010; Wallace et al., 2010; Duren et al., 2013).

The Cis-Baikal data allows analysis of age related trends in accrual of robusticity for several sections in each limb, interlimb robusticity ratios, shape, and asymmetry. Consideration of these different variables will be guided by the following questions:

- 1. Do different variables and cross-section locations show different patterns of age related change, and is the relationship between age and variables stronger in certain regions of the appendicular skeleton?
- 2. What factors explain changes in skeletal robusticity and morphology during growth? Reconstructions of development must be based on an understanding of the extent to which body mass, body shape, hormones, and behavior control the development of bone robusticity and form. Comparing sections within limbs also sheds light on localized variations in mechanical environment, the force applied by certain muscles and differences in range of motion, throughout each limb.

Although, as discussed in Chapter 9, the Cis-Baikal sample contains several sub-groups that exhibited differences in the accrual of CSG with age, pooling of the samples was advisable for preliminary discussion of general developmental patterns. General similarities in body plan and growth exist within *H. sapiens*, and an understanding of these general patterns will serve as the basis for interpreting group differences.

#### 8.4: Ontogenetic Trends in Cross-Sectional Area and Second Moments of Area

TA, CA, and SMAs increase in all sections from birth to late adolescence (Chapter. 5.1). Compared to other area measures, MA increases more slowly. Faster expansion of the periosteal diameter than the endosteal diameter produces a concurrent increase in Percent CA (%CA) as diaphyses become more filled in with age. Fitting of LOESS lines to bivariate plots of these properties against age detected an uptick in growth around age ten, for TA, CA, and SMAs but not MA. The detection of this pattern suggests a growth spurt in early adolescence for these properties. After the age of 15 years, individuals fall into the young adult range and the slope of the LOESS line decreases for TA and SMAs. Still, some of the young adults produce the highest values of TA and SMAs, implying that accrual of bone robusticity continues into the third decade of life, albeit at a slower pace than observed from birth to mid-adolescence. MA ceases to expand earlier than other area measures, after the age of ten years. Evaluating the extent to which these growth patterns relate to general changes in body mass and hormone concentrations contextualizes behavioral interpretations in the following chapter.

In the following discussion, growth trends in robusticity are evaluated in light of the widely accepted model of how periosteal and endosteal bone dimensions change during growth and respond to loading (Frisancho et al., 1970; Garn, 1970; Ruff et al., 1994; Pearson and Lieberman, 2004). During growth, cross-sectional size and strength increase to keep pace with growth in body size and greater activity levels. From birth to early adolescence, apposition of new bone occurs at the periosteal surface while bone is resorbed at the endosteal surface. Increases in mechanical loading primarily increase the rate of periosteal deposition, and they may also decrease the rate of endosteal resorption. In middle adolescence, the endosteum switches to a state of deposition while the rate of periosteal apposition gradually declines (Ruff et al., 1994; Bass et al., 2002; Pearson and Lieberman, 2004). Consequently, starting in adolescence, mechanical loading will engender endosteal deposition, while the sensitivity of the periosteum to mechanical loading gradually declines with age.

Analysis of general ontogenetic patterns in area and SMA measures (Ch. 5.1), demonstrates that the Cis-Baikal sample shows the same general patterns of age related change in cross-sectional area and measures of bending/torsional rigidity as prior investigations of growth in both archaeological and modern populations (Ruff et al, 1994; Ruff, 2003a: Ruff, 2003b; Harrington, 2010, Gosman et al., 2013). Growth profiles for TA and CA parallel each other throughout growth. This is expected since increased mechanical stimulus engenders bone formation solely on the periosteal surface into mid-adolescence (Ruff et al., 1994; Gosman et al., 2013). Medullary area also increases, but since diaphyses become more in-filled with age, the rate of periosteal apposition from birth to adolescence outpaces the rate of endosteal resorption in all human populations.

Increased cross-section size and ability to withstand bending/torsion with age reflects adaptation to both increases in activity levels and increases in body size. Correlations between body size and area/SMA measures are high in the Cis-Baikal sample ( $R^2 > 0.85$  for TA, CA, and SMAs) (Table 5.1). Furthermore, the increased rate of bone accrual during adolescence suggested by LOESS lines for TA, CA, and J occurs around the same age as the growth spurt in body weight and stature, two major determinants of load magnitude (Figures 5.1.1-5.1.4). Indeed, a plot of body mass estimates against age shows a very similar growth pattern as plots of TA, CA, and SMAs against age (Figure 5.1.6). Longitudinal studies of bone robusticity growth in a modern sample directly linked the increase in adolescent CSG to changes in body size (Ruff, 2003a, 2003b; Bass et al., 1991). For example, Ruff's (2003a) longitudinal examination of a modern sample demonstrated that both body size and bone strength show a concurrent peak in growth velocity during adolescence, implying that the former drives the latter.

The Cis-Baikal dataset is cross-sectional, so it is not directly measuring individual changes in growth rates. Still, detection of the same growth spurt by prior cross-sectional and longitudinal studies increases confidence that the acceleration in bone robusticity accrual in adolescence adequately approximates a true trend in the ontogeny of bone robusticity (Ruff et al, 1994; Loro et al., 2000; Goldman et al., 2009; Gosman et al., 2013). The slower increase in robusticity in late adolescence/young adulthood also proves consistent with a strong relationship between body mass and bone robusticity. After the body ceases to grow in stature, it continues to

gradually accrue muscle and fat. The increased mechanical load imposed by new tissue stimulates continued reinforcement of the skeleton (Ruff et al, 1991; Ruff et al., 1994).

In addition to the close relationship between body size and area/SMAs, the Cis-Baikal skeletal growth profiles may track hormone concentrations. Ruff et al. (1994) note that the magnitude of periosteal apposition engendered by changes in body size and activity levels during growth may depend on growth hormone concentrations. Insulin-like growth factor 1 (IGF-1) stimulates periosteal apposition, and it has been often identified as the hormone exercising the greatest control over bone growth (Ruff et al., 1994; Ruff, 2003a; Orwoll, 2003). As the concentration of growth hormone peaks in adolescence and declines thereafter, the growth spurt in TA, CA, and SMAs observed in adolescent Cis-Baikal individuals likely reflects a peak in the concentration of growth hormones, as well as changes in body size and activity levels.

Importantly, the rapid growth in bone size and robusticity during adolescence indicates that puberty constitutes an optimal window for bone deposition in the Cis-Baikal populations (Carter and Beaupré, 2001). In this period, high growth hormone concentration will make the skeleton extremely responsive to changes in load magnitudes, regardless of whether they arise due to increases in body size or activity levels. Due to the subsequent decrease in growth hormone production, the periosteal envelope will show a reduced response to mechanical stimulation thereafter. Histological studies of bone growth concur with this model, indicating that rates of bone deposition peak around the onset of puberty and decline thereafter (Goldman et al., 2009).

The sexual dimorphism in size-unstandardized bone robusticity observed in Cis-Baikal older adolescents and young adults further calls attention to the influence of sex hormones on skeletal growth (Figures 5.1.7 and 5.1.8). Testosterone and estrogen have unique effects on skeletal tissue. Estrogen inhibits periosteal apposition and stimulates endosteal deposition (Garn, 1970; Orwoll, 2003). Testosterone has the opposite effect. It causes greater periosteal apposition and maintains endosteal resorption (Orwoll, 2003). Therefore, hormonally stimulated increases in periosteal apposition may partially account for the greater TA and J of Cis-Baikal males. Hormones may also increase dimorphism indirectly, because testosterone stimulates greater muscle growth and body mass accrual in males (Ruff, 2003a). In turn, this increases the

mechanical loading on the skeleton. It is challenging to parcel out the exact extent to which direct and indirect hormonal influences contribute to greater male robusticity.

Another complicating factor is the skeletal changes theorized to occur during pregnancy and lactation. The fetus takes approximately 30 grams of calcium from the mother to develop the skeleton in-utero (Holmber-Martilla et al., 1999; Oliveri et al., 2004; Ward et al., 2005). After birth, calcium is further lost to breast-milk, and this may require the resorption of bony tissue, especially if the calcium content of the diet is poor (Ward et al., 2005). The extent to which this affects the maternal skeleton remains unclear, especially given the complex effect of pregnancy and nursing on hormonal levels. The limited number of studies conducted have demonstrated bone resorption during pregnancy and nursing, but it appears to predominantly occur in certain skeletal regions (e.g. metacarpals, femoral neck) (Holmber-Martilla et al., 1999; Oliveri et al., 2004; Ward et al., 2005). Clinical studies show that after weaning, bone density appears to return to pre-pregnancy levels, but whether this would be the case when diets lack sufficient calcium remains unclear (Ward et al., 2005). Pregnancy and breastfeeding may therefore be affecting the females under study, especially since hunter-gatherer populations tend to breastfeed longer than modern populations. Marked seasonal variations in diet may also have affected the ability of mothers to rebuild bony tissue following pregnancy. Whether any of the females under study had given birth cannot be assessed. Still, maternal loss of calcium may be an additional factor contributing to sexual dimorphism in bone size and strength.

Chapter 9 evaluates the extent to which males are more robust than females after standardization for differences in body size. Accounting for hormonally modulated differences in bone sensitivity to loading and muscle power will prove more difficult, since higher testosterone levels may stimulate greater periosteal apposition irrespective of body size.

Medullary area shows a different pattern of age related change than TA and CA. This must also be understood in the context of both mechanical factors and developmental changes in sex hormone concentrations. Regression showed that the correlation between MA and body mass and age is much lower than that observed for TA, CA, and SMAs (TA  $R^2$ = 0.86-0.9, MA  $R^2$ = 0.28-0.47) (Table 5.1). This unique growth pattern indicates that the endosteum responds to mechanical, hormonal, and health related stimuli differently than the periosteum. The enlargement of this space through resorption of bone until late adolescence may at first seem

paradoxical, since more material would impart greater strength. However, bone deposited further from the cross-section center makes a greater contribution to strength than bone close to the centroid. Thus, bone primarily responds to increases in loading through periosteal apposition during growth. Concurrent endosteal resorption optimizes bone form, removing tissue that makes only a small contribution to bone strength (Sparacello and Pearson, 2010).

The plateau in MA values after the tenth year is consistent with the onset of sex hormone production, which leads to cortical bone formation on the endosteal surface ((Frisancho et al., 1970; Garn, 1970; Ruff et al., 1994). While some Cis-Baikal adolescents have larger MA than younger individuals, others do not. Previous studies of adolescent growth have generally found that the production of sex hormones causes the endosteal surface to switch from a state of bone resorption to bone deposition. This leads to a subsequent contraction in medullary area during later adolescence (Frischano et al., 1970; Garn, 1970; Bass et al., 1991; Ruff et al., 1994; Wang et al., 2005; Neu et al., 2001; Pearson and Lieberman, 2004; Kontulainen et al., 2005; Ruff et al., 2006; Goldman et al., 2009). This happens earlier, and the contraction is more pronounced in females, because estrogen increases the sensitivity of the endosteum to loading. Testosterone has the opposite effect. Indeed, one study found no evidence of endosteal deposition in males up to age 20 (Neu et al., 2001). The earlier initiation of this process in females than males may explain why there is no clear evidence of contraction in the Cis-Baikal sample by the 16<sup>th</sup> year, the latest point in development for which endosteal dimensions are available. Although sex estimates are unavailable due to the indeterminate nature of pelvic morphology, the highest values in the adolescent sample may belong to males, who are still experiencing endosteal resorption. The lower values may represent females beginning endosteal deposition. The linkage of pregnancy and nursing to bone resorption may also contribute to sexual differences in MA, though whether any of these individuals had given birth by the age of 16 years could not be assessed (Ward et al., 2005).

Alternatively, the lack of compelling evidence for endosteal deposition could reflect biological reality rather than an inability to account for sexual differences. A sizeable number of studies have suggested that endocortical contraction may begin at different ages in different regions of the skeleton. For instance, while studies of the metacarpals have detected adolescent contraction in medullary area in both sexes during adolescence, studies of the distal radius and tibia have not (Frischano et al., 1970; Bass et al., 1991; Neu et al., 2001; Kontulainen et al., 2005; Gabel et al., 2015). Instead, these have shown that resorption may continue in both sexes until young adulthood, though males resorb endosteal bone faster than females (Gabel et al., 2015). The study of this biological transition is further complicated by the fact that some studies have detected the onset of endosteal deposition at different ages even in the same diaphyseal location (*e.g.* Neu et al., 2001; Wang et al., 2005). The factors determining the age at which endosteal resorption begins in different regions of the skeleton are currently unclear. The ambiguous results suggest that future studies must account for the influence of genetics, health, and activity levels to better understand what factors control bone accrual and resorption at the endosteal surface. Regardless, the Cis-Baikal data is consistent with a slowdown in endosteal resorption in both the upper and lower limb during adolescence. However, it is unclear if any individuals have actually begun to experience endosteal contraction by the age of 16 years, or if this occurs later in development in the diaphyseal locations under consideration.

The analysis of the factors affecting growth in bone area measures and bending/torsional rigidity provides a useful foundation for bioarchaeological interpretation. It demonstrates how reconstructions of behavior based on bone robusticity must be contextualized by an understanding of the dramatic changes in body mass and hormone concentrations that occur during growth. In the Cis-Baikal sample, the rate of increase in TA, CA, and SMAs is consistent with adaptation to increased loading throughout growth, which reflects a combination of increases in body mass, behavior related loading, and age-related variations in hormone concentrations. A nuanced interpretation of growth trends that acknowledges the interaction of these factors identifies adolescence as a time of especially marked skeletal sensitivity to activity induced loading. Around puberty, elevated levels of growth and steroid hormones increase the sensitivity of the skeleton to loading. While medullary area may also respond to behavioral stimuli throughout growth, the ontogeny of this property suggests mechanical and hormonal influences affect endosteal resorption differently than periosteal deposition.

#### 8.5: Ontogeny of Interlimb Robusticity Ratios

The analysis of interlimb robusticity ratios allowed comparison of how the weight bearing lower limb accrues robusticity relative to the non-weight bearing upper limb. In the Cis-Baikal sample, analyses of these ratios show that the femur and tibia midshaft accrue cortical bone and increase their resistance to bending and torsion faster than the humerus midshaft from shortly after birth to approximately the age of ten years (Figure 7.1.1, 7.1.2, 7.1.3). Subsequently, the ratio indicates equivalent growth in both limbs in early and middle adolescence. Ratios decline thereafter, as the upper limb becomes relatively more robust in some, but not all older adolescents. The last trend is more pronounced for the tibia/humerus ratios. A less marked later adolescent decline when the femur represents the lower limb likely reflects the greater size of this element compared to the tibia. Conversely, MA ratios did not show a statistically significant relationship with age, indicating that the endosteal dimensions of the upper and lower limb grow at a more equivalent rate (Figure 7.1.3). This implies endosteal dimensions do not respond as strongly to the same factors driving changes in ratios of TA, CA, and SMA measures. The following discussion considers mechanical explanations for ontogenetic patterns, as well as the reasons that little age-related change occurs in ratios of endosteal dimensions.

Prior developmental studies of interlimb robusticity ratios all detected the same general pattern across populations (Ruff, 2003b, Cowgill, 2008, Harrington, 2010, Osipov et al., 2016). Lower limb robusticity increases faster than humeral robusticity from birth to adolescence. Some groups subsequently demonstrate an increase in relative upper limb strength in late adolescence. Thus, the ontogenetic pattern for TA, CA, and J detected within the Cis-Baikal sample is common to *H. sapiens*. The more rapid increase in lower limb robusticity from birth to adolescence has been linked to functional adaptation to bipedal locomotion (Ruff, 2003b). The onset of bipedality requires the femur to become more reinforced as it supports the weight of the entire body, which increases during growth. The upper limb, which does not support the entire body, is less affected by body size increases (Ruff, 2002; Ruff, 2003a). Concurrently, the faster growth in lower limb musculature necessitated by bipedality also increases mechanical strain on the lower limb (Ruff, 2003b). In contrast, quadrupedal primates, which load both limbs equally, show almost no change in ratios during development. Consequently, while no difference exists at birth, human children exhibit ratios values that are 40% greater than those of quadrupedal primates by the age of three years, demonstrating a link between bipedality and increases in interlimb ratios during growth (Ruff, 2003b).

The subsequent decrease in femur/humerus and tibia/humerus ratio in late adolescence may reflect either sexual dimorphism or changes in behavior. Ruff (2003b) first noted a sexual difference in interlimb robusticity ratios, based on his examinations of a longitudinal sample in which sex was known. Interlimb ratio values decrease in late adolescent males, but not females. Ruff (2003b) attributed dimorphism to a genetically and hormonally mediated gain in upper limb muscle mass among males. Thus, the decline detected in archaeological samples might partly reflect sexual differences in the development of upper limb musculature rather than behavior, provided that the samples of indeterminate sex being examined contains more males than females. This proves inconsistent with the pattern of sexual dimorphism detected in adolescent and young adult Cis-Baikal individuals. LN/EBA females showed markedly higher values than males for the femur/ humerus ratio but not the tibia/humerus ratio (Figure 7.2.10). However, the same differentiation was not seen between EN males and females for any measure of interlimb robusticity. Previous studies of Cis-Baikal adults detected the same patterns, so a lack of EN dimorphism is not an artifact of small sample size (Stock et al., 2010; Lieverse et al., 2011). Harrington (2010) also detected a similar decrease in adolescent interlimb ratios among Later Stone Age South African foragers, but no sexual differentiation by young adulthood. While Cowgill (2008) did not include sex estimates, the same decrease emerged in the multiple archaeological samples included in her analysis.

Rather than a preponderance of males, an unlikely scenario in multiple samples, the relative increase in late adolescent humeral robusticity may reflect late adolescent changes in activity levels. The modern middle class urban sample used in Ruff's (2003b) study likely engaged in less physically demanding activity than adolescents in non-modern or non-urban populations, which would experience significant upper limb loading during foraging or agricultural work (Cowgill, 2008). Therefore, the dip in ratio values observed in Middle Holocene Cis-Baikal populations likely captures a general increase in humeral loading during adolescence as individuals begin to work harder (Figures 7.1.1 and 7.1.2). Indeed, previous studies have linked greater relative loading of the upper limb to reductions in interlimb robusticity related to upper limb use. For instance, gymnasts, who utilize their upper body more than the average population, develop relatively stronger upper limbs compared to lower limb than is the case for non-athletes (Eser et al., 2009). Since gymnasts primarily train and compete prior to young adulthood, this interlimb differentiation must develop by early

adolescence. As puberty represents an optimal window for functional adaptation, increased upper limb loading will be especially likely to affect interlimb robusticity ratios within this age range.

The sensitivity of interlimb robusticity ratios to age-related changes in mechanical environment calls further attention to the potential influence of body mass. Interlimb robusticity ratios tend to be employed as "size free" measures of how intensely the upper limb is loaded relative to the lower during activity (Lieverse et al., 2011; Ruff, 2009; Ruff, 2016; Shaw and Stock, 2013). That results of such comparisons conform to behavioral patterns inferred from other lines of evidence supports this approach (Lieverse et al., 2011; Shaw and Stock, 2013; Ruff, 2016). However, one must note that, while more rapid increases in lower limb musculature play a role, faster increase in lower relative to upper limb robusticity during growth also reflects greater weight bearing by the lower limb. For this reason, it is conceivable that interlimb robusticity ratios will be higher in heavier individuals.

Two studies that have explicitly considered this possibility did not detect patterning consistent with body mass having a large effect on ratios in either adults or juveniles (Shaw and Stock, 2013; Osipov et al., 2016). However, these studies did not utilize populations with a range of body mass well-suited for robust testing of this hypothesis. Both investigations employed Later Stone Age South African Cape hunter-gatherers. Compared to other populations, this group was an outlier in terms of both body size and terrestrial mobility. The skeletal gracility, small stature, and lean build of Holocene Cape foragers has been extensively documented (Pfeiffer, 2012). Multiple lines of archaeological evidence also indicate a high level of terrestrial mobility, matched by few other Holocene populations (Stock, 2006; Shaw and Stock, 2013). Both juveniles and adults from this population produce higher interlimb ratio values than groups with significantly higher body masses but lower levels of terrestrial mobility (Shaw and Stock, 2013; Osipov et al., 2016). Initially, this would suggest that interlimb robusticity ratios primarily reflect differences in behavior rather than body size, since higher ratios correlate with stronger lower limbs. Indeed, on theoretical grounds, one would expect body size effects to be small, since lower limb CSG shows only a slightly higher correlation with body size than upper limb CSG (Ruff, 2000; Ruff, 2003a). However, the high differentiation in mobility between Later Stone Age South Africans and other groups may obscure a smaller body mass effect on ratios.

Accounting for this possibility may prove more important in comparisons of populations where differences in levels of terrestrial mobility were less substantial.

While ratios of TA and J appear strongly affected by adaptation to bipedal locomotion during growth, ratios of MA do not. Neither the femur/humerus or tibia/humerus ratio increases markedly with age, and curve fitting does not find a statistically significant relationship between ratio values and age (Figure 7.1.4; Table 7.1). As heavier mechanical loading has been theorized to decrease the rate of endosteal resorption during growth, one would expect that bipedal locomotion slows resorption in the lower limb relative to the humerus (Ruff et al., 1994; Pearson and Lieberman, 2004). The Cis-Baikal data shows that adaptation to bipedality primarily occurs through interlimb differentiation in the rates of periosteal apposition. Stronger mechanical adaptation in periosteal dimensions is unsurprising, since adding bone externally leads to greater increase in bone strength than changes in internal diameter (Sparacello and Pearson, 2010). However, as was the case for detecting endosteal deposition in adolescence, the cross-sectional nature of the sample and potential sexual heterogeneity in endosteal area ratios with age reinforces the idea that this property does not track changes in mechanical loading as closely as measures of periosteal size, at least prior to the age of 16 years.

Overall, interlimb robusticity ratios demonstrate a strong correspondence to age-related changes in mechanical environment. The general growth pattern exhibited by variables heavily influenced by changes in periosteal diameter- TA, CA, and SMAs- tracks skeletal adaptation to bipedality until late adolescence, when increases in upper limb use and musculature may exert a greater influence over ratio values. Importantly, these ratios may also not be entirely size free, since body mass variation will have a somewhat greater influence on lower limb than upper limb robusticity. Little age-related change is detected in endosteal dimensions, suggesting that mechanical loading exerts less influence over endosteal resorption than periosteal apposition, especially prior to adolescence.

#### 8.6 Ontogeny of Limb Shape

Limb shape, as measured using ratios of bending rigidity, showed varying ontogenetic patterns throughout the upper and lower limb. As using ratios of SMAs from the same cross-section location controls for differences in body mass, heterogeneity in ontogenetic patterns

should primarily reflect variation in the local mechanical environment, how the limb moves during activity. In the Cis-Baikal sample, correlations between shape and age were generally weaker in the upper limb than the lower limb (Table 6.1-6.4). Furthermore, different patterns of age related change were detected in different regions of each limb. For this reason, the following discussion considers the upper limb and lower limb separately.

As a foreground to the discussion of general growth patterns, it is necessary to emphasize the information shape ratios convey about loading orientation. Predominantly unidirectional bending induces greater bone deposition about a single axis, causing the diaphysis to become less circular. As a result, SMA ratios will be markedly greater or lower than one (Ruff and Hayes, 1983a). Nearly equivalent bending about two or more axes produces a more circular diaphysis and SMA ratio values close to one. Even reinforcement about perpendicular axes can also result from adaptation to torsional strain, since a circular diaphysis best withstands twisting (Warden et al., 2009). Note that two ratios were used in this investigation, the quotient of anteroposterior and mediolateral bending rigidity (I<sub>x</sub>/I<sub>y</sub>) and the quotient of maximum and minimum bending rigidity (I<sub>max</sub>/I<sub>min</sub>). These two ratios can show different developmental patterns if axes of maximum and minimum bending rigidity are offset significantly from the anatomical axes.

### 8.6.1: Upper Limb Shape

The development of upper limb shape and how it varies across different limb segments has not been extensively explored in the anthropological or anatomical literature. Most studies of upper limb shape as an indicator of habitual activity have used adult samples and focused on only one or two elements (Stock and Pfeiffer, 2004; Rhodes and Knüsel, 2005; Warden et al., 2009; Shaw et al., 2012). Studies of juveniles have been more limited, and only some employed shape ratios for multiple elements (Cowgill, 2008; Harrington, 2010). This restricts the discussion to tentative reconstructions of growth related change in mechanical environment. Analysis of how ontogenetic patterning varies between cross-section locations uses clinical and anthropological studies of adults to identify pertinent differences in range of motion and muscle activity. Such an approach proves appropriate, because this investigation is primarily concerned with identifying potential causes of variation that can inform bioarchaeological reconstruction of behavior. Future studies can pursue more detailed exploration of which factors have the greatest effect on upper limb morphology, incorporating analysis of more section locations. General

similarities across sections are discussed first. Subsequently, the exploration of section specific patterns emphasizes the influence of range of motion and local mechanical environment on growth.

In the upper limb,  $I_x/I_y$  values are predominantly distributed around 1.0 throughout development, and only at the distal humerus and ulna midshaft section does this ratio show a significant correlation with age (Figure 6.1.1; Table 6.1). The distal humerus becomes more reinforced anteroposteriorly with age, and the ulna midshaft becomes more mediolaterally reinforced. However, R<sup>2</sup> coefficients indicate a stronger change in distal humerus shape with age. Imax/Imin values are higher than 1.0 in all sections (Figure 6.1.2). Thus, while upper limb sections experience fairly even loads along the anatomical axes, this does not mean that loading along other axes is equivalent. This ratio decreases with age at the clavicle midshaft, indicating that the section becomes more evenly reinforced with age. Conversely, humerus and ulna midshaft Imax/Imin increase with age as the sections become less circular. However, these increases are very weak. For both Ix/Iy and Imax/Imin, visual inspection of the plots and low R<sup>2</sup> coefficients emphasize that inter-individual variation in upper limb shape is considerable at all ages (Figure 6.1.1, 6.1.2; Table 6.1.1, 6.1.2).

The high inter-individual variability in upper limb shape from shortly after birth may arise due to both considerable genetic heterogeneity in bone form and the complexity of the mechanical environment. Diaphyseal shape is partly determined by genes. While the extent of genetic control remains debated, it appears to matter substantially less than mechanical environment (Volkman et al., 2004; Ruff et al., 2006; Cowgill and Hager, 2007). It is more pertinent that hunter-gatherer lifeways involve a range of manipulative behaviors (*e.g.* carrying, throwing, crafting tools, processing game and hides). These behaviors recruit different combinations of upper limb muscles. Furthermore, the combination of flexion, extension, circumduction, pronation, and supination involved in most manipulative tasks introduces bending about many different axes and torsion (Stock, 2006). Given the complexity and unpredictability of upper limb movement, weak patterns of age related change in all sections are to be expected. A lack of strong change with age likely reflects adaptation to multiaxial bending and torsion throughout the entire upper limb. Despite the weakness of age related change, section specific patterns are consistent with some regional diversity in range of motion and the effects of different muscles. The clavicle midshaft shows little change in  $I_x/I_y$ , and a decrease in maximum relative to minimum bending rigidity with age (Figure 6.1.1.; Figure 6.1.2). Only for the clavicle,  $I_x$  corresponds to superior-inferior bending rigidity and  $I_y$  measures anteroposterior bending rigidity. No clear change in the relative magnitude of strain along these anatomical planes occurs during growth. Therefore, a decrease in  $I_{max}/I_{min}$  with age is best interpreted as the clavicle adapting to greater loading along many different axes or greater torsional forces as the range and intensity of activities grows with age. This interpretation fits with the clavicle's primary function as a support strut that anchors the upper limb to the appendicular skeleton (M.A. Harrington et al., 1993; Auerbach and Raxter, 2008). The rotation of the entire upper limb about this strut engenders torsion. In addition, many large muscles and ligaments attached to the clavicle bend the diaphysis in many different directions. Indeed, previous studies have attributed the clavicle's unique double curvature or "S" shape to the substantial multiaxial shear forces experienced by this element (M.A. Harrington et al., 1993).

Different patterns of age related change in the shape of the two humeral sections further demonstrates variation in local mechanical environments within the upper limb. The distal section experiences anteroposterior reinforcement while the midshaft shows a weak increase in  $I_{max}$  relative to  $I_{min}$  with age (Figures 6.1.1, 6.1.2). More marked change at the distal humerus may reflect its proximity to the elbow joint, which allows the greatest range of motion along the anteroposterior plane. Thus, the growing strains engendered during flexion and extension of the elbow by the *M. brachialis* and *M. triceps brachii* may stimulate the anteroposterior buttressing of the diaphysis (Rhodes and Knüsel, 2005; Bowden and Bowden, 2010). Even though flexors and extensors of the elbow also attach near the midshaft, only minor increase occurs in  $I_{max}/I_{min}$  ( $R^2$  for Avg Hum Mid <0.1) (Table 6.2). This suggests bending and torsion engendered through rotation and circumduction of the upper limb are equally important determinants of shape at midshaft. Several major rotators of the humerus, *M. deltoidus*, *M. latissimus dorsi*, and *M. pectoralis major*, attach on the proximal half of the humerus, and contraction of these muscles produces significant torsion on the humeral diaphysis (Rhodes and Knüsel, 2005; Taylor et al., 2009; Bowden and Bowden, 2010). As this would stimulate even bone deposition about the

entire periosteal circumference, it may obscure anteroposterior buttressing due to flexion and extension (Taylor et al., 2009).

Like the humerus midshaft, the ulna midshaft showed very weak change with age for both ratios ( $R^2 < 0.1$ ) (Tables 6.1 and 6.2). Still a statistically significant decrease in  $I_x/I_y$  and increase in I<sub>max</sub>/I<sub>min</sub> occurs during development. This ontogenetic pattern indicates that the axis of maximum bending resistance lies close to the mediolateral plane (Ruff, 2008). Relatively faster increase in I<sub>max</sub> and I<sub>y</sub> is consistent with movement of the forearm primarily along the mediolateral axis, as occurs in a chopping motion. In addition to mediolateral movement, mediolateral buttressing may also reflect the development of the interosseous crest. This structure anchors the interosseous membrane, which connects the ulna and radius, and has several important mechanical functions (Poitevin, 2001; McGinley and Kozin, 2001; Orbay et al., 2016). The membrane maintains the space between the radius and ulna, dividing the forearm into anterior and posterior muscle compartments. It also plays an important mechanical role, distributing forces between the radius and ulna, especially during compression of the distal end (Orbay et al., 2016). As individuals grow, the muscles acting on the forelimb would generate greater strain. Consequently, the interosseous membrane would have to withstand and transfer more force between the radius and ulna. This could produce an increase in mediolateral loading regardless of if the forearm moves about this axis. Thus, the weak mediolateral expansion of the ulna midshaft may arise either through mediolateral movement of the forearm or due to the enlargement of the interosseous crest.

Previous studies of upper limb shape ontogeny have been rare. Harrington (2010) employed a similar sampling strategy, analyzing changes in shape at the clavicle, humerus, and ulna during growth using a sample of Later Stone Age South African juveniles.  $I_{max}/I_{min}$  was only calculated for the humerus midshaft. The clavicle midshaft, distal humerus, and ulna midshaft were represented by  $I_x/I_y$ . While this difference in methodology limits comparability to the current study, her examination also detected anteroposterior strengthening of the distal humerus and increasing disparity in  $I_{max}/I_{min}$  at the humerus midshaft with age. She considered the mediolateral strengthening of the ulna non-significant, though visual analysis of scatterplots shows the same weak trend evident in the Cis-Baikal sample (Harrington, 2010, p. 94, Figure 4.56). The detection of the same general patterns in two samples provides tentative evidence that developmental changes described using the Cis-Baikal sample may represent a general pattern of morphological adaptation to local mechanical environment. However, further study of a larger set of samples is needed to asses this possibility.

In summation, the extent to which shape changes in various upper limb locations with age appears to depend on the relative magnitude of bending forces experienced about different planes. Cowgill's (2007) study of humeral head retroversion provides a good example of how the development of upper limb morphology change depends on the balance between opposing inputs. At birth the humeral head is oriented along the anteroposterior axis. Subsequently, the head becomes more medially oriented with age. This change reflects the humeral head being pulled in in opposing directions by the muscles of medial and lateral rotation. Nearly equivalent push and pull results in the twisting of the head so that it faces along the mediolateral axis in adulthood. However, when one set of muscles generates markedly more power, as is the case for athletes such as baseball players, who overdevelop medial rotators, the humeral head reverts to a more anteroposterior orientation. In the same way, one can think of diaphyses as adapting to multi-axial bending and torsion during growth. When opposing strains remain relatively "balanced" during growth, no change should occur. Conversely, when limb use alters the magnitude of opposing strains, shape will change. Most noticeably, at the distal humerus, the predominantly uniplanar movement permitted by the elbow joint and attachment of major flexor/extensor muscles in this region stimulate anteroposterior diaphyseal reinforcement with age.

The Cis-Baikal data indicates that upper limb shape development reflects regional variation in musculature and range of motion. Overall, developmental patterns are weak, and shape shows considerable inter-individual heterogeneity with age. The lack of strong age-related change speaks to the importance of multi-axial bending and torsion in upper limb loading. Still the detection of limited developmental variation between sections is unsurprising. The clavicle and humerus midshaft develop in a mechanical environment dominated by multi-axis bending and torsion. This results in circularization of the clavicle with age. Conversely, the distal humerus becomes strengthened anteroposteriorly with age, possibly to resist strains generated by flexion and extension at the elbow. The weak mediolateral buttressing of the ulna midshaft could reflect slight increase in loading along the mediolateral axis with age. However, it could also

arise from increased loads placed on the interosseous membrane as it ensures structural cohesion of the forearm bones. This raises the possibility that interpretations of forearm loading might benefit from consideration of the radius and ulna together due to their function as a unit (Shaw and Stock, 2009b). While the developmental patterns seen at each section may be similar across human populations, further research is needed to confirm this.

#### 8.6.2: Lower Limb Shape

The importance of human bipedal locomotion to understanding the evolution of the species has motivated extensive studies of lower limb shape. Consequently, a larger body of literature then was available for upper limb interpretations informs analysis of ontogenetic trends. Analysis is also simplified by the fact that, unlike the upper limb, the lower limb primarily performs a single task throughout life, locomotion. This makes the range of motion more predictable. Walking and running predominantly bend the limb in two directions. The offset of the lower limb from the midline of the body at the hip joint produces mediolateral strain. Concurrently, extension and flexion of the limb creates bending along the anteroposterior axis. Variation in the relative magnitude of bending along these axes in different portions of the limb accounts for most differences in ontogenetic patterns between cross-section locations. The following discussion identifies the extent to which shape ratio development appears responsive to differences in body shape and locomotion throughout the lower limb.

In a seminal paper, Ruff and Hayes (1983a) laid out how the mechanical environment of the lower limb varies across the length of the femur and tibia, and these findings have been supported by subsequent studies of CSG (Shaw and Stock, 2011; Davies and Stock, 2014). The study utilized *in-vivo* and theoretical models of adult human locomotion to map out the relative magnitude of strains engendered during locomotion along the length of these two elements. The resulting diagram illustrating the relative intensity of anteroposterior, mediolateral, and torsional strain along the femoral and tibial diaphyses is reproduced in Figure 8.6.1. In general, the mediolateral strains created by offset of the limb from the midline are highest close to the hip joint and decrease distally. Conversely anteroposterior strains initially increase with distance from the hip joint, exceeding mediolateral strains at the femoral midshaft. They then reach a maximum at the proximal tibia. Distal to the knee joint, both AP and ML bending strains decline. Torsional strain is much smaller and thus a less important determinant of shape than bending strains throughout the femur. In the tibia, the magnitude of torsion exceeds the magnitude of

mediolateral bending. However, only at the distal end of this element does the magnitude of torsion exceed the magnitude of bending experienced about the anteroposterior axis.





Ruff and Hayes (1983a) generated their model based on studies of adult locomotion. Consequently, as discussed below, this model does not address the fact that the mechanics of locomotion differ in very young individuals in some important ways. Still it provides a set of basic expectations regarding development of lower limb shape. Shape change in the proximal femur should track changes in pelvic breadth during growth, because ML loads predominate close to the hip joint, where displacement from the midline is greatest. Locomotion induced anteroposterior strains will have a greater effect on the shape of more distal cross-sections during development. The Cis-Baikal ontogenetic data aligns with these expectations, though it also captures important interactions between changes in body shape and locomotion during development.

At the femur subtrochanteric section,  $I_x/I_y$  decreases, indicating mediolateral reinforcement with age (Figure 6.1.3). This appears particularly pronounced in adolescence. The three more distal sections (femur midshaft, tibia nutrient foramen, and tibia midshaft) undergo anteroposterior reinforcement with age, and values of  $I_x/I_y$  increase.  $I_{max}/I_{min}$  values of the femoral sections do not show the same growth patterns as  $I_x/I_y$  (Figure 6.1.4). No change with age occurs in this ratio at the subtrochanteric section. Conversely,  $I_{max}/I_{min}$  follows a quadratic curve at the femur midshaft section, initially decreasing after birth and then increasing into adolescence. In the two tibia sections,  $I_{max}/I_{min}$  increases consistently with age like  $I_x/I_y$ .

Given the disjunction between shape ratios in the femur but not the tibia, it proves necessary to discuss sections from the two elements separately. All analysis of the femur subtrochanteric ontogenetic trajectories are made tentative by the fact that only a few young adults/ older adolescents are available. Still, if one treats the adult endpoint as provisional and refers to other ontogenetic studies of lower limb shape, it is possible to determine if the lack of older adolescents biases results.

Subtrochanteric femur shape follows a unique trajectory compared to other lower limb sections in that mediolateral reinforcement increases with age. A previous study also found mediolateral reinforcement of the proximal femur with age (Harrington, 2010). This is consistent with adaptation to changes in pelvic breadth, an expected result given the correlation between hip breadth and proximal femur CSG documented in adults (Ruff, 2000; Davies and Stock, 2014). Increased mediolateral reinforcement during adolescence may capture a period of accelerated change in hip joint morphology that displaces the proximal femur further from the sagittal plane. Previous studies of growth in hip joint and pelvic dimensions concur with this interpretation. The femoral neck becomes more mediolaterally oriented during adolescence in both males and females, and a growth spurt in pelvic breadth occurs during puberty in both sexes (Gasser et al., 1991; Pujol et al., 2014; Pujol et al., 2016). The latter would especially increase mediolateral strains experienced by the proximal femur.

The offset of the femur from the midline also appears to play a role in femur midshaft shape development. As made clear by the increase in  $I_x/I_y$  for most of development, AP strains increase faster than ML strains throughout growth at this location (Figure 6.1.3). This increase follows a roughly linear trajectory, which would suggest increasing mobility with age leads to greater AP reinforcement. Paradoxically  $I_{max}/I_{min}$  initially decreases, reaching a nadir around the age of ten years before increasing into young adulthood. Prior investigations of lower limb shape ontogeny have detected identical patterns in both ratios within modern and prehistoric populations, indicating that patterning in  $I_{max}/I_{min}$  is not an artifact of sample size or measurement error (Cowgill, 2008; Cowgill et al., 2010; Harrington, 2010).

Instead, the U-shaped growth trajectory of  $I_{max}/I_{min}$  can be attributed to gradual adduction of the distal femur below the body. Cowgill et al. (2010) extensively explored this issue. This study primarily attributed the initial decrease in  $I_{max}/I_{min}$  during the first decade of life to the development of the bicondylar angle. As illustrated in Figure 8.6.2A, the bicondylar angle is defined as the angulation of the distal femur underneath the body. This anatomical feature makes locomotion more efficient by bringing the knee underneath the center of gravity (Shefelbine et al., 2002). While characteristic of *H. sapiens* and ancestral species of habitually bipedal hominins, the bicondylar angle is not present at birth. Instead, it develops gradually after individuals begin to walk, and clinical studies have shown it will not form in the absence of such stimulus. As depicted in Figure 8.6.2B, the femoral diaphysis of a fetus (far right) is straight. During childhood, the distal end of the femur gradually angles underneath the body as walking stimulates greater bone deposition along the medial side of the distal femoral metaphysis. Adult values of angulation are achieved between the age of four to eight years (Shefelbine et al., 2002; Cowgill et al., 2010).

Because they lack a fully developed carrying angle, toddlers and young children locomote with a waddling gait. This generates relatively higher maximum strains than the mature gait of an eight-year-old child, and the axis of maximum bending rigidity lies close to the mediolateral plane. The decrease in maximum strains with maturation of the bicondylar angle drives the initial decrease in  $I_{max}/I_{min}$  values seen in previous ontogenetic studies and the Cis-Baikal sample. Note that the nadir in ratio values at approximately eight to ten years in the Cis-Baikal sample corresponds to the age at which the adult carrying angle has been fully established. Thereafter, an increase in  $I_{max}/I_{min}$  indicates increased anteroposterior strain since adduction reorients the axis of maximum bending close to the anteroposterior axis (Cowgill et al., 2010).

Figure 8.6.2: A. Illustration of adult bicondylar angle B. Ontogenetic series showing development of bicondylar angle (in-utero to 8.0 years of age). (Adapted from Shefelbine et al., 2002).



Unlike the femur, both tibia sections show a consistent increase in both  $I_x/I_y$  and  $I_{max}/I_{min}$ with age. This congruence in patterns reflects the position of the tibia directly underneath the body from shortly after birth (Salenius et al., 1975). As this orients the axis of maximum bending rigidity along the AP plane from the beginning of life, the two ratios show similar ontogenetic trends (Gosman et al., 2013). However,  $I_x/I_y$  shows a stronger correlation with age at the femur midshaft and tibia nutrient foramen than at the tibia midshaft (Tables 6.3 and 6.4). This may reflect the increasing importance of torsion in the distal tibia, which might offset the axis of maximum rigidity from the AP plane (Ruff and Hayes, 1983a). There are two other reasons that tibia midshaft  $I_x/I_v$  may not change as markedly with age. First, the fibula serves as a mediolateral brace during locomotion, thereby altering how loads created by locomotion are distributed in the tibia (Sparacello et al., 2014). Second, it has been hypothesized that tibia shape is modified by the action of adjacent musculature (Lanyon, 1980; Carpenter and Carter, 2008). Specifically, the soleus and tibialis anterior muscle press against the posterior and lateral surfaces of this element, and both static and dynamic surface pressure may "lead to bone resorption or a decrease in bone formation" (Carpenter and Carter, 2008, p. 228). Consequently, due to constraints imposed by adjacent musculature, changes in tibia midshaft shape may not be able to track changes in mobility induced AP loading as closely as the femur midshaft and tibia nutrient

foramen sections. Of course, for this interpretation to be valid, the tibia would have to be more affected by soft tissue pressure than the femur. Given the tapering of the distal leg segment, such that the tibia and musculature are tightly enclosed by subcutaneous tissue, this is not an unreasonable hypothesis. In other words, limb segments of smaller circumference may generate relatively higher pressure on the enclosed skeletal elements.

Regardless, considerable age-related change in shape between the femur and tibia midshafts suggests that these sections are showing an adaptive response to mobility levels. Therefore, these variables can be used to compare mobility levels of juvenile samples, though the weaker age-related change in  $I_x/I_y$  at midshaft tibia suggests this section may not capture differences in mobility as well as the two more proximal locations, a finding supported by other studies of juveniles and adults (Stock, 2006; Gosman et al., 2013).

In general, lower limb shape develops differently depending on the relative magnitude of mediolateral and anteroposterior loads, which varies predictably throughout the lower limb. Femur subtrochanteric shape adapts to changes in pelvic breadth. The anteroposterior loading of the lower limb during locomotion exerts a much larger influence on the morphology of the femur midshaft, tibia nutrient foramen, and tibia midshaft sections. The development of the carrying angle also alters the mechanical environment of the femur midshaft during growth to a considerable extent. At the tibia midshaft, the strains engendered by locomotion appear to be more offset from the anteroposterior axis than at the femur midshaft and tibia nutrient foramen section. Still, at the femur midshaft, tibia nutrient foramen, and tibia nutrient foramen, and tibia midshaft both  $I_x/I_y$  and  $I_{max}/I_{min}$  can be used to reconstruct mobility levels during ontogeny.

#### 8.6.3: Summary of Limb Shape Changes

In both limbs, bones adapt to bending about several different axes as well as torsion. Correlations with age tend to be stronger in the lower limb, because it is predominantly experiences bending about two planes. The upper limb performs diverse functions and habitually experiences a wider range of motion. This complex mechanical repertoire engenders multi-axial bending and significant torsion. As relative increases in anteroposterior strains cause significant changes in lower limb shape between the midshaft femur and tibia, sections in this region should best capture differences in mobility between populations. Although the upper limb undergoes weaker ontogenetic changes, the diversity of developmental patterns suggests that different sections respond to the influence of different muscles and motions. Thus, certain behaviors may have a greater effect on the morphology of specific portions of the upper limb.

# **8.7** Ontogenetic Variation in the Asymmetry of Cross-Sectional Areas, Second Moments of Area, and Shape Ratios

As discussed in sections 8.4 and 8.5, behavior and differences in body size have the capacity to influence growth in area and SMAs. Bone shape reflects differences in both activity and body shape. However, asymmetry in CSG should develop solely due to differences in limb loading, because using pairs of limbs from the same individual controls for differences in size, genetics, and health (Trinkaus et al., 1994). Although all upper limb sections demonstrated mild increases in absolute and directional asymmetry of area and SMAs with age, there is a noticeable difference in the age at which side dominance, the tendency for one side to be stronger in most individuals, manifests in different elements (Figures 5.5.1-5.5.6). This suggests that certain portions of the upper arm experience more asymmetric strains than others. Conversely, limb shape does not develop side dominance with age (Figure 6.4.1-6.4.4). Between section differences in the development of asymmetry in area and SMAs, particularly in the age at which side dominance with age (Figure 6.4.1-6.4.4). Between section differences in the development of asymmetry in area and SMAs, particularly in the age at which side dominance emerges, primarily depend on localized variation in limb loading. A lack of change with age in limb shape asymmetry suggests that Cis-Baikal juveniles used both limbs in a similar fashion. Even though loads were higher on the dominant limb, they were applied along similar orientations in both arms.

As shape did not show clear changes in side dominance with age, it proves beneficial to first focus on area and SMAs. This will inform consideration of why shape ratios did not demonstrate the same changes. While absolute percent asymmetry follows a similar developmental trajectory across sections throughout ontogeny, the clavicle and ulna midshaft do not demonstrate a clear right-side dominance in TA and SMAs until late adolescence (Figure 5.5.4, 5.5.5). In fact, the clavicle demonstrates a slight left side dominance early in life. Conversely, at both the midshaft and distal humerus sections, most individuals are right dominant after the age of five years. The eventual emergence of right side dominance in robusticity throughout the upper limb is not surprising, because most adults are right side dominant for all upper limb elements (Trinkaus et al., 1994; Auerbach and Ruff, 2006 and references therein; Auerbach and Raxter, 2008). In that context, the most important finding emerging from ontogenetic study of asymmetry in the Cis-Baikal sample is that right side

dominance does not develop in concert throughout the upper limb. It emerges significantly earlier in the humerus than in the shoulder girdle or forearm.

Cowgill (2008) and Harrington (2010) detected similar patterning in the ontogeny of humeral asymmetry, with clear right-side dominance firmly established after the sixth year of life. Thereafter, left handed individuals also demonstrated lower values of asymmetry than right hand dominant individuals. Ontogeny of asymmetry in the clavicle and ulna has received little attention in the developmental literature. Only Harrington (2010) analyzed CSG asymmetry for these sections using her Later Stone Age South African sample. In this population, the clavicle did not demonstrate side dominance from birth to adolescence. The ulna became right side dominant later than the humerus, after the age of 8 years. These prior studies generally concord with what is seen in the Cis-Baikal sample, lending support to the argument that side dominance emerges earlier in the humerus than other elements.

Differences in how elements develop as well as their functional role in the upper limb may explain why side dominance emerges at different ages. Developmental differences should primarily affect the clavicle, as it grows in a unique way. The clavicular diaphysis is the first upper limb bone to begin ossification, and the last to complete growth (medial epiphysis fuses between 18-25 years). It is further differentiated from other limb bones in that the diaphysis forms through intramembranous ossification, direct ossification of the embryonic tissue in utero, and it develops its adult morphology and curvature largely prior to birth (Scheuer and Black, 2004; Auerbach and Raxter, 2008). Conversely the diaphyses of the humerus and ulna emerge and grow through endochondral ossification (Scheuer and Black, 2004; Auerbach and Raxter, 2008). Its unique development may explain why, while all other long bones tend to be longer on the side which is more robust, clavicles are usually longer on the more gracile side (Ljunggren, 1979; Auerbach and Raxter, 2008). Studies utilizing multiple populations have also determined that this element shows the greatest variation in cross-sectional properties of any bone (Stock, 2006). The clavicle's tendency to be longer on the left side is particularly intriguing. Perhaps the early formation of the diaphysis directly from cartilage encodes a weak left side dominance. Even if loading tends to generally become greater on the right with age, it may take a long time to overwrite this encoded bias given the great deal of intrinsic variability in this element's shape and size.

Late development of clavicular side dominance must also be considered in the context of mechanical environment. As described in the discussion of limb shape, the clavicle acts as a supporting strut, which anchors the upper limb to the thorax and transfers force from the upper limb to the axial skeleton (M.A. Harrington et al., 1993). Simultaneously, the sizeable ligaments attached to the clavicle restrict its range of motion (M.A. Harrington et al., 1993; Auerbach and Raxter, 2008). Indeed, it has been noted that the medial two thirds of both clavicles combined with the sternum form a singular functional unit responsible for stabilizing both shoulder joints (Ljunggren, 1979). The paired humeri and ulna do not share the same functional link, and powerful muscles responsible for flexion, extension, and rotation attach along their diaphyses. Therefore, these elements, especially the humerus, may experience greater bilateral differences in bending and torsion than the clavicle.

As many activities require loading of both the humerus and ulna, it is unexpected that the former should develop right side dominance earlier than the latter. Precocious humeral side dominance may reflect differences in the mechanical role of the upper and lower arm. It is possible high power unimanual activities preferentially load the upper limb segment. For instance, throwing, an activity capable of creating high asymmetry, produces greater changes in the shape and robusticity of the humerus than the radius or ulna (Warden et al., 2009; Shaw and Stock, 2009b). This is not to imply that earlier side dominance in Cis-Baikal humeri stems from throwing. Rather this example demonstrates that the most powerful or fast movements of the entire upper limb may predominantly load the humerus.

While the importance of the humerus for generating power may underlie precocious side dominance in humerus CSG, the age gap between the emergence of humeral and ulnar side dominance may also depend on the behavioral repertoire of juveniles. For instance, unlike baseball players, racquet sports players exhibit high asymmetry relative to non-players in both the humerus and forearm (Haapsalo et al., 2000; Warden et al., 2009). As both activities require similar rapid movements of the arm, the difference may result from the addition of high velocity impact loads on the forearm of racquet players over a significant portion of the growth period (Warden et al., 2009).

Of course, neither ball or racquet sports provide good behavioral analogues for huntergatherer children. Rather these examples raise the critical point that different types of loading
can affect the forelimb and the proximal segment to different extents. This raises an intriguing possibility. If greater or different types of mechanical loading are required to affect the asymmetry of the forelimb than the proximal segment, the later emergence of right side dominance at the clavicle and ulna may result from increases in workloads or increased behavioral heterogeneity in adolescence. The decrease in interlimb robusticity ratios during late adolescence, consistent with increased loading of the upper limb, supports this conclusion. If the later emergence of side dominance at the ulna and clavicle reflects increases in load magnitude or behavioral diversification, this implies that the age at which this occurs will likely vary between populations. Juveniles that work more intensively or practice certain behaviors that engender more asymmetric loads will develop right side dominance in the forelimb and clavicle sooner. The earlier emergence of right ulna dominance in Later Stone Age South African huntergatherers than in the Cis-Baikal sample may provide an example of this (Harrington, 2010).

While measures of robusticity become more asymmetric and develop right side dominance with age, shape measures do not. The range of absolute asymmetry does not increase as markedly with age, and analysis of directional asymmetry does not detect the emergence of side dominance (Figure 6.4.1-6.4.4). As discussed in the section on bone shape, lack of side dominance may partly reflect genetically encoded high heterogeneity in bone shape. The detection of greater inter-individual variation in clavicle midshaft shape asymmetry than other elements supports this possibility, since CSG properties of this element show the least correlation to activity levels (Figures 6.4.1 and 6.4.2; Stock, 2006).

From the perspective of functional adaptation, the lack of strong developmental change in absolute percent asymmetry and side dominance in Cis-Baikal upper limb shape suggests that considerable amounts of activity required a similar use of both limbs. Shape does not measure the overall magnitude of loading. Instead, it reflects the relative magnitude of loading along perpendicular axes. An abundance of studies indicates that shape is sensitive to bilateral differences in mechanical environment. For instance, athletes that throw at high velocities exhibit circularization of the dominant limb relative to the non-dominant limb (Warden et al., 2009; Shaw and Stock, 2009b). Predominantly unimanual use of tools could also lead to shape asymmetry in prehistoric populations (Macintosh et al., 2014b). Absence of such patterning in the Cis-Baikal sample strongly suggests that a substantial proportion of foraging activities

required similar use of both arms. Indeed, studies of past populations have associated the use of certain tools like digging sticks, axes, and two-handed scrapers with the movement of both arms along the anteroposterior plane (Stock and Pfeiffer, 2004; Shaw et al., 2012). Although less discussed, pottery making also requires similar movement of both arms (Macintosh et al., 2014b).

It is important to draw a distinction between relative strain magnitude and overall loads. For instance, spear thrusting and use of a digging stick requires loading of both arms predominantly along the anteroposterior plane, but the arm placed on the rear of the implement generates the most force (Shaw et al., 2012). Thus, it is important to remember that huntergatherers performed a diversity of tasks. A lack of side dominance in shape does not mean that individuals did not frequently engage in activities that predominantly loaded one arm, such as spear throwing or harpooning. Rather, it suggests that individuals invested considerable time into practicing activities involving similar movements of both arms.

The entire upper limb shows mild increases in percent asymmetry with age for area and SMAs, particularly in adolescence. While all elements eventually exhibit right side dominance in area and SMAs, right side dominance emerges first at the humerus, then the clavicle and ulna. This may reflect differences in both bone growth as well as local mechanical environment. The early side dominance of the humerus may result from the generation of large forces in this limb segment during fast and powerful movement of the entire limb. Additionally, the later emergence of right side dominance in the shoulder girdle and forearm could indicate a substantial increase in workloads or behavioral diversity towards the end of growth as individuals begin foraging like adults. Shape does not become more asymmetric or develop a clear side dominance with age, suggesting the way the left and right limbs were used was less differentiated than the loads placed upon them. Overall the variability in the ontogeny of side dominance testifies to the heterogenous mechanical environment of the upper limb during growth. This variation is not captured in studies of adults, which show right side dominance in all upper limb elements. Thus, ontogenetic study of bone robusticity provides a unique perspective on bone functional adaptation and the sensitivity of different elements to mechanical stimuli (Auerbach and Raxter, 2008).

## Section 8.8: Conclusion: Implications for Interpretations of Growth Differences between Populations

Identifying general trends in the ontogeny of skeletal robusticity and shape makes an important contribution to understanding what factors determines the size and shape of the adult skeleton. Given the limited number of ontogenetic studies in the literature, this section addressed the need to quantify how development of robusticity and shape varies throughout the appendicular skeleton. Also, it attempted to ascertain the extent to which different factors such as body mass, body shape, behavior, hormones, and genetics influence ontogenetic trajectories. Such analysis provides a foundation for nuanced bioarchaeological interpretations of bone robusticity. The evaluation of general growth trends undertaken here reveals that different variables are affected by different factors. Consequently, they are best suited to reconstructing different aspects of growth. Here, the perspectives each type of data can provide on differences in juvenile behavior and health are summarized to contextualize the bioarcheological comparison of groups in Chapter 9. Measures of area and SMAs as well as asymmetry in these measures, respond to changes in load magnitudes and capture the rate at which bone is added or removed. These will provide insight into workload as well as changes in body size. Shape allows reconstruction of how limbs move, and this measure can be used to interpret localized differences in body shape, muscle attachment, and range of motion.

Measures of area and SMAs change with age in a manner consistent with increase in both activity levels and body size during growth. Thus, differences in both aspects of growth can be detected using these variables. Adaptation to loading will primarily occur through periosteal apposition. Medullary Area (MA) shows a distinct growth profile compared to Total Area (TA) and Cortical Area (CA). The Cis-Baikal data is consistent with changes in periosteal dimensions and hormone concentrations controlling rates of endosteal bone resorption and formation, though activity levels and health status may also have some affect. Interlimb robusticity ratios of TA, CA, and SMAs primarily carry a behavioral signature. Conversely, endosteal ratios appear stable throughout ontogeny further emphasizing the importance of non-mechanical factors in determining endosteal bone activity. Rapid changes in bone size and robusticity as well as a decrease in interlimb robusticity ratios in adolescence identify puberty as a critical window for bone gain during which the skeleton should show an especially strong response to loading.

Therefore, analysis of adolescent skeletal remains may provide an especially good record of how individuals learn adult forms of foraging.

Studies of bone shape and asymmetry indicate that bone morphology proves sensitive to differences in body shape and range of motion throughout both limbs. Given the proximity of the hip joint and lack of considerable change with age, the subtrochanteric femur section should primarily be used to assess differences in body breadth between groups. In contrast, shape ratios of the femur midshaft, tibia nutrient foramen, and tibia midshaft show ontogenetic patterns consistent with adaptation to locomotion engendered strain. Comparisons of these sections between populations will be useful for analyzing variation in mobility during development.

Upper limb shape and asymmetry show ontogenetic similarities, exhibiting weak patterns of age related change and high inter-individual heterogeneity. Still, the changes or lack thereof detected at each section are consistent with localized differences in range of motion and muscle attachment. In addition, the humerus appears most sensitive to asymmetry in loading since side dominance emerges earliest at this location. This may result from the fact that movement of the humerus generates the most powerful and high velocity motions of the arm. For this reason, the humerus may provide the best record of differences in loading between populations, and this result concords with prior studies of adults (Stock, 2006). Also, an increase in right side dominance in late adolescence/young adulthood at the shoulder girdle and forelimb is consistent with increased workloads during adolescence. A lack of side dominance in shape asymmetry implies that Cis-Baikal populations used both arms in similar ways, even though higher loads were placed on the dominant limb.

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## **Chapter 9: Discussion Part 2- Bioarchaeological Interpretations**

### 9.1: Introduction and Structure of Discussion

The goal of this chapter is to improve understanding of the lives of Middle Holocene Cis-Baikal children and adolescents, primarily addressing what bone robusticity and morphology reveal about chronological and inter-cemetery variation in genetics, developmental stress, and behavior. Interpretation proceeds based on consideration of the environmental and social context in which growth and development occur. Ethnographies of child foraging behavior, especially those grounded in human behavioral ecology, provide a heuristic background for reconstructing child behavior in the past. Contextualizing interpretations with this information allows a consideration of how specific features of the environment and social influences interact with the developing mental and physical capabilities of growing foragers to shape their behavioral development.

This chapter makes bioarchaeological interpretations of the three results chapters by applying the data to several major questions about the development of Cis-Baikal individuals from birth to young adulthood.

- To what extent might variation in genetics and health between archaeological periods and groups using different cemeteries explain differences between groups? Consideration of this question also deals with how differences in body mass not removed through size standardization affect comparisons.
- 2. If differences cannot be explained completely by genetics and health, what does the data indicate about variation in workloads and the types of behavior practiced by juveniles from different archaeological periods and cemeteries?
- 3. Lastly, are previously reported adult patterns of sexual dimorphism and chronological differences in Cis-Baikal bone robusticity evident by young adulthood?

To address these issues, the discussion first briefly summarizes ethnographic and theoretical studies of juvenile foraging based on the precepts of behavioral ecology. The literature review highlights some basic observations about factors determining child behavior, which are then deployed in behavioral interpretations of the data. Subsequently, measures of size standardized and non-size standardized CSG, shape ratios, and interlimb robusticity for individuals of indeterminate sex younger than sixteen are used to address the first two questions. The effect of health on bone robusticity is specifically considered through analysis of size unstandardized area and SMA measures as well as body mass estimates regressed on age. As discussed below, a strong possibility exists that limitations of current juvenile body mass estimation methods prevented full control of differences in body size. For this reason, these variables are also critically compared to size standardized CSG to determine how this problem may affect comparisons. Variation related to genetics is explored through evaluation of the age at which differences emerge between groups, and where in the skeleton they occur. Evaluating the potential effect of health and genetics foregrounds the discussion of behavioral differences and similarities. First, variation in CSG detected among juveniles of indeterminate sex younger than 16 years of age is discussed. Subsequently, the emergence of adult levels of sexual and chronological differences in behavior is addressed through the analysis of older adolescent/ young adult comparisons. Reconstructions of genetics, health, and behavior are contextualized through comparison to prior bioarchaeological studies of variation in behavior, health, and diet among Middle Holocene Cis-Baikal populations, as well as ethnographic studies of how huntergatherer children forage and learn adult behaviors.

### 9.2: Survey of the Ecological and Social Determinants of Juvenile Foraging Behavior

An understanding of how ecological and social factors determine the extent to which children forage and what types of activities they perform in hunter-gatherer societies strengthens interpretations of sample comparisons. Ethnographies of hunter-gatherer groups from a diversity of environmental contexts demonstrate that considerable variation exists in the amount of time forager juveniles devote to foraging. Research has frequently employed the interpretive framework of human behavioral ecology to explain this variation. Human behavioral ecology considers variation in human behavior as "phenotypic adaptation" by individuals "to varying social and ecological conditions" that serves to enhance their fitness (Smith and Winterhalder, 2003, p.1). In other words, human behavior is adaptable, and behavior will vary in ways that improves individuals' ability to survive and reproduce.

Child foraging constitutes a specialized sub-field of human behavioral ecology (Winterhalder and Smith, 2000). Studies of child behavior must account for the fact that the cognitive and physical abilities of children change with age, and adults exercise substantial control over how juveniles spend their time (Kaplan et al., 2000; Bock, 2005; Guerven and Kaplan, 2006). These investigations have shown that the physical and mental competence required of a juvenile forager is environmentally specific, because each environment presents different physical as well as mental challenges. The age at which children begin to forage and what foraging behaviors they perform depends on if they have the prerequisite physical ability and skill to target available resources (Bock, 2002, 2005; Guerven and Kaplan, 2006). Furthermore, their unique physical constraints will lead them to target different resources than adults (Bliege Bird and Bird, 2002). Adults, who provision offspring for much of the growth period, also play a role. They may either discourage or facilitate child foraging and labor, and this decision making is also shaped by aspects of the environment (Bock, 2002; Bock, 2005). The following discussion summarizes key findings of past child foraging studies, examining the basic factors that control how much children forage and what resources they target. The concluding section summarizes how this research can be integrated with interpretations of skeletal evidence.

The forthcoming discussion considers the interrelated topics of juvenile foraging choices, foraging ability, and the characteristics of the environment that either favor or discourage foraging prior to physical maturity. Consideration of these subjects requires adoption of the theoretical framework of behavioral ecology, particularly that subset of it falling under the heading of Optimal Foraging Theory (OFT). As the name suggests, OFT treats foraging behavior as oriented towards achieving an optimal outcome. The goal of the individual is to acquire food in the most efficient manner possible, one that maximizes benefits and limits costs (Winterhalder and Smith, 1981; Smith, 1991; Smith and Winterhalder, 2003). Whether a foraging behavior proves optimal or efficient depends on two factors. First, the most efficient behavior will maximize benefits. In terms of foraging, this usually means obtaining as much energy as possible, but the "currency" maximized need not be energy. Foraging can also aim to maximize the acquisition of certain nutrients (e.g. fat, protein, etc.). The goal may also be the acquisition of resources for uses other than consumption (e.g. material for clothes and tools). Additionally, an optimal behavior minimizes costs. The most obvious cost of foraging is that time and energy spent foraging cannot be allocated to other fitness enhancing activities (e.g. making tools, building social networks, learning new skills, etc.). As foraging may also be dangerous, minimizing foraging time further decreases the chance of injury or death. As each behavior has

specific costs and benefits, an individual will choose the behavior that provides the greatest benefit at the least cost.

Behavioral options are evaluated considering constraints (Winterhalder and Smith, 1981) and references therein; Smith, 1991). Physical and mental constraints are partially inherent to the individual. For instance, humans have age-dependent levels of stamina, strength, and cognitive ability. The magnitude of these constraints is also environmentally specific. Each environment contains a specific set of resources that are distributed in a certain way. This alters the time and energy that humans must expend to harvest certain resources. The technology available will also influence this. One can therefore model human foraging choices as selection between several conditional strategies (Smith, 1991b; Winterhalder and Smith, 2000). Basically, hunter-gatherers must obtain enough food to survive. Doing so in such a manner that either maximizes the yield or minimizes the time spent doing so is advantageous for the reasons discussed above. Faced with environmentally specific constraints, individuals will generally choose the foraging behavior that optimizes the foraging outcome. Smith (1991b) summarizes this as "If the environment or payoff matrix looks like x, then behave in manner y," with y being the behavior or suite of behaviors that accrues the greatest benefit to the individual (p. 17). Consequently, "behavioral variation arises as individuals match their conditional strategies to their particular current socioecological settings" (Smith and Winterhalder, 2003, p. 2).

The application of OFT to child foraging behavior raises several unique issues. Notably, the physical and mental capabilities of children change markedly throughout the growth period. The changing nature of constraints makes the costs and benefits of different foraging behaviors age specific. Also, adults provisioning of offspring provides the bulk of calories for at least some portion of development (Bliege Bird and Bird, 2002; Kaplan et al., 2000). Lastly, overcoming mental constraints and ensuring an individual can competently forage in adulthood requires skill development (Kaplan et al., 2000; Bock, 2002; Bock, 2005). Thus, juvenile foraging may serve to build adult competence, even if it provides little immediate nutritional benefit. Considering these major issues highlights that the time juveniles devote to foraging behavior should vary considerably due to age-specific differences in physical and mental competence. Children's foraging activity also depends on the extent to which adults can provide for their nutritional needs and the amount of learning required to become a productive adult forager.

Consideration of child foraging from the perspective of human behavioral ecology has generated a large corpus of literature. Specifically, this work has examined whether children make significant contributions to their own subsistence, and what types of foraging behaviors children practice at different ages. As growth involves significant gains in both physical strength and mental capability, a debate has emerged as to whether children's foraging behavior is shaped primarily by constraints of knowing (learning) or constraints of growing (physical ability) (Kaplan et al., 2000; Bliege Bird and Bird, 2002; Bock, 2002; Bird and Bliege Bird, 2005; Bock, 2005). The talk of constraints makes the applicability of OFT clear. Limitations of strength and skill determine the costs of engaging in specific foraging activities.

The first school of thought has emphasized physical factors such as strength, stamina, and coordination as the most important constraints on child foraging. Learning is conceived of as a fairly rapid process, meaning adult levels of foraging efficiency emerge quickly once individuals attain the prerequisite levels of physical ability (Bliege Bird and Bird, 2002; Bird and Bliege Bird, 2002; Bird and Bliege Bird, 2005). This hypothesis concurs with the age at which individuals begin to engage in simple foraging tasks. Provided environmental conditions are favorable, infants and toddlers accompanying their mothers begin gathering as soon as they are able, in early childhood (Hawkes et al., 1995). For simple tasks, juvenile foragers quickly reach adult levels of foraging return rates. For instance, juvenile shellfish collectors forage as efficiently as adults (Bird and Bliege Bird, 2002; Bliege Bird and Bird, 2002). However, due to their unique physical abilities, they target different species until they achieve adult levels of strength. Multiple other studies have similarly observed that children target a different set of resources and forage in different areas of the environment than adults (e.g. Bird and Bliege Bird, 2005; Tucker and Young, 2005). Children consistently pick resources that require less strength to harvest, and these prey items tend to be close enough to camp that children can easily travel to them (Bird and Bliege-Bird, 2005; Tucker and Young, 2005; Guerven and Kaplan, 2006). In such cases, the difference between adult and juvenile foraging reflects the physical constraints imposed by children's small bodies, not a lack of knowledge. Physical limitations also explain why juveniles tend to be excluded from big-game hunting until early adolescence (MacDonald, 2007). Pursuing and killing a large animal requires a high degree of stamina and strength achieved only at the end of growth.

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Paradoxically, studies have also highlighted that children performing simple tasks underproduce, harvesting less than they could, even though acquiring more energy would benefit growth. In the context of OFT, this only appears contradictory until one considers the effect of adult provisioning. When adults provide most or all the food that children need, children gain little by maximizing time spent on simple foraging tasks (Tucker and Young, 2005). They can derive greater benefit from investing time into alternative activities such as learning more complex tasks or building social ties.

Other studies, most notably those of Kaplan et al. (2000) and Bock (2002, 2005), while not eschewing the importance of strength, have argued that learning, the so called "constraint of knowing," may prove an equally significant determinant of juvenile foraging behavior. Success in some foraging tasks requires children to attain a basic threshold of mental competence. Either the resource proves hard to locate and pursue, or the technology employed requires considerable skill. For instance, some plant resources require complicated processing to extract edible portions. The mongongo nut and palm hearts provide the classic examples (Jones et al., 1994; Hawkes et al., 1995; Bock, 2005). Processing efficiency increases gradually from childhood until middle adulthood as individuals sharpen their skills (Jones et al., 1994; Hawkes et al., 1995; Bock, 2005). Similarly, physical stamina alone does not ensure success in hunting. Hunters spend years learning to track animals, predict their movements, and approach undetected (Bock, 2002; Walker et al., 2002; MacDonald, 2007). Thus, the high mental constraints associated with certain behaviors make them an inefficient or suboptimal foraging activity until children master necessary skills.

The significant strength and considerable mental aptitude required for hunting demonstrates the important point that many foraging activities require a considerable level of both strength and mental ability (Guerven and Kaplan, 2006). Consequently, mental and physical constraints interact to shape the types of behavior children engage in. Bock (2002; 2005) has proposed an influential theory of how physical and mental constraints act as interacting determinants of juvenile foraging efficiency. Each foraging task requires a base level of physical and mental competence or "threshold of ability" (Bock, 2005, p. 113). The relative importance of the physical and mental threshold will depend on the complexity of these task. Once children have grown strong enough to begin foraging, increases in the efficiency of simple tasks may

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occur rapidly (Bock, 2002; 2005). This occurs, because, once a certain level of strength has been attained, the process of learning by doing will quickly build competence. Thereafter, additional increases in the productivity of simple foraging tasks will reflect additional growth in body size and, to a lesser extent, refinement in skill (Bock, 2002; Bock, 2005; Guerven and Kaplan, 2006). For instance, children can fish successfully once they are strong enough to use the equipment required (Bock, 2005). Practice improves their ability as it teaches them to locate the best fishing grounds. Further gains in strength will also allow them to capture larger fish.

Alternatively, very complex behaviors such as hunting or tool making may require significantly longer periods of learning, even once an individual possess the prerequisite levels of strength to practice them (Guerven and Kaplan, 2006). Compared to low skill tasks, it will take longer to refine initially crude attempts. For instance, ethnographic study of complicated tasks, such as processing hard to extract plant parts, shows that efficiency increases at steady rate from childhood to middle adulthood (Bock, 2002; Guerven and Kaplan, 2006). Similarly, the physical demands of big game hunting preclude serious training in this activity until adolescence. Time spent in play hunting around camp in childhood probably inculcates a base level of knowledge in tracking and pursuit (MacDonald, 2007). Even so, success in big game hunting rises slowly from adolescence to middle adulthood, indicating that learning takes considerable time once juveniles are strong enough to practice (Walker et al., 2002). Individual hunting returns peak in middle adulthood, but time spent hunting is greatest in young adulthood (Walker et al., 2002; Guerven and Kaplan, 2006). This disjuncture between the age of peak time investment and peak returns is exactly what one would expect if mental competence rather than physical strength constitutes a more important determinant of foraging success for complex tasks.

Clearly, both mental and physical constraints determine how much children forage and what resources they target. The magnitude of these constraints is environmentally and socially specific. Each of these factors can alter the magnitude of physical and mental thresholds that successful foragers must surpass. Environment will have a considerable effect, because the difficulty of foraging depends on the resources available and the environmental hazards individuals must contend with. Two case studies illustrate how differences in environment can dramatically alter child foraging. Early influential studies of the !Kung created a widespread impression that hunter-gather children seldom forage (Draper, 1976; Jones et al., 1994; Hawkes

et al., 1995). However, subsequent study of the Hadza found that children in this group were precocious foragers. Further studies of other forager societies demonstrated considerable variability exists in how much children forage (Hawkes et al., 1995; Hewlett and Lamb, 2005 and references therein)

The discrepancy between the !Kung and Hadza demonstrates the primacy of environmental constraints on child behavior. The !Kung inhabit a desert environment, and the physiology of children makes them particularly susceptible to dehydration (Hawkes et al., 1995). Likewise, a lack of landmarks and presence of large predators makes navigation of the terrain both mentally challenging and physically dangerous. Foraging is further precluded by the fact that resources patches are located far from camps, so children would expend more energy traveling than they would harvest. For these reasons, adults discourage foraging or travel far from camp until children are much older, though children sometimes do assist in processing the resources that adults return to camp (Jones et al., 1994; Hawkes et al., 1995). Consequently, high physical and mental constraints create a situation in which foraging costs far outweigh the benefits for !Kung children. The reverse proves true for Hadza children, who forage in an environment that is easier to navigate and water is not scarce. It is also worth noting that Hadza children also have access to more easily harvested resources such as fruit. By contrast, the main plant resource available to the !Kung, the mongongo nut, must be processed with considerable skill to avoid spoilage (Jones et al., 1994; Hawkes et al., 1995). This restricts processing to older children that have acquired the necessary dexterity and cognitive ability.

Within a similar environment, technological differences also influence the magnitude of physical and mental thresholds that an individual must surpass to forage. The mental competence and physical strength required to use a tool effectively varies based on its size and complexity (Lancy, 2017). It will also depend on if children are provisioned with adequately scaled down versions of foraging equipment (Bock, 2005). Even if technology is simple enough to use from an early age, one must also not overlook that children must also learn how to manufacture these tools. As with subsistence tasks, different types of manufacturing require varying levels of strength, dexterity, and cognition (Lancy, 2017). Once these are present, children learn some simple tool making techniques very quickly, but others take considerable time to perfect (Lancy, 2017). As is the case for foraging behavior, producing crude facsimiles of adult implements may

constitute a vital learning process that accelerates the development of necessary physical and mental abilities (Bock, 2002, 2005).

In addition to the effect of environment and technology on child behavior, intergenerational interaction and social factors influence how children spend their time. Children do not make choices independently. Directly or indirectly, they receive cues from adults and older children (Kaplan et al., 2000; Bock, 2005). In some cases, foraging, while ostensibly play, mimics the behavior of adults, and, in favorable circumstances, this can result in the harvest of a large amount of calories (Tucker and Young, 2005). Adults may further manipulate the extent to which children forage by including them on foraging expeditions and providing encouragement or specially made tools (Bock et al, 2002; Bock et al, 2005). Jones et al. (1994) note that adults benefit from child foraging as it raises the overall return rate of the "group," the child, their siblings, and adult relatives. For instance, a Hadza mother raises the cumulative return rate of foraging when she includes her children on foraging trips. Importantly such encouragement is not restricted to foraging. Children, particularly females, are often recruited for domestic labor such as child care or transporting resources (Henry et al., 2005; Guerven and Kaplan, 2006).

The time and energy adults save by recruiting children into foraging or domestic tasks can be invested into additional offspring or other activities that raise adults' fitness (Bock, 2005). Indeed, the variable contribution of child foragers to subsistence has been posited as one reason that the fertility rates of hunter-gatherer groups exhibit marked variation worldwide (Kelly, 1995). Alternatively, parental encouragement of foraging may assist in the long running learning processes necessary for the mastery of complex tasks. Of course, the example of the !Kung discouraging children from foraging provides a counterexample, in which parents maximize reproductive success by protecting their children from danger. In addition, adults may not recruit child labor as much as they could, because it minimizes the time available for learning other tasks or forming social networks with other members of the group (Bock, 2005; Guerven and Kaplan, 2006). These examples again call attention to the fact that whether adults encourage child foraging depends on if its benefits outweigh the costs to themselves and their offspring (Bock, 2005).

During adolescence, juveniles take on adult roles. Partly, this arises due to a decrease in parental provisioning towards the end of growth. Adolescents must now provide for themselves

what they no longer obtain through inter-generational transfers (Bliege Bird and Bird, 2002). In addition, they may now have to support dependents (mates and children). To achieve these goals, adolescents and young adults work harder and begin targeting hard to acquire but high value resources such as large game. Assumption of adult behavior in adolescence also represents an investment in learning, because a period of failure may be acceptable if it ensures success in high payoff foraging as an older adult (Bock, 2005). However, one must not make the simplifying assumption that adolescents and young adults will engage in high skill activities as much as older adults. It takes a long time to master some activities such as big game hunting, even after a forager achieves the prerequisite levels of strength and endurance. Sugiyama and Chacon (2005) point out that, if ensuring adequate food intake is important, adolescents may also devote more time than older adults to low skill activities with more reliable yields. For instance, among the Yora, adolescents devote considerable time to hunting, but they fish more than older adults (Sugiyama and Chacon, 2005). This may reflect a balanced investment that ensures adolescents/young adults have both opportunities to learn and obtain enough food for themselves and their dependents. In addition, reproduction may uniquely influence female adolescent behavior, as pregnancy and child care (e.g. nursing, carrying infants) affect the distances they can travel, the resources they can target, and the amount of food they must acquire.

Lastly, a growing focus on difficult to harvest resources in adolescence may also reflect growing individual agency in time allocation, particularly if certain behaviors enhance social status (Bliege Bird and Bird, 2002; Bliege Bird et al., 2001; Smith, 2004). According to costly signaling theory, adolescents may actively invest extra time into foraging behaviors that confer social capital, particularly those that signal their suitability as a mate or leader (Bliege Bird et al., 2001; Smith, 2004). For instance, if the goal of foraging is solely to maximize energy acquisition, it is puzzling that adolescent devote great energy to game hunting. Such hunts rarely succeed, and they would acquire more energy fishing or gathering (Bliege-Bird and Bird, 2002b; Sugiyama and Chacon, 2005; MacDonald, 2007). While the importance of "learning by doing" can explain such behavior, targeting highly valued resources also allows adolescents and young adults to demonstrate their potential as a mate and accrue social capital (Bird et al., 2001; Guerven and Kaplan, 2006; Smith, 2004). Note that the exact utility of social capital remains debated. Accrual of prestige has often been linked to attracting mates. However, it may also

need (for a fuller consideration of these scenarios see Smith, 2004). Ethnographic studies of costly signaling predominantly analyze male behavior. However, females may also change their foraging patterns and workloads as they approach the age of first reproduction to build prestige and signal readiness to provision children (Bliege Bird and Bird, 2002). These examples show that social factors may be as important as environmental factors in determining child and adolescent foraging choices. Relatives may encourage or discourage child foraging as a way of promoting their own reproductive fitness. In adolescence, maturing foragers may also make choices that seek to maximize social capital as well as foraging efficiency.

This brief consideration of the factors shaping juvenile foraging has relevance to reconstructions of juvenile behavior in past populations. Studies of juvenile foraging call attention to the importance of both physical and mental constraints in determining the extent of child foraging and the types of behavior juveniles undertake. Based on these studies it is also possible to lay out a general "roadmap" of how foraging behavior changes with age. If environmental conditions are conducive to small children foraging at all, they will exploit resources that require low skill and low strength to harvest. As they grow older, children generally devote more time to foraging, and they also begin to focus on resources that take more skill to harvest successfully. How hard children work will also depend on the extent to which adults recruit their labor. As individuals approach adolescence, sexual differences in behavior will also tend to increase. Male adolescents potentially invest more time into big game hunting while females may focus more on domestic labor and provisioning children.

Consideration of environmentally specific physical and mental constraints can contextualize analysis of skeletal robusticity throughout the growth period. Biomechanical analysis measures how strength varies in relation to both body size and activity, though some differentiation may also reflect genetic and health related variation. Controlling for growth in size allows exploration of how hard individuals are working at different ages. Therefore, the age at which differences in CSG emerge between individuals or groups can be considered in light of the physical and mental abilities attained at certain stages of growth. For instance, the detection of differences between groups in childhood would suggest that children in one group are more engaged in low skill and low strength activities. Conversely, the emergence of differences in adolescence would be more indicative of variation in activities that require high levels of strength and skill. One should also evaluate the significance of behavioral differences considering what motivates these individuals at different ages. Children may forage merely out of a desire to mimic adults or as play (Tucker and Young, 2005). Alternatively, adults may be recruiting their labor to maximize resource acquisition or perform domestic tasks (Bock, 2002, 2005). During adolescence, the speed with which individuals assume adult behaviors may depend on how much adolescents must contribute to their own subsistence, how much time they must invest in learning, and a desire to build social status.

#### 9.3: Summary of Group Comparisons

Comparisons of cross-sectional geometric properties demonstrate chronological and geographic differences. Prior to size standardization, Late Neolithic (LN) juveniles aged 0-16 years demonstrate generally higher measures of area and SMA measures relative to Early Neolithic (EN) individuals throughout the upper and lower limb (Chapter 5.4). Following size standardization, LN individuals still showed a tendency towards TA and SMAs in all sections but the subtrochanteric femur section and humerus midshaft and distal sections (Figures 5.2.1, 5.2.2, 5.2.3; 5.3.1, 5.3.2, 5.3.3). This difference reached statistical significance in the lower limb (Tables 5.3, 5.6). Examinations of internal dimensions found that EN individuals have significantly smaller medullary cavities and higher %CA at the humeral midshaft than LN Ust-Ida individuals (Figures 5.3.4, 5.3.5; Table 5.6). The same difference was not apparent in the lower limb (Figures 5.2.4, 5.2.5; Table 5.3). The lower limbs of EN individuals younger than 16 years were significantly more anteroposteriorly reinforced than those of LN individuals (Figures 6.2.1, 6.2.2; Table 6.5). Comparisons of upper limb shape and asymmetry did not show any clear differences between individuals younger than 16 years old (Figure 6.3.1, 6.3.2; Table 6.5). Comparison of interlimb ratios indicate that EN individuals either had relatively stronger upper limbs or relatively weaker lower limbs than LN individuals (Figures 7.2.1-7.2.3). However, ratio comparisons only reached statistical significance for CA ratios (Table 7.2).

Comparing the two cemeteries that make up the EN sample, Lokomotiv and Shamanka, separately to LN Ust-Ida, demonstrated cemetery specific patterns. Comparisons of sizeunstandardized area and SMA measures showed that the EN Lokomotiv sample produced the lowest TA, CA, and SMA measures, and body mass estimates (Figures 5.4.5-5.4.7, 5.4.9; Table 5.14). Conversely, comparisons of size-standardized upper and lower limb area and SMAs, as well as lower limb shape ratios, reveal that LN Ust-Ida and EN Shamanka exhibited the most statistically significant differences (Tables 5.4, 6.6). EN Lokomotiv individuals show few statistical differences compared to the other two groups for size-standardized variables and lower limb shape. Only for measures of interlimb robusticity ratios did Lokomotiv to Ust-Ida comparisons detect more differences than Shamanka to Ust-Ida comparisons (Table 7.3). Differences reached statistical significance predominantly for ratios of CA rather than ratios of TA or SMAs. That inter-cemetery patterning in interlimb ratios resembles that of body mas comparisons suggests that body size is affecting these ratios.

Adolescent/young adult females and males show sexual dimorphism for TA, SMAs, and limb shape in both periods (Figures 5.2.15, 5.2.16, 5.3.14, 5.3.15, 6.2.6, 6.2.7, 6.3.7, 6.3.8). In addition, LN/EBA females are markedly more gracile than EN females, but there is no clear evidence for differentiation between males from different time periods for TA and SMA comparisons (Figures 5.2.15, 5.2.16, 5.3.14, 5.3.15). There is also no evidence for chronological change in lower limb shape between individuals of the same sex (Figures 6.2.6, 6.2.7). LN/EBA females have higher femur/humerus TA and J ratios than all other individuals, implying that this group placed markedly higher loads on the femur than the humerus (Figure 7.2.10). However, the tibia/humerus comparisons do not show the same pattern.

## 9.4: Differences in Postcranial Robusticity Attributable to Genetics and Developmental Stress (Indeterminate Sex Individuals Aged 0-16 Years)

Examination of whether genetics and developmental stress can explain differences in bone robusticity between groups must precede behavioral interpretations. Some percentage of skeletal size and form is heritable, and variation in nutrition and disease load during development can also produce differences in body mass, a major determinant of skeletal robusticity (Ruff et al., 2006a; Cowgill, 2008; Cowgill, 2010; Duren et al., 2013; Ruff et al., 2013; Adams and Ackert-Bicknell, 2015).

## 9.4.1: Differences in Genetics

The data does not support genetic variation in mechanosensitivity, baseline levels of bone size, or body shape being the primary factors responsible for differences in robusticity and bone shape between EN and LN populations. Differences between individuals from different archaeological periods emerge at points in development during which activity should have a greater influence on bone morphology than genetics.

The possibility of genetically encoded differences in robusticity among Middle Holocene Cis-Baikal populations had to be considered, because prior genetic analyses of Cis-Baikal populations revealed a chronological change in mtDNA and Y-chromosome haplotype frequencies between the EN and LN/EBA periods (Mooder, 2004; Mooder et al., 2006; Mooder et al., 2010; Moussa, 2015; Moussa et al., 2016). As discussed in Chapter 2, genetic differences could have produced variation in bone robusticity for two reasons. Firstly, specific alleles may code for different baseline levels of bone robusticity, differences in shape, or variable sensitivity to loading (Churchill, 1999; Robling and Turner, 2002; Lovejoy et al., 2003; Wallace et al., 2010; Zemel, 2011; Roseman and Auerbach, 2015). Secondly, populations adapted to colder climates have broader bodies to minimize heat loss, and this difference is present from birth (Ruff, 1994; Holliday, 1997; Weaver, 2003; Cowgill et al., 2012). A wider body generates greater mediolateral strain during locomotion, so, levels of mobility being equal, broader bodied individuals would exhibit stronger and more circular lower limbs, and the effect would be most evident sections closer to the hip joint. (Ruff and Hayes, 1983a; Ruff, 2000; Weaver, 2003; Ruff et al., 2006b; Shaw and Stock, 2011; Davies and Stock, 2014; Pearson et al, 2014). Genetic differences persist for many generations, and it is possible that the ancestral lineages which gave rise to EN and LN/EBA populations underwent long term adaptation to different climates prior to their arrival in the Cis-Baikal (Mooder et al., 2010; Schurr et al., 2010). Therefore, the issue at hand is not whether the Cis-Baikal was colder during the EN or LN/EBA, but whether these populations descended from ancestral lineages that evolved morphological adaptations to different temperature ranges.

Importantly, studies of genetic variation in CSG must acknowledge that the extent to which genes influence the ontogeny of bone robusticity and shape varies remains poorly understood. Studies have produced widely varying estimates of the percentage of variation in limb bone size and shape accounted for by genetic factors (Ruff et al., 2006a; Wallace et al., 2012; Adams and Ackert-Bicknell, 2015). Such investigations are complicated by the fact that research is just beginning to identify genes that influence CSG, and the genes linked to such variation appear to be highly site-specific, affecting only certain regions of the skeleton (Wallace et al., 2012; Adams and Ackert-Bicknell, 2015). Also, it is unclear if variation reflects genes coding directly for differences in structure or differences in mechanosensitivity. Alternatively, genes can affect CSG indirectly by coding for differences in muscle and body size, thereby

altering mechanical environment (Adams and Ackert-Bicknell, 2015). Thus, while bone robusticity and shape are clearly heritable, it has never been conclusively demonstrated that variation attributable to genetics can be greater than that brought about through functional adaptation. Specially bred mouse lineages do show differences in CSG (Wallace et al., 2010, 2012). However, these may not be good models for real world human populations, and functional adaptation may have a greater influence on morphology in larger mammals (Wallace et al., 2012).

When trying to identify genetic differences in CSG, it is more important that differences attributable to genetics should be most apparent within certain age ranges. Current theories postulate that the influence of autosomal genes on CSG should be greatest during infancy, when behavioral differentiation is minimal (Carter and Beaupré, 2001; Wallace et al., 2010; Duren et al., 2013 and references therein). Subsequently, the influence of genes should decline throughout childhood as adaptation to behaviorally induced loading becomes a more considerable influence on Cross-Sectional Geometry (CSG). Indeed, pronounced differences in loading may overwrite genetically encoded differences between groups (Cowgill, 2010; Wallace et al., 2010). Once individuals reach puberty, sex chromosomes play an important role in modulating the rate and manner of bone accrual (Frisancho et al., 1980; Ruff et al., 1994; Carter and Beaupre, 2001; Pearson and Lieberman, 2004; Ruff et al., 2013). In sum, differences between groups attributable primarily to genetics should be most strongly expressed early in ontogeny, while the sex chromosomes will lead to sexual dimorphism after puberty.

When compared to the expectations above, the Middle Holocene Cis-Baikal biomechanical data does not show patterning consistent with variation between groups being attributable to genetic differentiation prior to puberty. Few differences in area and SMA measures are present in infancy. Instead, differences between EN and LN indeterminate sex juveniles younger than 16 years emerge around the age of five years for measures of area, SMAs, lower limb shape, and interlimb robusticity ratios (Figures 5.2.11-5.2.12, 5.3.12; 6.2.5; 7.2.9). At this point in development, the influence of genes should be decreasing as behaviorally induced loadings become more important determinants of bone form (Carter and Beaupré, 2001; Duren et al., 2013). Admittedly, few individuals in the sample are younger than 5 years, raising the possibility that differences are present before this. Still, this would not explain why difference

are maintained throughout development, making functional adaptation a more parsimonious explanation. Only for comparisons of upper limb shape did differences between samples appear most pronounced at birth and decrease with age (Figures 6.3.5, 6.3.6). Thus, as discussed in Chapter 8, upper limb shape may show high levels of idiosyncratic variation compared to lower limb shape. This difference may have a genetic basis, but further study is needed to confirm this hypothesis.

At the femur subtrochanteric section, the location at which pelvic breadth should exert the greatest influence over morphology, the EN and LN samples show the least differentiation in size-standardized robusticity and shape of any lower limb section, implying that that EN and LN individuals exhibit equivalent ranges of body breadth for age (Figures 5.2.1-5.2.2; 6.2.1-6.2.2). Thus, descent from founding populations adapted to different climates is unlikely to explain variation in lower limb shape. The result concurs with prior analysis of Cis-Baikal adults, which detected only slight increases in bi-iliac breadth from the EN to the LN/EBA (Stock et al., 2010). The small magnitude of the difference made it unlikely it would affect biomechanical analysis (Lieverse et al., 2011).

While genetic differences do not appear a convincing explanation for differences between individuals younger than 16 years, genetically modulated increases in sex hormone production may account for a considerable portion of the sexual dimorphism seen in size-standardized TA and SMAs within the adolescents/young adult females and males (Figures 5.2.15, 5.2.16, 5.3.15, 5.3.16). As discussed in Chapter 8, production of testosterone promotes periosteal apposition in males during adolescence (Garn, 1970; Frisancho et al., 1970; Ruff et al., 1994; Goldman et al., 2009; Gosman et al., 2013). Conversely, higher levels of estrogen in females decrease the mechanical sensitivity of the periosteum (Orwoll, 2003). As a result, loading of equivalent magnitude produces greater gains in periosteal diameter among males, and they will appear more robust even once body size has been controlled for. The extent to which these hormonally modulated differences between sexes can be controlled for during behavioral reconstruction will be considered in greater detail in the section dealing with sexual differences with behavior.

## 9.4.2: Differences in body mass and their potential effect on size-standardized comparisons

While genetic variation between EN and LN groups does not appear a major cause of differences in CSG prior to puberty, chronological differences in body mass may have a more

significant effect on comparisons of size-standardized measures of area and SMAs. LN juveniles younger than 16 years generally produce a higher range of size-standardized robusticity than EN individuals in both limbs, except at the femur subtrochanteric and humerus sections where the two samples produce equivalent ranges (Figures 5.2.1-5.2.3, 5.3.1-5.3.3). By contrast, EN adults produce a higher range of size-standardized robusticity in both limbs (Stock et al., 2010; Stock and Macintosh, 2016). In addition, both prior studies of adults and juveniles have shown that body mass was lower in the EN than the LN (Stock et al., 2010; Temple et al., 2014). As CSG may be more sensitive to the loads produced by body mass than joint dimensions, body size differences may explain the discrepancy between juvenile and adult comparisons (Lieberman et al., 2001; Cowgill, 2010). This is especially the case due to the significant methodological limitations of juvenile body mass estimation. This section investigates how well body mass estimation techniques controlled for body mass differences between groups, and how this could affect behavioral interpretations. The relevance of CSG as an indicator of variation in developmental stress is the subject of the following section.

The reasons that area and SMA measures are more sensitive to differences in body mass than joint dimensions has been discussed in detail in Chapters 2 and 4. Here it is most pertinent to emphasize that joint surfaces show considerably more genetic canalization in developmental trajectory than diaphyseal dimensions. The need for joints to fit together and maintain structural integrity throughout growth limits the extent to which joint dimensions respond to fluctuations in body mass (Cowgill, 2010; Davies and Stock, 2014). The transverse dimensions of long bone diaphyses do not face the same constraint. Furthermore, CSG shows a closer relation to body size throughout life, because it "is very sensitive to alterations in all mechanical loads, including muscular loadings as well as the gravitational loading produced by body weight" (Ruff et al., 1991, p. 411). Ruff et al.'s (1994) ontogenetic study supports the greater sensitivity of CSG than joint dimensions to body mass changes during growth. The growth curve for joint dimensions parallels that for long bone length, whereas that of CSG more closely corresponds to that of body mass (Ruff et al., 1994). Indeed, over the entirety of the life course, the correlation between joint dimensions and body mass peaks in late adolescence, while CSG shows a closer relationship to changes in body mass throughout life (Ruff et al., 1991; Ruff, 2003a; Ruff, 2007). Given the sensitivity of diaphyseal measures to all mechanical loads, some researchers have recommended using CSG to evaluate differences in both *body mass and activity levels* when comparing individuals *from the same species* (Lieberman et al., 2001). Joint dimensions provide more appropriate estimates of body mass than CSG for inter-species comparisons, because body mass differences are more likely to be genetic in origin (Lieberman et al., 2001). Of course, activity also exerts a large effect on CSG, so the multifactorial nature of such data cannot be overlooked to extrapolate either body size or activity levels without consideration of the other (Robbins et al., 2010). The preceding discussion does not imply that joint surfaces are insensitive to differences in body mass. Rather, behavioral reconstructions of juveniles must account for the possibility that smaller alterations in body mass accrual would be required to alter growth in bone robusticity than the growth of joint surfaces.

The issues raised by using joint dimensions to standardize properties more sensitive to changes in body weight may have been exacerbated by the poor preservation of some Cis-Baikal individuals. The Ruff (2007) equations require measures of femoral joint surfaces and age estimates accurate enough to fit an individual into the appropriate year wide age cohort. In addition to dental development, this study employed diaphyseal length and skeletal fusion to estimate the age of individuals without preserved teeth. Thus, the inherent limitations of age estimates make it unclear if the correct body mass equation was employed in all cases. More importantly, a lack of the relevant femoral dimensions for a substantial number of individuals necessitated the estimation of these measures from other skeletal measurements or from regression of body mass on age. It was not possible to do this separately for EN and LN individuals, due to the small sample sizes for each regression equation. This raised the possibility that archaeological period specific standards would produce unrealistic estimates for certain age ranges, and this was indeed the case in preliminary investigations. Thus, the use of combined sample regressions for estimating body mass when femur dimensions were lacking may have further homogenized the range of body mass estimates produced for different archaeological periods.

In this investigation EN individuals tended to show a slightly lower range of body mass estimates than LN Ust-Ida individuals ((Figure 5.4.9). This concurs with both prior studies of adults and juveniles (Stock et al., 2010; Temple et al., 2014). Regression of size-unstandardized

CSG on age also demonstrated the same pattern (Figures 5.4.1-5.4.4). Given the strength of the relationships between body mass and TA, CA, and SMAs ( $R^2>0.9$ ), this is consistent with body mass indeed being slightly lower during the EN than the LN (Table 5.1). Thus, joint dimension-based estimates account for at least some variation in body mass. However, since CSG exhibits greater sensitivity to body mass than joint dimensions, it remains unclear if size-standardization completely removes patterning due to differences in body mass.

Given the strong evidence for change in body size between archaeological periods, all behavioral interpretations must consider the possibility that size-standardization based on joint dimensions did not completely remove the effects of body size on CSG. Consequently, EN juveniles may appear gracile compared to LN individuals due to differences in body weight rather than lower workloads. However, body mass differences cannot explain all patterning in size-standardized measures. Importantly, the tendency for LN individuals younger than 16 years to appear more robust than their EN predecessors reaches statistical significance in the lower limb, but not the upper limb. At the two humerus sections, the EN individuals appear as strong as LN individuals, but slightly more gracile at the clavicle and ulna midshaft sections (Figures 5.3.1 and 5.3.2). If patterning was attributable solely to unaccounted differences in body mass, LN individuals should also appear more robust at the humeral sections. Thus, patterns of variation between archaeological periods cannot be attributed entirely to differences in the loads engendered by body mass.

### 9.4.3: Insights into Variation in Developmental Stress

In addition to guiding behavioral interpretation of size-standardized variables, the analysis of differences in body mass and size-unstandardized CSG adds to understanding of variation in levels of developmental stress during the Middle Holocene. In general, lower EN body mass estimates and size-unstandardized CSG for age concur with the hypothesis that EN individuals experienced greater developmental stress than LN individuals. The results further build on previous studies of health by revealing that developmental stress may have varied between populations using different cemeteries in the EN.

Size-unstandardized CSG and body mass estimates in juveniles younger than 16 years are lower in EN populations, and EN Lokomotiv produces the lowest range of size-unstandardized CSG (Figures 5.4.1-5.4.8). The multiple lines of evidence for lower EN body mass concurs with several previous studies that suggested greater developmental stress in the EN than the LN (Lieverse et al., 2007b; Lieverse, 2010; Waters-Rist, 2011; Waters-Rist et al., 2011; Temple et al., 2014). EN individuals from Lokomotiv and Shamanka showed a higher frequency of linear enamel hypoplasia (LEH), an indicator of disruption in enamel secretion, compared to LN Ust-Ida individuals. This is consistent with more episodes of developmental stress during growth (Waters-Rist, 2011). Both Lieverse et al. (2007b) and Waters-Rist (2011) hypothesized that higher frequency of LEH in the EN reflected more frequent or more severe seasonal food shortages. This was based on ethnographic observations that high latitude hunter-gatherers often struggle with periods of resource scarcity, due to marked seasonal fluctuations in resource abundance. The denser concentration of EN populations in the Angara River Valley and South Baikal during the EN may have resulted in more severe depletion of local resources, particularly the large terrestrial game (Lieverse et al., 2007a; Weber and Bettinger, 2010; Waters-Rist, 2011; Losey et al., 2017). As a result, they may have experienced more frequent or severe seasonal shortages of food. Evaluation of growth in long bone length and body mass concluded that greater developmental stress in the EN lead to reductions in long bone growth and body mass accrual (Temple et al., 2014). It should be noted that Temple and colleagues (2014) used a smaller sample composed only of individuals for which both dental age and femoral dimensions used to calculate body mass were available. Perhaps for this reason, the difference in body mass between the EN and LN samples appears slightly more pronounced in that study than the current investigation. This further supports the previously discussed possibility that methodological limitations prevented a complete control for chronological change in body mass. Regardless, Temple and colleagues (2014) study still shows the same patterning as the body mass estimates and size-unstandardized CSG in the current investigation. Thus, multiple lines of evidence indicate that EN juveniles experienced greater developmental stress than LN juveniles, and this disparity resulted in reductions in body mass between archaeological periods.

Interestingly, the body mass estimates generated in this dissertation also demonstrate that differences in body size emerge early in life, around the age of two years (Figures 5.4.10, 5.4.11). However, the fact that there are few LN Ust-Ida individuals younger than this makes the interpretation tentative. Despite this limitation, the result supports prior studies, which proposed that differences in developmental stress levels between EN and LN individuals emerge early in life (Waters-Rist et al., 2011; Temple et al., 2014). For example, isotopic study of weaning in

Middle Holocene groups indicates that a substantial proportion of EN infants died while still breastfeeding. This suggests a "considerable stressor was affecting the population to the point at which the capacity of breastfeeding to buffer infants from malnutrition and/or disease was impaired" (Waters-Rist et al., 2011, p. 238). Thus, differences in developmental stress levels and body mass between archaeological periods appear to have emerged early in life.

The comparison of size-unstandardized CSG and body mass estimates also detected intercemetery variation in body mass during the EN. This was somewhat unexpected since similarities in Lokomotiv and Shamanka LEH frequencies suggest fairly equivalent levels of developmental stress (Waters-Rist, 2011). One cannot entirely exclude the possibility that differences between EN groups is an artifact of sample size, since there are fewer Lokomotiv individuals than Shamanka individuals. Alternatively, lower body mass estimates and sizeunstandardized CSG in the Lokomotiv sample than the Shamanka sample reflects geographic variation in stress levels within the EN, with Shamanka individuals experiencing less compromised growth. This could stem from geographic differences in resource abundance related to population density. Lokomotiv was one of several large EN cemeteries in the Angara River Valley, but Shamanka is the only large cemetery in the South Baikal microregion (Weber and Bettinger, 2010). If, as Weber and Bettinger (2010) hypothesize, the number and distribution of burials correlates with population density, then it is possible that the larger and more densely concentrated EN population in the Angara River Valley depleted local resources more than populations in the South Baikal (Lieverse et al., 2013). Zooarchaeological analysis of Angara River Valley habitation sites supports the occurrence of prey depression, which appears to have begun in the Late Mesolithic (Losey et al., 2017). This may have increased the frequency and severity of seasonal resource shortfalls. Note that the scenario discussed specifically refers to depletion of terrestrial game rather than fish. Hunter-gatherer populations would not have been large enough to deplete aquatic resources (Kelly, 1995). Furthermore, Shamanka individuals exhibit greater variability in  $\delta^{15}$ N than the entire EN Angara skeletal sample, which comes from several cemeteries including Lokomotiv (Weber et al., 2016b). The heterogeneity in isotopic values implies that "those buried at Shamanka II constitute a more heterogeneous group in terms of their places of origin, and hence with respect to their diets, than the Angara groups" (Weber et al., 2016b, p. 248). Consequently, Shamanka individuals may have experienced less seasonal resource stress during growth than their Lokomotiv contemporaries, because groups using this

cemetery may have been more distributed about the landscape. Such a difference in population distribution could have also lowered population pressure on resources.

## **9.4.4: Summary of Differences in Genetics and Body Size and their Effect on Robusticity Comparisons**

Examining the extent to which differences in juvenile bone accrual reflect variation in genetics and health between groups does more than evaluate how these factors can affect behavioral interpretations. It also provides additional insight into how much Cis-Baikal populations differed from each other in terms of genetics and health. EN and LN Cis-Baikal populations are genetically distinct (Mooder et al, 2010; Moussa et al., 2016). However, this is not a convincing explanation for variation in bone robusticity and shape. Most differences arise after five years of age, rather than at birth. In addition, a lack of differentiation in variables associated with differences in body breadth indicates that differences in body shape do not have a significant effect on comparisons of lower limb strength and shape.

Limitations inherent to standardizing for body mass using estimates from joint dimensions raised the possibility that differences in body mass had not been fully controlled for. Estimates of body size from joint dimensions and size-unstandardized CSG suggested lower body mass in the EN compared to the LN. This agrees with prior studies, which hypothesized that EN individuals experienced more frequent and severe developmental disturbances (Lieverse, 2007b; Waters-Rist, 2011; Waters-Rist et al., 2011; Temple et al., 2014). Of the three cemeteries compared, EN Lokomotiv juveniles exhibited the lowest body masses. Thus, high population density may have led to a greater depletion of resources in the Angara River Valley than in other microregions during the EN. In terms of how differences in body mass will affect behavioral analysis, one must keep in mind that area and SMA measures likely show greater sensitivity to changes in body mass than joint dimensions. Consequently, increase in body mass between the EN and LN may partly explain the general tendency for LN Ust-Ida individuals to produce higher ranges of size-standardized limb robusticity.

# 9.5: Behavioral Interpretations of Differences in Robusticity9.5.1: The Lower Limb: Individuals Aged 0-16 Years

The lower limbs of EN individuals younger than 16 years old are relatively more reinforced along the anteroposterior axis than the mediolateral axis and less robust than those of LN individuals. These results are consistent with decrease in terrestrial mobility and increase in body mass between the EN and LN. Importantly, differentiation between groups is most pronounced in sections of the limb that show the greatest sensitivity to differences in mechanical loading, which demonstrates the consistency of these patterns with functional adaptation. It is also probable that shape and robusticity respond to different mechanical influences. The more anteroposteriorly reinforced diaphyses of EN juveniles indicate they traveled greater distances prior to adulthood, possibly due to differences in resource distribution and abundance between the EN and LN. Conversely, chronological increase in lower limb robusticity is consistent with LN juveniles bearing heavier loads during locomotion. Given the differences in limb shape, the greater robusticity of LN juveniles likely reflects differences in body mass not removed by sizestandardization. The greater differentiation of Shamanka than Lokomotiv from Ust-Ida may partly reflect small Lokomotiv sample size. If it does not, Shamanka juvenile mobility levels may have differed more from Ust-Ida, because the incorporation of lakeshore foraging into the seasonal round influences mobility levels. Alternatively, the uniqueness of this cemetery may reflect greater variation in mobility levels among groups utilizing this cemetery compared to Lokomotiv and Ust-Ida.

Differences in lower limb shape and size-standardized robusticity reach statistical significance in the locations prior studies have identified as most sensitive to differences in mechanical loading (Stock, 2006; Gosman et al., 2013; Davies and Stock, 2014; Sparacello et al., 2014). Shape comparisons reach significance at the femur midshaft and tibia nutrient foramen, but not the tibia midshaft (Tables 6.5 and 6.6). Such patterning likely reflects a closer link between shaft morphology and terrestrial mobility levels in these sections, as the relative magnitude of AP relative to ML strains engendered by locomotion peaks close to the knee joint (Ruff and Hayes, 1983; Gosman et al., 2013; Ch.8 this study). Thus, sections close to this location, femur midshaft and tibia nutrient foramen, should provide a good record of locomotor engendered strain. The reasons that femur midshaft shape is more sensitive to activity differences than tibia midshaft shape, even though these sections lie roughly equidistant from the knee joint, have only been the subject of a limited number of investigations (Ruff, 2006b; Stock, 2006; Wescott, 2014). Still, several studies of adult populations, for which archaeological evidence allowed inference of mobility levels, support the hypothesis that femur midshaft shape provides a better indicator of mobility levels than tibia midshaft shape (Holt, 2003; Stock, 2006; Sparacello et al., 2014). Differences in mechanical environment may explain why tibia midshaft shape

shows a lower correlation with mobility levels. As discussed in Chapter 8, while the femur and proximal tibia experience primarily AP and ML strain, locomotion generates relatively greater torsional forces in the midshaft and distal regions of the tibia (Ruff and Hayes, 1983a; Figure 8.6.1). This may limit the extent of anteroposterior buttressing that occurs in this region of the diaphysis. The presence of the fibula, which acts as a mediolateral brace, may further weaken the relationship between tibia midshaft shape and mobility (Sparacello et al., 2014). In addition, the pressure imposed on the lateral and posterior tibia shaft surface by adjacent musculature may further constrain the ability of shape to reflect differences in AP and ML load distribution (Carpenter and Carter, 2008). As discussed in Chapter 8, this hypothesis for why tibia midshaft shape shows a lower correlation with mobility levels than more proximal sections would only be valid if the musculature of limb segments of the distal limb segment. Further testing is needed to confirm the assumption.

It remains unclear why significant differences are detected for  $I_x/I_y$  but not  $I_{max}/I_{min}$  at the femur midshaft and tibia nutrient foramen sections. Possibly, this discrepancy relates to the fact that the relative magnitude of  $I_{max}$  to  $I_{min}$  responds to differences in both body shape and mobility levels. As discussed in Chapter 8, due to the lack of a carrying angle, the waddling gait of toddlers and young children engenders relatively higher maximum strains than the "adult" form of bipedal locomotion (Cowgill et al., 2010). Consequently, at the femur midshaft, the magnitude of I<sub>max</sub> relative to I<sub>min</sub> decreases for much of the first decade, and it then increases in adolescence (Figure 6.1.4). The ratio of  $I_x/I_y$  shows the opposite pattern, increasing throughout ontogeny as terrestrial locomotion generates progressively greater loads in the AP plane than the ML plane (Figure 6.1.3). For these reasons, the two ratios provide slightly different records of locomotor activity. As both EN and LN individuals undergo similar changes in body shape, I<sub>max</sub>/I<sub>min</sub> may not distinguish these samples as well as  $I_x/I_v$ , which solely tracks the relative increase of AP loads due to locomotion. Still, this should not negate the fact that both ratios are higher in the EN sample, indicating a greater disparity in load distribution regardless of which axes are used for ratio values (Figure 6.2.1 and 6.2.2). As terrestrial locomotion produces unequal bending loads about perpendicular planes, these findings concord with functional adaptation to greater terrestrial mobility in the EN, though statistical significance is achieved only for measures of  $I_x/I_y$ .

Differences in area and SMAs between Cis-Baikal juveniles achieve statistical significance at the tibia sections but not the femur midshaft (Table 5.3). Again, this finding supports prior research suggesting that mechanical load levels show a closer concordance with tibia rather than femur area and SMA measures (Stock, 2006; Davies and Stock, 2014; Shaw et al., 2014). The closer correlation between tibia strength and mobility levels has been attributed to the principle of tissue economy. According to this principle, the more gracile distal segments of the limb must be "strong enough to prevent fracture, yet light enough to minimize... the energetic requirements of movement" (Stock, 2006, p. 195-196). Since the cost to accelerate material increases with distance from the origin of the force, more proximal segments may face less pressure to optimize form. Retention of unnecessary tissue here does not raise the energy required to move the limb as much as additional material in the distal portion of the limb (Pearson and Lieberman, 2004). Thus, individuals experiencing higher loading will tend to have more robust tibiae, because the structural benefits outweigh the energetic cost of maintaining and accelerating extra bony tissue. Importantly, Carpenter and Carter (2008) suggest that crosssection size may be more sensitive to loads engendered during movement, while periosteal pressure created by adjacent soft tissue has a greater effect on shape, the axes along which the cross-section expands in response to strain. Thus, the fact that cross-section size and strength appear more correlated to mechanical loads in the tibia than femur, does not contradict a closer correlation between activity and shape at sections proximal to the tibia midshaft.

Overall, quantifications of shape suggest higher mobility in the EN, while sizestandardized area and SMAs indicate more robust lower limbs in the LN. This discrepancy demonstrates that shape and area/SMA measures do not respond to the same mechanical influences. Previous investigations have made the important distinction that robusticity measures (area and SMAs) capture differences in load magnitude, but shape captures differences in load distribution (Trinkaus et al., 1991; Marchi et al., 2006; Marchi et al., 2011; Sparacello et al., 2014). Importantly, terrestrial mobility, while a major influence, is not the sole determinant of load magnitude. Body mass also applies a constant load to the lower limb.

## 9.5.1.1: Lower Limb Shape

Given the potential effects of body mass on robusticity, it proves beneficial to discuss shape results first. Shortcomings of juvenile body mass estimation cannot affect this variable. The more anteroposteriorly expanded lower limb diaphyses of EN Cis-Baikal juveniles indicate that, on average, juveniles in this group habitually traveled greater distances than LN Ust-Ida individuals, and this difference becomes apparent in individuals older than five years (Figures 6.2.1, 6.2.2, 6.2.5). The chronological difference in shape ratios is entirely consistent with studies of adults, which found that EN females and males had less circular lower limb diaphyses than LN/EBA individuals (Stock et al., 2010; Lieverse et al., 2011; Stock and Macintosh, 2016). As the current investigation deals with an ontogenetic series, the detection of differences after five years must be understood within both an ecological and developmental context: how much and why do juvenile hunter-gatherers travel around a boreal forest landscape? The implications of detecting differences in juvenile samples for understanding chronological changes in mobility levels is also explored.

As previously discussed, ethnographic studies of juvenile foragers show that children primarily move over long distances when the entire group relocates or when caretaking adults, usually females, take them on foraging excursions (Hawkes et al., 1995; Henry et al., 2005). When adults forage alone, children spend most of their time in or around camp under the supervision of either older children, grandparents, or other adult relatives (Marlowe, 2005). Independent foraging outside camp can occur, but it depends on the presence of easily harvestable resources (Bird and Bliege Bird, 2002; Tucker and Young, 2005). Additionally, adults actively discourage child foraging when environmental hazards pose a risk to their safety (Hawkes et al., 1995; Henry et al., 2005). When children do accompany adults on foraging trips, it is usually the mother. The inclusion of juvenile males on hunting forays, particularly longdistance ones, rarely occurs prior to adolescence (Hawkes et al., 1995; Henry et al., 2005; MacDonald, 2007).

In the Cis-Baikal, one can largely discount the possibility that extensive solo foraging by children explains differences between EN and LN samples. Five-month long winters during which temperatures are regularly below 0° Celsius would constrain juvenile mobility, especially since children are less resistant to temperature extremes than adults (Weber et al., 2002; Cowgill et al., 2012 and references therein). Furthermore, navigating a boreal forest also requires long term learning. Interviews with modern central Siberian Evenki, who practice a combination of reindeer pastoralism, hunting, and gathering, reveal that individuals in these groups rely on memory, interpretation of landscape features, and trail markers to navigate the landscape (Sirina,

2006; Turov, 2010). Acquiring such knowledges takes many years. These constraints on juvenile mobility recall the example of !Kung foragers discussed above. Just as extreme heat and the cognitive difficulty of navigating a desert restricts travel by juvenile !Kung, Cis-Baikal juveniles would have been seasonally limited by extreme cold and a lack of the necessary mental skills necessary to navigate the landscape by themselves (Jones et al., 1994; Hawkes et al., 1995).

Thus, mental and physical constraints make it logical to consider juveniles as proxies for group mobility or, if juveniles went on foraging trips, the mobility of adults caring for children. Consequently, the more anteroposteriorly reinforced diaphyses of EN juveniles indicate that EN groups habitually traveled over longer distances. However, it is not clear if this means that moves occurred over longer distances in the EN or were more frequent than in the LN. In addition, children may have accompanied caretaking adults on either longer or more frequent foraging trips. Furthermore, based on general similarities in the types of subsistence practices engaged in, one can largely exclude the possibility that differences in non-mobility related habitual activities lead to chronological alterations in load orientation (Ruff, 1999; Wescott, 2014).

Greater group mobility in the EN may reflect a reduced abundance of terrestrial resources relative to the LN. Based on the distribution of cemeteries, EN groups in the upper Angara River Valley (portion closest to the lake) and adjoining South Baikal microregions appear to have been concentrated into "a few rather large" communities, as evidenced by the presence of several large EN cemeteries in these two microregions (Weber and Bettinger, 2010, p.499). It has been further suggested that EN groups greater reliance on fish effectively tethered them to "specific waterways for longer periods of time" in the year than was the case in the LN/EBA (Lieverse et al, 2013, p.8). Either one of these factors or both could have depleted local populations of ungulates, the primary non-aquatic food source. The recent discovery that populations became more dependent on fish throughout the EN supports this hypothesis (Weber et al., 2016a,b). Importantly, EN groups would only have been concentrated next to particularly rich rivers and lakeshore fisheries on a seasonal basis, when fish were particularly abundant (Lieverse et al., 2011). Due to the depletion of local non-aquatic resources, they may have been more mobile or exploited a larger area during other parts of the year.

By contrast, the more circular diaphyses of LN juveniles younger than 16 years suggest foraging groups using Ust-Ida habitually moved shorter distances during residential moves or during daily foraging trips. Perhaps this reflects more even distribution of the population during the LN (Weber and Bettinger, 2010). If this change in population density reduced population pressure on terrestrial game, groups may not have needed to travel as frequently or as far to find productive patches (Waters-Rist, 2011). Alternatively, ungulates may have been more abundant and less dispersed in the LN due to environmental differences between the EN and LN. Reconstructions of Middle Holocene climate suggest that a period of increased aridity may have increased the prevalence of habitats that "acted to concentrate game in particular localities" in the LN (White and Bush, 2010, p.19-20). This greater resource abundance may have decreased the likelihood that hunting depleted local ungulate populations, regardless of chronological changes in population size and distribution. Also, if game populations were less dispersed around the landscape, groups would have had to travel shorter differences between hunting grounds.

Greater travel by EN groups for at least part of the year, perhaps to exploit a wider area, concurs with ethnographic study of how boreal forest/arctic groups deal with scarce or patchily distributed ungulate populations. When hunting success drops, moving the entire group more frequently reduces the distance male hunters must travel, as long distance "foraging in cold northern climates can be exhausting" (Kelly, 1995, p.124). In addition to increasing the distance and frequency of residential moves, population pressure on resources may have also required individuals to conduct more intensive local foraging for small game, the sparse plant resources, and fish (Lieverse et al., 2011; Lieverse et al., 2013). Such foraging activities are well within the cognitive and physical abilities of children older than five years. This parallels the finding that both adult EN males and females have more ovoid diaphyses than LN/EBA individuals (Stock and Macintosh, 2016). The chronological decrease in adult female mobility proves particularly significant, since they are more likely than males to combine child care and foraging. Thus, the more ovoid diaphyses of EN juveniles may reflect both more intensive local foraging by their caretakers and differences in the distance covered by entire groups during the seasonal round.

The proposal that entire EN groups habitually traveled greater distances should not be seen as contradicting the hypothesis, proposed in several previous papers, that logistical mobility may have been more extensive in the EN than the LN (Weber et al., 2002; Lieverse et al., 2007a;

Lieverse et al., 2011; Lieverse et al., 2013; Stock and Macintosh, 2016). As a reminder, residential mobility refers to the movement of entire groups to resource patches. As residences are placed close to resources, foraging typically occurs over a short distance. Groups following a logistic mobility strategy place their main camp in a key location that may not be near one or several important resources. Small task-specific groups then undertake excursions to acquire these resources and return them to the main group base (Kelly, 1995). Consequently, logistic forays tend to occur over greater distances than the daily foraging excursions undertaken by foragers practicing a residential strategy.

It has been proposed that logistic mobility would have been an especially important component of EN male mobility patterns during periods of the year that groups were tethered to waterways rich in fish (Weber et al., 2002; Lieverse et al., 2007a; Weber and Bettinger, 2010; Lieverse et al., 2011). If seasonal reduction in mobility depleted local ungulate populations, males would have had to hunt at a greater distance from the main camp (Lieverse et al., 2011). Rather than entirely discounting the possibility of greater logistic mobility in the EN, the preceding interpretations of juvenile limb shape call attention to the fact that differences in resource abundance and distribution affect mobility in complex ways. Differences in skeletal indicators of mobility most directly measure the distance and intensity of terrestrial travel, not whether it was residential or logistic in nature (Ruff and Larsen, 2014; Stock and Macintosh, 2016). The interrelation between logistic and residential movement further complicates interpretations. For instance, during a residential move, hunters may range away from the group, perhaps for an extended period, to find and pursue game (Kelly, 1995). Also, multiple unsuccessful logistic hunting forays often induce the relocation of the entire group's residence, allowing hunters to forage logistically in another, potentially more productive, location (Kelly, 1995). These examples highlight that changes in logistic mobility likely affect levels of residential mobility and vice versa.

Furthermore, the EN and LN populations depended on the same two resources, fish and ungulates. This limits behavioral options, and one should not expect enormous differences in foraging strategy (Weber and Bettinger, 2010; Weber et al., 2011). In all archaeological periods and microregions, both residential and logistic moves would have been important for ensuring access to resources throughout the seasonal round (Stock and Macintosh, 2016). This

fundamental similarity in foraging strategies may account for the considerable overlap in shape ratios between individuals from different archaeological periods and cemeteries (Figures 6.2.1-6.2.4). Indeed, Kelly's (1995) survey of ethnography finds that boreal forest groups generally invest considerable energy into both residential and logistic foraging. Thus, both EN and LN foraging strategies involved both residential and logistic mobility, but the frequency and distance of residential and logistic moves may well have changed between archaeological periods. Since juveniles do not participate in big game hunting prior to adolescence, the shape differences detected speak most directly to a chronological change in either the length or frequency of residential moves or the intensity of localized foraging (MacDonald, 2007).

#### 9.5.1.2: Lower Limb Area and SMA Measures

Detection of lower size-standardized robusticity in EN juveniles compared to LN juveniles runs contrary to the detection of greater adult robusticity in the EN by previous studies of adults (Stock et al., 2010; Stock and Macintosh, 2016). Furthermore, as terrestrial mobility is a significant determinant of robusticity, the increase in juvenile lower limb robusticity between the EN and LN is unexpected given the early emergence of adult differences in shape consistent with higher terrestrial mobility in the EN (Figures 5.2.1-5.2.3). Studies of osteoarthritis and muscoskeletal markers also support greater terrestrial mobility in EN populations (Lieverse et al., 2007a, 2013). Since, as discussed above, area and SMA measures exhibit greater sensitivity to body mass than joint dimensions, uncontrolled for differences in body mass may account for the higher size-standardized robusticity of LN juveniles (Lieberman et al., 2001; Cowgill, 2010). It has been shown that the rate of femoral bone accrual increases markedly after individuals begin to walk, and both locomotion and weight bearing drive this ontogenetic pattern (Ruff, 2003b). Importantly, comparisons of TA and SMAs between archaeological periods primarily reach statistical significance in the lower limb but not the upper limb (Tables 5.3, 5.6). Given the greater correlation between lower limb CSG and body mass, one would expect exactly this pattern if body mass accounts for a substantial portion of the differentiation in area and SMA measures (Ruff, 2002).

Patterning in interlimb robusticity ratios further supports the hypothesis that greater LN lower limb robusticity reflects differences in body mass. LN Ust-Ida individuals produce a higher range for ratios of TA, CA, and J than their EN predecessors, particularly those buried at Lokomotiv (Figures 7.2.1-7.2.3, 7.2.5-7.2.7). Most bioarchaeological studies using interlimb

ratios have treated these variables as size free measures of loading. This approach was based on the premise that bones of the same individual should be equally affected by differences in body mass (Ruff 2003b; Cowgill, 2008; Stock et al., 2010; Shaw and Stock, 2013; Osipov et al., 2016). However, as discussed in Chapter 8, this assumption may not be entirely valid. The increase in interlimb robusticity ratios with age occurs "due to continuing adaptation of the [lower limb] to increases in body size, coupled with a continuing decline in humeral strength relative to body size" (Ruff, 2003b, p.335). Consequently, more rapid accrual of body weight could lead to a higher ratio of lower/ upper limb strength, because femoral and tibial robusticity track increases in body size more closely than upper limb sections. Prior studies support a link between interlimb robusticity ratios and body size. In a longitudinal study of a modern population, where changes in body mass could be tracked, fluctuations in interlimb robusticity ratios with age were directly linked to changes in body mass (Ruff, 2003b).

Two more aspects of the sample comparisons support a link between interlimb robusticity ratios and body mass. First, most significant differences between EN and LN groups emerge in comparisons of CA ratios (Table 7.2). This is important, because cortical area most directly reflects resistance to compressive loads, the kind directly engendered by weight bearing (Ruff, 2008). Second, Lokomotiv produced the lowest CA ratios, and these were significantly lower than those of Ust-Ida individuals (Figures 7.2.5- 7.2.7, Table 7.3). This group also produced the lowest body mass estimates and size-unstandardized CSG. Thus, inter-cemetery patterning in interlimb ratios resembles that seen in comparisons of proxies for body mass (estimates of mass from joint dimensions and size-unstandardized CSG).

While body mass may account for generally greater LN lower limb robusticity, critical evaluation of which SMAs differ significantly between groups offers some additional support for greater terrestrial mobility in the EN. Although EN individuals exhibit significantly or nearly significantly lower ranges of size-standardized I<sub>y</sub>, I<sub>max</sub>, I<sub>min</sub>, and J in several lower limb crosssections, I<sub>x</sub>, which represents bending rigidity in the AP plane, exhibits no chronological change at the femur midshaft, tibia nutrient foramen, or tibia midshaft section (Tables 5.3 and 5.4). Locomotion primarily generates AP strains (Figure 8.6.1). Therefore, chronological homogeneity in I<sub>x</sub> is consistent with greater terrestrial mobility in the EN compensating for the loads imposed

by greater body mass in the LN along other axes. This results in a diaphysis more reinforced in the AP plane, as demonstrated by higher ratios of  $I_x/I_y$  in the EN sample.

Given the ambiguities created by limitations in body mass standardization, it remains unclear when during development the more robust lower limbs characteristic of EN adults emerged during development. However, the more anteroposteriorly reinforced lower limbs of EN individuals after the age of five years are consistent with the emergence of differences in mobility. As mobility constitutes "the most repetitive aspect of loading" on the lower limb other than body size, it is not unreasonable to hypothesize that greater EN limb strength relative to body size also emerges around this age (Stock, 2006, p. 194).

## 9.5.1.3: Inter-Cemetery Differentiation in Lower Limb CSG

In addition to chronological variation, comparing the EN Shamanka and Lokomotiv juveniles separately to LN Ust-Ida detects differentiation between specific cemeteries. While visual analysis of boxplots makes clear that individuals from both EN cemeteries have less circular and more gracile lower limbs compared to Ust-Ida, the difference reaches statistical significance only for Shamanka to Ust-Ida comparisons (Tables 5.4, 6.6). Conversely, there were no significant differences between Shamanka and Lokomotiv individuals. It is possible that detection of significant differences between Shamanka and Ust-Ida but not between Ust-Ida and Lokomotiv reflects differences in sample size. The Shamanka and Ust-Ida samples are both approximately twice the size of the Lokomotiv juvenile sample. Visual analysis of boxplots shows that Lokomotiv and Shamanka appear more similar to each other than Ust-Ida in terms of lower limb shape and size-standardized measures (Figures 5.2.6-5.2.10, 6.2.3, 6.2.4). Therefore, it may simply be the case that the smaller size of the Lokomotiv sample reduces statistical power, preventing the detection of significant differences in comparisons to Ust-Ida. The overlap in isotopic values between Shamanka and Lokomotiv adult individuals also implies that foraging ranges overlapped considerably, an expected result given the proximity of the cemeteries (Weber et al., 2011). As this similarity in diet implies exploitation of the same or nearby habitats, it is unlikely that behavior differed markedly between EN individuals from these two cemeteries.

If not totally an artifact of sample size, greater differentiation of Shamanka from Ust-Ida might reflect "the specific uniqueness of Shamanka II and/or its South Baikal locale" (Lieverse et al., 2016, p.168). As Lokomotiv is in the same microregion as Ust-Ida, behavior may have
varied less at these two sites due to ecological similarities. Most obviously, individuals buried in these cemeteries may have focused more on riverine aquatic resources, while many the individuals utilizing Shamanka depended more on lake fish (Weber et al., 2011; Weber et al., 2016b). Differences in the foraging strategies of riverine and lakeshore foragers may have altered mobility patterns and workloads, and this could account for the distinctiveness of the Shamanka individuals (Losey et al., 2012; Losey and Nomokonova, 2017).

Importantly, the above interpretation may only apply to some of the groups burying their dead at Shamanka. Stable isotope analysis of Shamanka burials indicates substantial dietary variation (Weber et al., 2016b). Indeed, the individuals buried here show a greater range of  $\delta^{13}$ C and  $\delta^{15}$ N isotope values than all individuals from the EN Angara sample, which consists of individuals from multiple cemeteries "separated by a distance of over 250 km" (Weber et al., 2016b, p. 247). The most parsimonious explanation for this is that individuals burying their dead at Shamanka represented "a more heterogeneous group in terms of their places of origin, and hence with respect to their diets" (Weber et al., 2016b, p.248). Some of the individuals buried at this cemetery obtained fish from the local lakeshore, but others appear to have acquired aquatic resources elsewhere. Based on isotopic values, Weber and colleagues (2016b) hypothesized that these individuals foraged in the Middle Irkut river valley to the west, the Selenga River to the east, or another location not yet isotopically sampled. Isotopic signatures do not, in and of themselves, provide information about how far individuals exploiting different aquatic resources traveled over the course of a seasonal round or throughout their lives. Still, the exploitation of aquatic resources from different locations suggests that groups burying their dead at Shamanka may have exhibited considerable variation in terms of distance traveled and intensity of foraging. Importantly, if foraging groups using Shamanka had distinct foraging ranges, there could be substantial inter-individual variation in mobility, which exceeded that present in Ust-Ida and Lokomotiv groups. Thus, if not due to sample size, the clearer differentiation of Shamanka than Lokomotiv from Ust-Ida could reflect intra-cemetery heterogeneity in mobility in the Shamanka group. In other words, certain groups burying their dead at Shamanka may have differed more in terms of mobility from Angara River Valley groups than others.

It is also pertinent that dependence on aquatic resources increased throughout the EN at both Lokomotiv and Shamanka (Weber et al., 2016a; Weber et al., 2016b). If dependence on aquatic resources affects mobility patterns, a well-documented phenomenon, one cannot ignore the possibility of chronological change in distance traveled and load bearing by juveniles within both EN groups (Kelly, 1995). Indeed, during portions of the EN when groups depended less on aquatic resources, juvenile mobility may have been more like that of LN individuals buried at Ust-Ida. Investigating the effect that increased dependence on aquatic resources had on juvenile mobility requires further analyses. These would account for when during the EN individuals were buried.

The last factor that could potentially contribute to the more anteroposteriorly reinforced lower limbs of Shamanka juveniles is terrain. Shamanka is close to the Eastern Sayany mountains. Additionally, the terrain immediately surrounding Shamanka and Lokomotiv is "occupied by extensive stretches of rolling hills" which reach heights of 1,000-1,100 meters (Weber, 2003, p.53). Around Ust-Ida, the landscape becomes flatter (hills 400-600 meters high). Several bioarchaeological studies have linked the traversal of mountainous terrain to increases in AP reinforcement of the lower limb (Ruff, 1999; Marchi et al., 2006; Ruff et al., 2006b). Thus, in addition to higher mobility, traversal of more rugged terrain may have contributed to the anteroposterior expansion of EN juveniles' lower limb diaphyses, particularly in Shamanka populations. However, it is unclear if Shamanka groups included the Sayany mountain area in their foraging round or if juveniles would have commonly accompanied adults into this area. Furthermore, the variation in topographical relief may not be large enough to explain the more circular lower limbs of Ust-Ida individuals. 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 traversed may well have been larger than those between Ust-Ida, Lokomotiv, and Shamanka, especially if Shamanka individuals did not habitually forage in the Sayany mountains. Pastoralism also involves the travel of considerable distances, so behavior may still account for differences detected in these studies. Consequently, it is more parsimonious to assume that differences in limb shape between Cis-Baikal juveniles from different cemeteries primarily reflect variation in distance traveled rather than differences in terrain traversed.

The comparison of the lower limb in individuals of indeterminate sex younger than 16 years underscores the complexity of reconstructing mobility using CSG. However, these

variables differ most in locations expected to reflect differences in mechanical loading. Considering the mobility of juveniles as related to either group mobility or the mobility of adults caring for children produces some important insights. Chronological change in limb shape indicates EN groups may have utilized a larger foraging range, possibly due to the depletion of terrestrial game close to areas of seasonal aggregation. Alternatively, terrestrial game may have been less plentiful or more patchily distributed around the Cis-Baikal in the EN than in the LN. LN juveniles had more robust lower limbs and higher interlimb indices. Given the limitation in size-standardization, greater body mass in the LN may account for elevated lower limb CSG and interlimb robusticity in this period. Comparison of individuals from different cemeteries revealed the most marked distinctions between Shamanka and Ust-Ida. The failure to detect differences between Ust-Ida and Lokomotiv may simply be an artifact of small sample size. Alternatively, the uniqueness of Shamanka may reflect its location, or substantial variation in mobility among groups utilizing this cemetery.

#### 9.5.2 The Upper Limb: Individuals Aged 0-16 Years Old

The following discussion first considers the significance of LN individuals appearing more robust at the clavicle and ulna but not the humeral sections, where EN individuals produce an equivalent range of standardized residuals. As in the examination of the lower limb, the potentially higher body mass of the LN sample must be considered. Consequently, EN individuals may have had slightly more robust humeri than LN juveniles younger than 16 years, and differentiation in endosteal measures at the humerus midshaft supports this possibility. This result indicates EN juveniles placed higher loads on their upper limb than LN juveniles. A greater reliance on fish in the EN may have favored the greater involvement of juveniles in fishing. Despite this potential difference in workloads, it remains unclear if juveniles from different archaeological periods devoted different amounts of time to different activities. The complicated nature of upper limb loadings raises the issue of equifinality. Either EN and LN juveniles practiced similar types of behavior, or different behaviors may load the upper limb in a similar way.

## 9.5.2.1 Upper Limb Area and SMAs

As in the lower limb, the possibility that size-standardization does not completely control for the effects of body mass differences complicates interpretations. Still, critical comparison of patterning at different cross-section locations allows identification of some potential differences in load levels. LN individuals produce higher ranges of clavicle and ulna midshaft robusticity, which may represent residual body mass effects (Figures 5.3.1-5.3.2). However, the same difference does not exist at the humerus midshaft and distal sections, where the EN and LN samples demonstrate an equivalent range of values for TA, CA, and J (Figures 5.3.1-5.3.3). The tendency for LN ulnae to be more robust does reach statistical significance (Tables 5.6, 5.7-5.9). However, this may be an artifact of sample size, because the LN sample was one-third smaller for this comparison. Indeed, comparison by cemetery highlights that this significant difference between archaeological periods is primarily driven by differences between Lokomotiv and Ust-Ida, where Lokomotiv average n=4. Thus, it is not clear if differences in ulnar robusticity reflect actual differences in mechanical loading, or if they are artifacts of small sample size.

It is unlikely that LN clavicle and ulna size-standardized robusticity reflects adaptation to greater behaviorally induced loading. The humerus, which should provide the best record of functional adaptation, does not show the same differentiation. Stock's (2006) study of correlations between activity levels and CSG found that humerus and ulna size-standardized CSG showed equally strong correlations with inferred loading levels, while the correlation for the clavicle was markedly lower. However, both the clavicle and ulna showed more idiosyncratic variation unrelated to activity levels than the humerus. For this reason, "the humeral diaphysis may represent the most straightforward relationship between mechanical loading and morphology" (Stock, 2006, p. 201). The analysis of changes in side dominance during growth discussed in Chapter 8 offer further support for this hypothesis. The humerus exhibits a marked right-side dominance much earlier in development than the clavicle or ulna. Thus, either the humerus is more sensitive to differences in loading, or the most intensive loadings of the limb predominantly affect the upper arm. Critically accounting for the possibility that sizestandardization did not completely remove the effects of body mass produces additional insights into potential chronological change in juvenile upper limb loading. If one corrected the EN sample for potentially unaccounted differences in body mass, the EN humerus would be more robust.

Significantly smaller medullary cavities and higher percent CA at the humerus midshaft further support higher upper limb loading during growth among EN juveniles (Figures 5.3.4 and 5.3.5; Table 5.6). It has been hypothesized that increased loading prior to puberty primarily

stimulates greater periosteal apposition, and, to a lesser extent, reductions in endosteal resorption (Ruff et al., 1994; Pearson and Lieberman, 2004). During puberty, the sensitivity of the periosteal envelope to loading gradually decreases, and the endosteum switches from a state of net bone resorption to bone formation. Consequently, after puberty, greater loading results in endosteal deposition, though periosteal apposition also occurs into the third decade of life, particularly among males (Orwoll, 2003; Neu et al., 2001; Gabel et al., 2015). As the differences between Cis-Baikal groups are apparent after the age of five years, one cannot attribute reduced EN medullary area solely to greater endosteal deposition in adolescence (Figure 5.3.12). While deposition in adolescence may play a role, EN individuals must also exhibit a slower rate of endosteal resorption prior to puberty.

In isolation, a tendency towards medullary stenosis in the EN would represent an inefficient adaptation to greater loading. Conserving bone on the endosteal surface provides less increase in strength than deposition of new bone on the periosteal surface (Ruff et al., 1994; Pearson and Lieberman, 2004). However, accounting for potential body mass related patterning could potentially remove this discrepancy. Homogeneity in humerus TA, CA, and SMAs possibly results from greater upper limb loading in the EN compensating for greater body mass induced loads in the LN. In turn, lower MA and higher %CA in the EN reflects reductions in the rate of endosteal resorption due to higher loading among the EN group. Importantly, MA shows a lower correlation to body mass than other area measures (TA  $R^2$ = 0.86-0.9, MA  $R^2$ = 0.28-0.47) and %CA is a size free ratio (Table 5.1). Therefore, it is reasonable to suggest that, because these variables show less correlation with body mass, limitations in juvenile body mass estimation have a smaller effect on group comparisons than was the case for TA, CA, and SMAs.

Somewhat higher upper limb robusticity in EN juveniles would concord with the sole previous study of upper limb strength in adults, which concluded that EN populations had more robust upper limbs than LN/EBA populations (Stock et al., 2010). Importantly, the available evidence also suggests that EN juveniles appear to have placed higher loads on their upper limb than their lower limb. Except for the femur subtrochanteric section, EN and LN juveniles only show parity in size-standardized CSG at the humerus. Also, EN individuals show more marked endosteal differentiation from LN individuals in the upper limb than the lower limb. Tibia midshaft MA is also slightly smaller in the EN sample (Figure 5.2.4), but only at the 10% alpha

level (p=0.067). Lower limb %CA also does not differ significantly between archaeological periods (Table 5.6). The lower interlimb robusticity ratios of EN individuals would further support relatively higher loading of the upper limb, but, as discussed above, this difference may also reflect higher body mass in the LN.

Ethnographic analogy provides some basic guidelines for interpreting possibly higher upper limb loading in the EN. Certain resources in the Cis-Baikal region would have been especially suited for child foraging from an early age. A review of the behavioral ecology of child foraging indicates that, when juveniles forage, they focus on resources that require low skill and low strength to harvest (Bird and Bliege Bird, 2005; Bliege Bird and Bird, 2002; Guerven and Kaplan, 2006). Indeed, ethnographies, including those of high latitude groups in environments similar to that of the Cis-Baikal, show that children frequently harvest berries, mushrooms, small game, waterfowl, eggs, and, most importantly, fish (E. Smith, 1991; Weber et al., 2002; Hewlett and Lamb, 2005 and references therein; Katzenberg et al., 2012 and references therein). This is not to say that harvest of flora and small game entirely explains greater upper limb robusticity of EN juveniles, since such resources were only available for brief periods of the year. However, when present, these other foods may have been important supplements to the diet, and even the youngest foragers could have harvested them.

Given the known importance of fish to the Middle Holocene diet, it is more significant that ethnography highlights the ubiquity of fishing as a childhood activity among huntergatherers (Watanabe, 1972; Weber et al., 2002; Bock, 2005; Guerven and Kaplan, 2006; Weber and Bettinger, 2010; Weber et al., 2011; Losey and Nomokonova, 2017). Children acquire the physical and mental ability to fish early in life. By the age of five years, children have begun fishing from shore or simple watercraft, and they employ a combination of hook and line, baskets, and nets (Bock, 2005; Sugiyama and Chacon, 2005; Guerven and Kaplan, 2006). The riverbanks and lakeshore of the Cis-Baikal would have offered similar opportunities, and similar technology would have been available (Losey et al., 2008, 2012). Additionally, children may have harvested and processed fish from traps and weirs (Watanabe, 1972; Turov, 2010; Losey et al., 2012). These ethnographic descriptions highlight the biomechanical relevance of fishing as a potential explanation for differences in upper limb loading. Use of fishing gear would have required repetitive and intense upper limb loading. In addition, other related activities such as boring holes for ice fishing, transporting the catch back to campsites, and processing of the fish would have further engendered considerable upper limb loading.

Ethnographies rarely address the specific amount of time devoted to fishing by foragers of different ages, though they do note that engagement in this activity increases with age (Smith E., 1991; Bock, 2005; Guerven and Kaplan, 2006; Turov, 2010). Ethnographies of high latitude and boreal forest foragers make passing references to the engagement of whole family units or bands in this task, especially during parts of the year that fish are abundant (Watanabe, 1972; Turov, 2010). Furthermore, Turov (2010) notes that, in the boreal forest, ice fishing was performed by the elderly, who were considered too weak to forage for game or other resources far from camp. For the same reasons, children may also have been involved in this activity. While such fishing provides low yields, it may prove particularly beneficial in winter months, when other resources are scarce (Losey et al., 2012). Juvenile fishing would also benefit adults seeking to maximize foraging yields, because it would allow juveniles to partly provision themselves or contribute to overall group yields (Hawkes et al., 1995; Bock, 2005). Thus, given the substantial benefits and low constraints, one would expect all juveniles growing up in the Cis-Baikal to devote considerable time to fishing, and this behavior would generate significant upper limb loads.

In addition, juveniles would have been involved in domestic tasks such as carrying loads, manufacturing, and processing food harvested by adults. This further highlights the potential importance of children as a potential labor pool capable of boosting the productivity of their adult kin. Additionally, childrens' involvement in domestic labor frees adults to devote more time to foraging or other activities (Hawkes et al., 1995; Bock, 2005; Henry et al., 2005).

Since stable isotope analysis indicates greater reliance on fishing in the EN, higher juvenile upper limb robusticity in this period is consistent with greater participation by EN juveniles in this activity (Weber et al., 2011; Weber et al., 2016a, 2016b). This concords with ethnographic evidence, and increased reliance on aquatic resources in the EN would have been a powerful motivation for adults to recruit children to fill "the specific labor needs of the household" (Bock, 2005, p. 114). The time devoted to fishing in the Angara and South Baikal microregions may have peaked during seasonal runs when "larger than average numbers of people could have been involved, and food production in excess of immediate needs was a good

possibility" (Losey et al., 2012, p. 140). While the time devoted may have fluctuated seasonally, it would benefit children to fish during all periods of the year. Maximizing fishing yields would have helped offset seasonal shortages of food, which studies of growth stress suggest were more severe or frequent in the EN (Lieverse et al, 2007; Waters-Rist, 2011; Waters-Rist et al., 2011; Temple et al., 2014). Alternatively, EN children may have been more involved in some aspects of domestic work, *e.g.* processing game, manufacturing tools and clothing. However, the latter is less likely for reasons discussed below.

#### 9.5.2.2 Upper Limb Shape and Asymmetry

The discussion of area and SMA measures indicates a possible decrease in the magnitude of upper limb loadings from the EN to the LN, though interpretations are complicated by uncertainties about differences in body mass. Conversely, comparisons of upper limb shape and asymmetry did not demonstrate chronological change in the way that loads were distributed within cross-sections or between limbs in indeterminate sex individuals younger than 16 years of age. Homogeneity in these variables is consistent with a generally similar behavioral repertoire. Individuals practiced the same types of behavior and used similar tools. Whether they devoted different proportions of their time to specific tasks remains unclear.

No clear differences were detected in shape or asymmetry. Only a weak differentiation in upper limb I<sub>x</sub>/I<sub>y</sub> was detected in the left arm, but this only reached significance at the ulna midshaft (Table 6.8). Furthermore, the same variables did not differ significantly in cemetery comparisons (Table 6.9). More importantly, I<sub>x</sub>/I<sub>y</sub> does not show consistent patterning between sections. EN individuals produce a slightly lower range for humerus sections but a higher one for the ulna midshaft (Figure 6.3.1). This emphasizes the weakness of the trends, and it remains unclear why the difference would appear most pronounced in the generally non-dominant limb. The detection of statistical significance in isolated variables may simply arise due to random chance. When multiple comparisons are made, the odds that at least one will achieve significance increases (Rice, 1989; Moran, 2003). Furthermore, differences between individuals from different archaeological periods and cemeteries appeared greatest at birth. As discussed above, such patterning is more consistent with differences being attributable to genetic variation rather than differences in limb usage. Similarly, asymmetry in upper limb robusticity and shape does not differentiate EN and LN juveniles younger than 16 years old, aside from sporadic detection of significant differences at the clavicle and ulna (Tables 5.15, 5.16). As discussed above, the

humeral sections develop side dominance early in ontogeny, implying this element provides a better record of asymmetric loading related to activity. Therefore, differences caused by activity should affect humeral sections as much if not more so than other elements. It is likely that detection of some statistically significant differences in the clavicle and ulna simply reflects inherently greater idiosyncratic variation in the morphology of these elements. Thus, similarity in humeral shape and asymmetry implies the employment of similar tools and loading of the arm in a comparable manner.

Homogeneity in shape and asymmetry is somewhat unexpected, given evidence for temporal change from greater dependence on aquatic resources in the EN to relatively greater dependence on ungulates during the LN, at least in the Angara River Valley (Weber and Bettinger, 2010; Weber et al., 2011). The transition in subsistence practices heightens the possibility that children would have behaved somewhat differently in the different archaeological periods (Weber et al., 2011). For example, using ethnographic survey data, Waguespack (2005) has shown that, as the amount of large game in the diet of hunter-gatherer groups increases, men spend more time hunting. Conversely, women devote more time to non-hunting tasks including burden carrying, manufacturing, and processing. The increases in female labor are often specifically linked to carrying supplies, manufacturing, butchery, and "moving and establishing new residential camps" (Waguespack, 2005, p. 671). This compensates for the greater time males devote to hunting. Fleming (2013) pointed out that, for the same reason, greater involvement of other non-hunting segments of the population in domestic labor would also prove beneficial. As women (female relatives as well as mothers) also tend to be most involved in child care, the situation favors the recruitment of children to assist with labor.

Stable isotope analysis provides the only direct evidence that terrestrial game constituted a greater proportion of the diet in the LN relative to the EN (Weber et al., 2011). Evidence for this affecting the behavior of juveniles is limited, but interpretations of grave goods offer tentative support for this possibility. Fleming (2013) found that Ust-Ida juveniles were frequently buried with needle cases, while EN individuals from Shamanka and Lokomotiv were not. She interpreted this as a potential indication that the increased focus on ungulates "created a labor demand and necessitated the work of more humans, including subadult individuals" (Fleming, 2013, p.119). Thus, it is possible Ust-Ida juveniles were more involved in manufacturing tasks

such as hide processing and clothes making. Of course, links between burial accoutrements and behavior during life are not straightforward. The inclusion of a tool does not imply an individual spent a significant amount of time using it during life.

Given the potential difference in juveniles' economic roles, it proves necessary to ask why, despite the evidence for chronological change in subsistence practices and greater upper limb robusticity in the EN, do upper limb shape and asymmetry comparisons show no clear differentiation between EN and LN juveniles? First, upper limb shape and asymmetry may not serve as very good recorders of time spent performing different activities, capturing broad rather than fine differences. Unlike the lower limb, the upper limb adapts to a much more complex mechanical environment. The range of motion is higher and less predictable. Also, different activities may engender similar levels of asymmetry and bending about the same axes. Thus, the potential equifinality of bone functional adaptation problematizes efforts to ascertain if individuals practiced different behaviors based solely on upper limb biomechanics. The problem of equifinality is attenuated by the fact that the chronological change discussed involves children devoting different proportions of their time to fishing and domestic labor, rather than the exclusion of one in favor of the other. It may not be possible to detect fine differences in time allocation, especially if different activities engender similar levels of asymmetry and loading about the same axes. Furthermore, it remains unclear exactly what percentage of the diet fish and terrestrial game constituted in any archaeological period, or how much this changed from the EN to the LN. Both resources remained important throughout the Middle Holocene. Indeed, the need to obtain access to terrestrial game has been postulated as a reason for greater mobility in the EN (Lieverse et al., 2011; Stock and Macintosh, 2016; this dissertation). Waguespack (2005) notes that female behavior only changes when the percentage of large game in the diet changes markedly. For that reason, small scale changes in dependence on terrestrial game may not lead to a dramatic alteration in juvenile behavior.

Lastly, inability to estimate sex may also confound behavioral reconstruction prior to late adolescence, when physical maturation allows sex estimation. Ethnographic studies have shown that girls are more involved than boys in domestic tasks, and sexual disparity in behavior increases with age (Henry et al., 2005; Sugiyama and Chacon, 2005; Tucker and Young, 2005; Guerven and Kaplan, 2006). The discussion of sexual dimorphism in older adolescents and young adults below will consider this possibility in greater detail.

## 9.5.2.3: Inter-Cemetery Variation

Shamanka exhibits significantly smaller medullary area and higher %CA compared to Ust-Ida (Tables 5.7-5.9). Lokomotiv does not show significant differences from the other two groups for these variables, though, as in the lower limb, visual analysis of boxplots indicate that Lokomotiv shows a similar range of values to Shamanka (Figures 5.3.10, 5.3.11). Again, the detection of statistical significance in comparisons of Shamanka but not Lokomotiv to Ust-Ida may reflect sample size. The Lokomotiv sample is approximately half as large as the Shamanka and Ust-Ida samples, which reduces statistical power.

The similarity of Shamanka and Lokomotiv juveniles follows from the geographic proximity and overlap in isotopic values, indicating foraging in an overlapping area (Weber et al., 2011). However, if the greater %CA and smaller MA of juvenile EN foragers reflects a greater behaviorally induced loading of the upper limb, it is somewhat surprising that Shamanka juveniles showed the greatest differentiation from LN Ust-Ida individuals. Given the presence of multiple large EN cemeteries in the Angara River Valley and the abundance of fish in the eponymous river and its tributaries, one would expect population pressure to favor a greater economic role for Lokomotiv juveniles (Weber and Bettinger, 2010; Losey et al., 2012). Depression of terrestrial game through hunting pressure would lead to a greater focus on aquatic resources. If not an artifact of sample size, the greater differentiation of Shamanka than Lokomotiv from Ust-Ida may most directly stem from the incorporation of the lakeshore as well as the nearby rivers into the foraging rounds of the groups interring their dead at Shamanka. However, the exact way in which this would affect the harvest of aquatic resources remains unclear.

As also discussed in the previous section, greater differentiation of Shamanka than Lokomotiv individuals from the Ust-Ida group may further reflect behavioral diversity at Shamanka. As both Lokomotiv and Ust-Ida foragers foraged in a riverine habitat, there may be slightly less differentiation between them, though a chronological change in both upper limb loading and terrestrial mobility appears to have occurred. In contrast, Shamanka individuals appear heterogeneous in terms of dietary signatures, suggesting distinct groups (family units or bands) using this cemetery exploited several distinct regions (Weber et al., 2016b). If foraging in different localities correlates with more behavioral diversity, this could explain why Shamanka is more differentiated than Lokomotiv from Ust-Ida.

A critical analysis of the potential effects of body mass on TA, CA, and SMAs suggest functional adaptation to higher upper limb loading in the EN. The smaller medullary area and higher %CA of EN individuals support this interpretation. Greater EN humeral robusticity potentially arises due to a greater involvement of EN children in fishing or domestic labor. This differentiation from LN juveniles appears particularly pronounced for the Shamanka juveniles, who differ significantly from Ust-Ida. Since the smaller Lokomotiv sample also shows lower medullary areas and higher %CA than Ust-Ida, the detection of statistical significance only for the Shamanka to Ust-Ida comparison may arise due to small Lokomotiv sample size. Alternatively, lakeshore foraging or greater behavioral diversity explain the greater differentiation of Shamanka than Lokomotiv from Ust-Ida. There is no clear difference in shape or asymmetry between birth the age of 16 years, which may indicate homogeneity in the types of behavior practiced by juveniles. However, this conclusion remains tentative. Differences in these variables may only appear when there are large differences in behavior. Furthermore, the fact that different behavior types may engender similar mechanical strains also raises the issue of equifinality.

# 9.5.3 Behavioral Differentiation During Adolescence and Young Adulthood (Individuals older than 16 years)

Older adolescents and young adults, for whom skeletal morphology was developed enough for sex estimation, constitute an important analytic target. Consideration of this subset of individuals allows examination of sexual differences in CSG established by the end of ontogeny. This section explores the adolescent transition to adulthood from a biomechanical perspective, making interpretations with reference to ethnography and behavioral ecology. Limitations of the small adolescent/young adult sample necessitate that attention focus less on statistical significance than on patterns suggested by visual inspection of the data. The general goal is assessing if patterning previously detected in studies of Middle Holocene Cis-Baikal adults emerges by the end of adolescence (Stock et al., 2010; Lieverse et al., 2011; Stock and Macintosh, 2016). This requires consideration of two distinct issues. First, do individuals exhibit sexual dimorphism consistent with past studies of adults? Second, is chronological change characteristic of adults seen in the adolescents and young adults? In general, the results indicate sexual dimorphism has emerged in both robusticity and limb shape, but chronological change in robusticity characteristic of adults is only evident for female comparisons.

Prior to behavioral interpretation, one must consider the limitations of this specific data set. Sample size and composition present the largest obstacle to comparisons, and the limitations arising from these factors must attenuate interpretations. Sex estimates could be attained for only a small number of adolescents and young adults with CSG data, raising the possibility that patterning detected reflects artifacts of small sample size. This limitation would especially have affected female comparisons, since the sample includes only two LN/EBA females. The sample composition also differs somewhat from that of the juvenile sample. The sample of indeterminate sex juveniles younger than 16 years, was composed of EN and LN individuals. The adolescent/ young adult sample of known sex also contains EBA individuals, three EBA males from Shamanka and one EBA female from Ust-Ida. As discussed in Chapter 8, this raises a methodological issue, since behavioral variation between LN and EBA samples may have been obscured. These samples were pooled, because the main goal of this section is a comparison to prior studies, which also combined LN and EBA samples (Stock et al., 2010; Lieverse et al., 2011; Stock and Macintosh, 2016). Otherwise, it would be difficult to tell if patterns are characteristic of adults have been established by the end of development. As discussed in Chapter 8, using only LN adults would raise the possibility that exclusion of EBA individuals leads to a failure to detect patterns seen in previous studies.

#### 9.5.3.1 Sexual Dimorphism

Examination of older adolescents and young adults grouped by sex estimate showed sexual dimorphism in size-standardized limb robusticity and limb shape in both the EN and LN/EBA samples. In general, the sexual dimorphism detected concords with prior studies of mature individuals (Stock et al., 2010; Lieverse et al., 2011; Stock and Macintosh. 2016). Like the current study, prior studies of adults showed that females produced lower values of size-standardized robusticity in both limbs and more circular lower limbs than males from the same archaeological period. The detection of dimorphism in humeral shape is an entirely novel finding, and it suggests important differentiation in habitual behavior between the sexes.

Two possibilities account for males exhibiting higher TA and SMAs by the end of adolescence (Figures 5.2.15, 5.2.16, 5.3.14, 5.3.15). First, as discussed above, high levels of testosterone heighten the sensitivity of the male periosteal surface to mechanical loading. Testosterone also prolongs the period during which the periosteal surface exhibits a "juvenile like" response to loading. Females exhibit an earlier reduction in periosteal sensitivity and an earlier transition to endosteal deposition (Ruff et al., 1994; Neu et al., 2001; Wang et al., 2005; Gabel et al., 2015). For these reasons, males will exhibit higher size-standardized CSG, even if activity levels did not differ.

If hormonal differences do not completely account for dimorphism in robusticity, then the results indicate that males practiced more physically demanding foraging behaviors than females in both archaeological periods. In that context, it is particularly notable that sexual dimorphism in TA and SMAs appears more pronounced in the LN/EBA sample of adolescents and young adults (Figures 5.2.15, 5.2.16, 5.3.14, 5.3.15). While small sample size could explain this difference (LN/EBA female n=2), prior studies of adults also detected greater sexual dimorphism in the LN/EBA (Stock et al., 2010; Lieverse et al., 2011; Stock and Macintosh, 2015). Interlimb robusticity ratios provide further evidence that levels of dimorphism in robusticity change from the EN to the LN/EBA. As in past studies of all adults, LN/EBA female adolescents/young adults produce higher values for femur/humerus ratios than all other groups (Lieverse et al., 2011; Figure 7.2.10). This result suggests that during adolescence, LN/EBA males engaged in activities that placed markedly higher loads on their upper limbs than females. The same differentiation was not seen in the EN.

Assessment of sexual dimorphism in limb shape does not have to contend with hormonal differences, since ratios assess the relative magnitude of bending loads about different axes within the same bone. In the lower limb, sexual dimorphism is apparent for  $I_x/I_y$  and  $I_{max}/I_{min}$  at the femur midshaft in both EN and LN/EBA samples by the end of adolescence (Figures 6.2.6, 6.2.7). At the two tibia sections, EN individuals show patterning consistent with sexual dimorphism, but LN/EBA males only produce a clearly higher range than females for  $I_{max}/I_{min}$ . Overall these findings are concordant with males in both periods traveling greater distances than females in adolescence and young adulthood. The discrepancy in LN/EBA femur and tibia shape dimorphism may reflect the fact that femur midshaft shape has been shown to exhibit greater

sensitivity to differences in mobility levels (Stock, 2006). Especially when sample sizes are small, this section would therefore be more likely to capture mobility differences. In general, the adolescent/young adult sexual dimorphism in lower limb shape concurs with prior studies of adults, which detected dimorphism in shape for both EN and LN/EBA individuals at the femur and tibia midshaft (Stock et al., 2010; Lieverse et al., 2011; Stock and Macintosh, 2016). Thus, sexual differences in mobility characteristic of adults appear to have been established by the end of adolescence in both the EN and LN/EBA.

As no previous study has considered upper limb shape, the finding that females have more anteroposteriorly reinforced and less circular humeri in both the EN and LN/EBA provides new evidence for the sexual division of labor during the Middle Holocene (Figures 6.3.7, 6.3.8). The shape difference exists in both the EN and LN/EBA groups, indicating that similar sexual differentiation in upper limb loading was present throughout the Middle Holocene. Recall that more circular diaphyses indicate resistance to nearly equivalent bending loads about multiple axes or torsion. Conversely, more unevenly reinforced diaphyses reflect adaptation to bending predominantly about a single axis. The more anteroposteriorly reinforced humeral midshaft and distal sections of females implicates repetitive unidirectional loading, most likely produced through flexion and extensions of the upper limb. Conversely, the more circular humerus of males could indicate either less repetitive application of loads about specific axes or adaptation to torsional loads. As discussed in Chapter 8, the detection of differentiation in the humerus may reflect the mechanical action of major flexors and extensors upon this element. The action of these muscles drives a general trend towards decreased circularity of the humerus during growth, especially towards the distal end of the diaphysis. Comparisons of males and females here suggest that, due to behavioral differences, females exhibit especially unequal reinforcement with age due to their behavioral repertoire. A lack of differentiation in other upper limb elements also conforms to expectations established in Chapter 8. Based on earlier development of side dominance in the humerus, it was proposed that the humerus is either more sensitive to loading or powerful motions of the arm preferentially load the humerus. This concurs with prior studies of adults, which showed a closer correspondence between humeral robusticity and activity levels than shoulder girdle and forearm robusticity (Stock, 2006). Furthermore, regardless of how the upper limb is used, the clavicle will predominantly experience torsion or multiaxial bending. In

the forearm, loads are distributed across two elements, and this may further obscure differences between females and male loading regimens.

Overall, biomechanical differentiation throughout the skeleton indicates a behavioral divergence between the sexes during adolescence. Males placed higher loads on their skeletons, traveled farther distances, and practiced a different range of habitual manipulative behaviors than females. This suite of differences likely relates to males participating in big game hunting, which requires significant long-distance travel and substantial physical exertion. Indeed, prior biomechanical studies have suggested this behavior explains a substantial portion of dimorphism in CSG of Cis-Baikal adults (Stock et al., 2010; Lieverse et al., 2011; Stock and Macintosh, 2016). MacDonald's (2007) ethnographic survey of how individuals learn to hunt shows that boys only begin to regularly accompany older male relatives on hunting expeditions in adolescence. By this age, they have acquired the necessary physical and mental abilities to productively and safely begin training in this physically demanding activity.

The difference in humeral shape is also consistent with males training as hunters and females devoting more time to processing or manufacturing. Stock and Pfeiffer (2004) found a similar sexual difference in humeral shape among Later Stone Age South African hunter-gatherers. Based on archaeological evidence, they suggested that the use of throwing spears and bows stimulated adaptation to torsional loads in males. Females experienced greater anteroposterior loads due to the use of digging sticks, processing shellfish, and grinding seeds and ochre. Given the presence of identical technology, the same behavioral model can explain adaptation to torsional loading in Cis-Baikal males (Weber and Bettinger, 2010). Stock and Pfeiffer's (2004) explanation for AP reinforcement among Later Stone Age females indicates the importance of processing and manufacturing, but it requires adaptation to a boreal forest context. Provisionally, one can suggest hide scraping, butchery, and the processing of aquatic resources as habitual behaviors that would have generated a repetitive anteroposterior load. Ethnographic studies support this, showing northern hunter-gatherer females devote substantial time to such activities (Shaw et al., 2012 and references therein).

It remains unclear if the sexual differentiation detected emerged entirely in adolescence, or if began to emerge in childhood. The latter scenario is more likely. Ethnographic studies have shown that female children devote more time to processing and other domestic tasks throughout childhood (Guerven and Kaplan, 2004; Sugiyama and Chacon, 2005). Thus, if sex was known, some chronological differentiation might be visible prior to the age of 16 years. However, since adolescence represents a time of considerable change in physical and mental capabilities, the magnitude of sexual differentiation in behavior likely increased considerably in this period. For instance, males only begin to accompany adults on hunting expeditions in adolescence (Walker et al, 2002; Macdonald, 2007). This reflects the high physical and mental thresholds that must be surpassed before an individual can safely and effectively train in this behavior. Also, in adolescence, provisioning by adults decreases, so individuals devote more time and energy to provisioning themselves, and perhaps their own dependents, in gender appropriate ways (Bliege Bird and Bird, 2002).

## 9.5.3.2: Chronological Change

Previous studies of adults found LN/EBA males and females exhibited decreased robusticity and more circular lower limbs compared to their EN predecessors (Stock et al., 2010; Lieverse et al., 2011; Stock and Macintosh, 2015). In the smaller sample of adolescents and young adults considered here, a clear chronological decrease in limb robusticity and interlimb robusticity ratios is primarily evident in comparisons of females but not males (Figures 5.2.15, 5.2.16, 5.3.14, 5.3.15, 7.2.10). Lower limb shape does not show the chronological trend towards greater circularity in the LN/EBA characteristic of adults of either sex (Figures 6.2.6, 6.2.7). If results are not artifacts of small sample size, they would suggest that chronological change in robusticity emerges earlier in females than in males.

Small sample size may account for an inability to clearly detect some of the chronological differences between EN and LN/EBA adults seen in previous studies (Stock et al., 2010; Stock and Macintosh, 2016). This explanation seems especially likely for analysis of lower limb shape, as comparisons of individuals aged 0-16 years old already showed differences between archaeological periods. Indeed, while prior studies of adults did detect significant chronological differences in lower limb shape ratios, there was considerable overlap in ratio ( $I_x/I_y$  and  $I_{max}/I_{min}$ ) ranges between individuals of the same sex from different archaeological periods (Stock and Macintosh, 2015). Consequently, limiting the sampling range to adolescents and young adults may have resulted in the selection of individuals that do not represent the true magnitude of chronological differentiation in some variables, especially lower limb shape.

Importantly, female comparisons of size-standardized TA and SMAs show clearer evidence of chronological reductions in size-standardized limb robusticity than male comparisons (Figures 5.2.15, 5.2.16, 5.3.14, 5.3.15). Despite the limitations of small sample size, the clearer evidence for chronological change in TA and SMAs among females than males has some potentially important implications. It supports prior hypotheses, made based on both CSG and muscle markers, that female workloads changed more from the EN to the LN/EBA than male workloads (Lieverse et al., 2011; Stock and Macintosh, 2016). Thus, even small sample sizes can detect such differentiation. Male behavior appears to have changed less markedly between the EN and LN/EBA, probably due to the involvement of males from both archaeological periods in ungulate hunting (Stock and Macintosh, 2016).

Furthermore, as in prior studies, the ratio of femur to humerus robusticity is highest in LN/EBA female adolescents and young adults (Lieverse et al., 2011; Figure 7.2.10). This indicates chronological decreases in female upper limb loading were larger than decreases in lower limb loading. Unlike previous studies, the current study also evaluated the tibia/humerus ratios. Problematically, LN/EBA adolescent and young adult females do not show the same elevated values when the tibia represents the lower limb. This complicates interpretations, because several studies have hypothesized that tibial robusticity shows higher correlations with activity related loading than femoral robusticity (Stock, 2006; Davies and Stock, 2014; Shaw et al., 2014). Thus, relative differences in upper to lower limb loading related to activity should be more evident for this variable. Due to this discordance between variables, it remains unclear if chronological decreases in female robusticity were truly more pronounced in the upper limb. Evaluating the issue will require further examination of a larger adult sample.

From an ontogenetic perspective, the greater chronological differentiation of female robusticity, in both the current study and prior examinations of adults, suggests females assume adult behavioral repertories earlier than males. Females mature faster, entering puberty before males. As sexual maturation often correlates with a transition to adult roles and status, it may be the case that a behavioral shift to fully adult modes of behavior occurs during this developmental period or shortly thereafter (Henry et al., 2005; Sugiyama and Chacon, 2005; Guerven and Kaplan, 2006). This is not to simplify the complexity of age related changes in social status and behavioral repertoire. While adolescence certainly constitutes an important period of interlinked changes in physiology, behavior, and social status, gender specific behaviors are also learned prior to and after this period (Derevenski, 2000; Joyce, 2000; Stoodley et al., 2000). However, ethnographic study does show that female children devote more time to processing, childcare, and other domestic labor throughout childhood than males, and this disparity increases with age (Guerven and Kaplan, 2006; Sugiyama and Chacon, 2005). Beginning in adolescence, reproduction may have also affected female behavior. Mothers may have altered their foraging strategies and workloads to provide both food and care for their children. The CSG patterning seen in Middle Holocene samples is also consistent with an earlier adoption of adult roles by females.

While the available evidence supports the emergence of chronological differences in female behavior by young adulthood, it remains unclear if the same was true of males. As discussed, small sample size could entirely account for homogeneity in male samples. The fact that chronological changes in male behavior were likely smaller than female changes reinforces this point (Lieverse et al., 2011; Stock and Macintosh, 2016). Detection of small differences may simply require larger sample sizes. Alternatively, a lack of clear differentiation in male robusticity may relate to the later onset of puberty and the nature of adult male foraging behavior. Males become sexually mature later than females, so the transition to adult roles may occur somewhat later. As a result, these differences may not have been fully established by the age of 25 years, the upper age limit of the current sample. Additionally, learning to hunt requires substantial long-term training, and initially failure rates are high. Peak hunting success is achieved in middle adulthood, around the age of 35 years (Walker et al., 2002; Guerven and Kaplan, 2006). Due to the high failure rate of hunting, adolescent males in hunter-gatherer groups have been observed devoting more time to fishing or other types of foraging that require less skill than older males (Walker et al., 2002; Sugiyama and Chacon, 2005). In this context, it is worth noting that the ethnography of boreal forest Evenki shows that adolescent/ young men invest considerable time in fishing (Turov, 2010). Indeed, fishing seems to serve as an additional form of hunting training, since group members correlate success in spear fishing with hunting ability. This example is not meant as a direct analogue for the behavior of Middle Holocene adolescents and young adults. Rather it highlights that considerable behavioral change occurred beyond adolescence. Although male individuals likely invested considerable time in learning

"adult" behaviors, they may have also continued to invest more time in other activities than older more experienced adults.

Consequently, it remains unclear if chronological differences in adult male behavior were established by young adulthood. Ethnographic studies provide compelling evidence that, at least in terms of hunting, adolescent males do not behave in the same way as older males. Thus, while small sample size may obscure incipient differences between archaeological periods, differences in CSG between EN and LN/EBA males may only become fully established after young adulthood. In that context, it is important that bone loses its heightened "juvenile-like" response to loading gradually after adolescence (Neu et al., 2001; Kontulainen et al., 2005; Ruff et al., 2006a; Gabel et al., 2015). For this reason, continued changes in male behavior after adolescence/young adulthood could lead to the emergence of clearer chronological differentiation in CSG later in life.

Lastly, humerus shape also shows tentative evidence of change between archaeological periods. LN/EBA females and males display more ovoid humerus midshaft sections compared to EN individuals of the same sex, and several comparisons of  $I_x/I_y$  and  $I_{max}/I_{min}$  are significant at the 10% alpha level (p<0.1) (Figures 6.3.7, 6.3.8; Table 6.10). However only the humerus midshaft  $I_{max}/I_{min}$  comparison for males reaches statistical significance at p<0.05. Given the evidence for greater consumption of ungulates in the LN/EBA than the EN, differentiation in upper limb use is not entirely surprising (Weber et al., 2011). Harvesting more ungulates may entail greater devotion of time to processing hides and butchery in the LN/EBA. However, comparisons reach statistical significance in only one variable among males. As one comparison among many can reach significance by chance, it remains unclear how much upper limb shape truly changed between the EN and LN/EBA. Chronological differentiation in adult upper limb shape, a heretofore unexamined issue, requires further study with larger sample sizes to confirm these tentative results.

In sum, the analysis of adolescents and young adults in which sex could be assessed shows strong evidence for sexual dimorphism throughout the Middle Holocene, but the evidence for chronological change in CSG is less convincing. Sexual dimorphism in area and SMA measures may partly reflect the differential effect of sex hormones on the periosteum and endosteum during adolescence. However, the extent to which hormonal differences rather than sexual disparity in workloads accounts for higher size-standardized male robusticity remains unclear. Limb shape, over which hormonal differences should have no influence, also shows sexual dimorphism. Males have more anteroposteriorly reinforced lower limbs and more circular upper limbs than females. Differences in limb robusticity and shape indicate sexual divergence in behaviors. In adolescence, males have likely begun training as hunters, which involves travel over greater distances and adaptation of the upper limb to torsional loading. At the same time, female adolescents and young adults may have devoted more time to localized foraging and fishing, as well as domestic labor. This may well have involved an upper limb loading regimen distinct from that of males.

While sexual differences in CSG are evident by the end of adolescence, the evidence for reductions between the EN and LN/EBA detected in previous studies is not as strong. There is a strong possibility that certain variables do not show patterns characteristic of adults due to small sample size. Despite this limitation, females show stronger evidence of chronological decreases in limb loading than males. The result suggests greater chronological change in female behavior and that females assume adult roles earlier than males. The lack of clear chronological differentiation between males has two explanations. First, small samples may lack the power to detect behavioral differences smaller than those seen in females. Second, males may not have fully assumed a fully adult behavioral repertoire by young adulthood. Ethnographic observations confirm that adolescent males train intensively as hunters, but, due to inexperience, they devote more time to other types of foraging than more experienced older males. Lastly, upper limb shape also shows tentative evidence of chronological change in both males and females. This difference may reflect a greater focus on the hunting and processing of ungulates in the LN/EBA, but larger sample sizes are required to confirm the result.

## 9.5.4: Summary of Behavioral Interpretations

Bioarchaeological interpretation of bone robusticity and shape show that studying how the skeleton accrues bony tissue contributes to understanding of variation in genetics, health, and behavior. This study does not find a strong link between bone robusticity, shape, and previously documented genetic differences among Cis-Baikal populations. Differences in body mass arise early in development, which may reflect decrease in developmental stress levels from the EN to the LN. Although uncertainties in body mass estimation complicate behavioral interpretations, the results support differences in juvenile behavior prior to the age of 16 years. EN juveniles appear to have traveled greater distances than LN juveniles, and they placed higher loads on their upper limb. This differentiation in juvenile behavior likely stems from chronological change in population density, foraging strategies, and resource distribution. EN groups may have habitually traveled greater distances than LN groups due to depletion of local terrestrial resources. EN juveniles may also have been more involved in fishing than LN individuals.

Although subdividing the sample of individuals younger than 16 years of age by cemetery reduces sample size, treating the data in this way offers potential insight into intercemetery heterogeneity in health and behavior during the EN. Lokomotiv individuals may have experienced greater developmental stress than EN Shamanka individuals. Shamanka individuals exhibit a unique range of postcranial robusticity and lower limb shape, and, with regards to these variables, they differ more from Ust-Ida individuals than Lokomotiv juveniles. This may reflect differences in foraging strategies due to the incorporation of lakeshore foraging into the behavioral repertoire of some groups that buried their dead at Shamanka. At the same time, one must not overstate the magnitude of differentiation detected, since environmental constraints likely exerted a strong homogenizing pressure on health and behavior. Thus, it is unsurprising that comparisons of individuals from different archaeological periods and cemeteries showed heavy overlap in the range of biomechanical properties throughout development.

Lastly, the analysis draws attention to adolescence as a time of transition. During this period, sexual differences in workloads are present, indicating females and males assume distinct behavioral repertoires. However, it remains unclear if chronological differences in robusticity and behavior characteristic of adults have been fully established. Comparisons of females from different archaeological periods show clearer differentiation than comparisons of males. If not an artifact of sample size, this finding may reflect the earlier assumption of adult roles by females.

# **Chapter 10: Conclusion**

This study addressed two large themes.

- As the ontogeny of biomechanical properties with age is still not fully understood, how does Cross-Sectional Geometry (CSG) change with age, and how does growth in body size and behavior shape the process of bone accrual?
- How does comparison of CSG ontogeny contribute to a better understanding of genetics, developmental stress, and juvenile behavior among Middle Holocene Cis-Baikal hunter-gatherer populations?

To conclude, this chapter summarizes new insights achieved by addressing these questions and identifies areas requiring further research.

# **10.1 General Developmental Patterns**

Overall, the analysis of how bony tissue accrues perpendicular to the long axis of diaphyses during growth in the Cis-Baikal sample supports the findings of prior studies (Ruff et al., 1994; Sumner and Andriacchi, 1996; Ruff 2003a,b; Cowgill, 2008; Goldman et al., 2009; Harrington, 2010; Gosman et al., 2013). The trajectory of bone accrual on the periosteal surface closely follows that of growth in body mass, emphasizing that one of the skeleton's primary function is to withstand the weight of the body during movement. Hormonal concentrations further modulate the rate at which bone accrues. An adolescent growth spurt in bone area and rigidity correlates with hormonally modulated increases in body size during puberty. The differential effects of sex hormones also contribute to the emergence of dimorphism in bone robusticity. As in prior studies, detection of rapid increase in bone robusticity during adolescence emphasizes that bone exhibits heightened sensitivity to loading during this phase of growth (Carter and Beaupre, 2001; Goldman et al., 2009; Tenforde and Fredricson, 2011; Gosman et al., 2013). Changes in interlimb robusticity ratios and increases in directional asymmetry in the upper limb with age further demonstrate changes due to functional adaptation during ontogeny.

It remains unclear how loading changes rates of endosteal resorption and deposition during growth. To some degree, medullary cavity size tracks periosteal size (Sparacello and Pearson, 2010). Loading levels may also have location specific effects on the endosteal surface. EN and LN Cis-Baikal juveniles exhibit some differentiation with regards to endosteal diameter at the humerus midshaft, indicating that load levels affect levels of endosteal resorption and deposition during growth. The extent to which endosteal dimensions track changes in mechanical loading remain incompletely understood. For instance, some studies, including the current investigation, have linked higher levels of loading to a reduced rate of endosteal resorption during growth (Bradney et al., 1998; Weatherholt and Warden, 2018). Other comparisons of active juveniles to controls have detected greater resorption in response to exercise (Ruff et al., 1994; Haapsalo et al., 2000; Bass et al., 2002). There is some indication that whether loading inhibits or stimulates endosteal resorption during growth depends on the type of loading experienced and the portion of the limb examined (Bradney et al., 1998; Haapsalo et al., 2000; Bass et al., 2002). Future clinical and anthropological studies can explore the issue in greater detail, especially if endosteal dimensions are measured throughout the diaphysis.

When during life the endosteum switches from a state of net resorption to a state of net deposition also remains unclear. While early studies suggested the change occurred in adolescence, newer investigations have suggested resorption continues at the endosteum into young adulthood (Frisancho et al., 1970; Garn, 1970; Neu et al., 2001; Gosman et al., 2013; Gabel et al., 2015). The Cis-Baikal data shows no evidence for endosteal deposition by the age of 16 years, though this may reflect an inability to differentiate females and males. Regardless, this finding is consistent with the prolongation of endosteal resorption into late adolescence.

Examination of ontogenetic trends further emphasized that the lower limb undergoes extensive adaptation to both bipedal locomotion and changes in body shape during growth. Interlimb robusticity ratios increase with age, reflecting the femur's greater involvement in weight bearing. The shape of the proximal femur exhibits a unique pattern of age related change, and increased mediolateral reinforcement of this section, particularly in adolescence, may well track increases in pelvic dimensions. Distal to this section the lower limb generally less circular and more reinforced in the antero-posterior plane during growth. Due to changes in carrying angle of the distal femur, the ontogenetic trajectory of femur midshaft shape differs from that of the tibia.

The consideration of upper limb shape and asymmetry ontogeny proves particularly important, as few previous studies have considered how shape and asymmetry develops throughout the upper limb (Harrington, 2010). Ontogenetic trends in shape change are weak.

This probably reflects that, due to the complexity of the mechanical environment, all sections experience substantial multi-axial bending and torsion. Differences in range of motion and the regional influence of different muscles and ligaments account for the detection of unique developmental patterns in several sections. The clavicle midshaft adapts to increased torsional or multi-axial bending with age, likely due to its function as a support strut. The distal humerus experiences greater AP bending with age due to the proximity of the elbow joint, and the ulna becomes more mediolaterally reinforced due to the developmental trajectories, with Cis-Baikal females exhibiting less circular and more AP reinforced humeri than males by the end of adolescence. Comparisons of directional asymmetry unexpectedly detected a later emergence of right arm dominance at the clavicle and ulna than in the humerus. High power motions of the dominant arm may preferentially load the upper limb segment. Further examinations of the development of shape ontogeny and side dominance in CSG using larger sample sizes and multiple populations are ongoing (Osipov and Harrington, 2017).

The comparison of Cis-Baikal individuals from different archaeological periods also has relevance to studies examining which regions of the skeleton provide the best record of differences in behavior. Chronological differences in lower limb shape reached statistical significance at the femur midshaft and tibia nutrient foramen section, whereas area and SMA measures differed significantly at the tibia nutrient foramen and tibia midshaft. These results are consistent with prior findings that loading environment shows the strongest correlation with limb shape at the femur midshaft and close to the knee joint (Ruff and Hayes, 1983a; Stock, 2006; Gosman et al., 2013). Conversely, tibia strength shows a closer correlation to load levels than femoral strength. The reasons for these patterns remain somewhat unclear. The relatively greater magnitude of torsion in the distal section of the tibia and load sharing with the fibula potentially complicates the relationship between tibia midshaft shape and strain distribution (Sparacello et al., 2014). The principle of tissue economy may account for closer linkages between load magnitudes and tibia robusticity than femur robusticity (Stock, 2006; Davies and Stock, 2014b). Although correspondence between upper limb CSG and activity has been explored less extensively, it has been hypothesized that humeral shape and strength show the closest correlation with activity levels (Stock, 2006). The results of this study concur with that hypothesis. Side dominance emerges earlier in humeral cross-sections than the clavicle and ulna,

implying that activity related differences in loading have a greater influence on this element. Furthermore, sexual differentiation in shape is only apparent in humeral sections. Further studies are needed to confirm these findings, particularly in adult samples, where shortcomings in juvenile body mass estimation do not complicate interpretations. Studies of juveniles should also explore additional approaches to account for allometric scaling in CSG.

Lastly, there is the potential to expand ontogenetic analyses of skeletal biomechanics beyond the examination of CSG. The study of bone microarchitecture encompasses both trabecular bone structure (e.g. volume, orientation, and density) as well as cortical bone microarchitecture (e.g. cortical bone porosity and density). Functional adaptation in bone microarchitecture is an emerging field of study, due to the growing availability of high resolution imaging modalities (e.g. HR-pQCT and micro-CT) and computers capable of processing these datasets. Recent analyses of micro-architectural properties demonstrate its potential to offer additional insight into workloads and developmental stress. Like CSG, micro-architectural properties appear to vary in relation to activity level and load orientation (Schilpilow et al., 2013; Wallace et al., 2013; Ryan and Shaw, 2015; Gabel et al., 2017). Examinations have found that femoral trabecular thickness differentiates hunter-gatherers from more sedentary agricultural populations, indicating that analysis of micro-architecture can discern differences in workloads and mobility levels (Ryan and Shaw, 2015). Trabecular organization and density, as well as cortical porosity also appear to vary in response to differences in nutrition (Agarwal, 2008; Schug and Goldman, 2014). However, it remains unclear how variation in behavior, developmental stress, and diet affects micro-architecture during development. Therefore, future explorations of growth in Cis-Baikal juveniles and other populations can consider the ontogeny of bone microarchitecture to expand on the study of CSG properties. Undertaking such research will improve understanding of how genetics, behavior, and developmental stress influence the biomechanical properties of long bones, enabling a more nuanced interpretation of variation in growth and behavior in the past.

## **10.2 Bioarchaeological Interpretations**

The following summary of bioarchaeological interpretations constructs a narrative of how Middle Holocene Cis-Baikal hunter-gatherer children grew and how they behaved from birth to young adulthood. Laying out the findings of bioarchaeological comparisons in this way provides an easy to follow summation of new insights into variation in Middle Holocene genetics, health, and behavior.

Despite changes in the mtDNA and Y-chromosome haplotypes of Middle Holocene populations from the EN to the LN, the effect of genetic differentiation on the development of postcranial strength and shape remains uncertain (Mooder et al., 2006; Mooder et al., 2010; Moussa et al., 2016). Inability to ascertain if EN and LN populations possessed genetically encoded differences in baseline robusticity or mechanosensitivity partly reflects a lack of certainty about which genes contribute to variation in CSG. Furthermore, the extent of gene flow between EN and LN populations remains unclear. Differences in size-standardized robusticity and shape do emerge early, around the age of five years. Since the sample contains relatively few individuals younger than this, one cannot totally exclude that some differences are present from birth. Even if they did, it would not explain why differences are maintained throughout the growth period, when mechanical influences should have a greater influence on skeletal development. Functional adaptation to load differences provides a more convincing explanation for differences in CSG properties. Also, comparisons of proximal femur morphology do not support a genetically encoded differentiation in body shape.

Stronger evidence exists for chronological change in levels of developmental stress. The analysis of body mass estimates and size-unstandardized CSG regressed on age is consistent with an increase in juvenile body mass from the EN to the LN. This concurs with prior studies of developmental stress, which hypothesized that EN individuals experienced more episodes of growth disruption, and this was associated with growth stunting. Differences in body mass for age between cemeteries were also investigated. Of the two EN cemeteries, Lokomotiv produces the lowest range for both body mass estimates from joint dimensions and size-unstandardized CSG. The lower range of body size indicates that individuals buried at this cemetery experienced more developmental stress than individuals buried at the contemporaneous Shamanka cemetery. However, the Lokomotiv sample is roughly half the size of the Shamanka sample. For that reason, one cannot discount the possibility that the greater differentiation of this cemetery from the LN Ust-Ida group is due to small sample size. If low body mass is not an artifact of sample size, population pressure on resources offers a potential explanation for higher developmental

stress at Lokomotiv than Shamanka. Like previous studies, the current examination also indicates differences in body mass emerged in early childhood.

Examination of ethnography and behavioral ecology provides a framework for the interpretation of behavior. Whether juveniles forage and how much they work depends on the environmental and social context. The characteristics of the local environment (*e.g.* temperature, terrain, types of resources available and their distribution) determine the physical and mental constraints facing juvenile foragers. Despite some evidence of chronological change in environment, EN and LN Cis-Baikal individuals would have learned to forage in a similar landscape and targeted similar resources. This would impose similar physical and mental constraints on behavior. Adults may also encourage child labor if it reduces the effort they must expend to provision their offspring.

Differences between groups attributable to behavior emerge after the age of five years. Again, the paucity of individuals representing the youngest part of the growth series makes it difficult to firmly ascertain the age at which differentiation occurs, but the chronological difference clearly emerges early in development. Analysis of shape avoids the uncertainties of body mass estimation in juveniles. Less circular and more anteroposteriorly expanded lower limbs suggest that EN juveniles began traveling greater distances than LN juveniles in childhood. Thus, the greater terrestrial mobility characteristic of EN adults emerged early in life. The mobility of EN juveniles is best interpreted as a proxy for group or caretaker mobility. Either EN groups moved over longer distances during their seasonal rounds, or EN juveniles accompanied adult caretakers on more frequent or extensive local foraging excursions. Chronological differentiation may have ecological correlates. It is possible that higher EN population density depleted local ungulate populations during times of aggregation, necessitating travel over longer distances compared to the LN, at least during certain parts of the year. Alternatively, ungulates were simply more dispersed in the EN due to environmental differences. The lack of clear differentiation in upper limb shape or asymmetry indicates that EN and LN juveniles performed similar types of foraging behaviors and domestic work.

Differences in lower and upper limb robusticity cannot be interpreted as easily as differences in shape, due to the potentially complicating influence of body mass. Again, this issue arises due to the greater sensitivity of CSG measures than joint dimensions to body mass.

While prior studies of adults indicated that EN individuals had more robust upper and lower limbs, the analysis of size-standardized TA, CA, and SMAs in indeterminate sex juveniles younger than 16 years of age did not show this pattern. Instead, LN juveniles produced a higher range of size-standardized values for most lower and the upper limb sections. The humerus constitutes a notable exception, where EN and LN groups show parity in size-standardized area and SMAs. The gracility of EN juveniles younger than 16 years old may therefore reflect lower body mass. In other words, the diaphyses of EN individuals are adapting to lower load magnitudes during growth, but this reflects the skeleton supporting a less massive body rather than differences in activity levels.

Adjusting for unaccounted body mass differences would, at least, homogenize the lower limb. Therefore, it remains unclear if the greater lower limb robusticity characteristic of EN adults develops prior to the age of 16 years. Limb shape does indicate greater terrestrial mobility in the EN after five years of age. As mobility constitutes the most repetitive aspect of loading on the skeleton, one would expect that lower limb robusticity would also become elevated within this age range, provided one could account for body size differences with greater accuracy (Stock, 2006). Accounting for lower body mass in the EN would also make the EN humerus more robust. The detection of greater humerus midshaft Percent CA and lower MA further supports higher loading of the upper limb in the EN. Consequently, EN juveniles may have been working harder than LN juveniles at activities that predominantly load the upper limb. This result could reflect a greater involvement in fishing by EN juveniles, since isotopic and archaeological evidence indicate a greater dependence on fish in the EN. Ethnographic studies also point to fishing as a common juvenile activity. As populations became more dependent on aquatic resources throughout the EN, juvenile labor may have become increasingly important for the harvest of these resources throughout this period.

There is also evidence of regional differences in CSG ontogeny. Of the two EN samples, Shamanka juveniles showed more differentiation than Lokomotiv from LN Ust-Ida for lower limb shape and the robusticity of both limbs. One cannot exclude the possibility that Lokomotiv to Ust-Ida comparisons fail to reach statistical significance simply because the Lokomotiv sample is roughly half as large as the Shamanka sample. Indeed, visual analysis of boxplots suggested that the Lokomotiv sample was more like Shamanka than Ust-Ida. If sample size does not totally account for a lack of statistical differentiation between Lokomotiv and Ust-Ida, the exploitation by Shamanka individuals of the lakeshore may account for their unique biomechanical signatures. One must also consider that Shamanka groups demonstrate greater heterogeneity in place of origin, which may correlate with behavioral heterogeneity. As a result, some Shamanka individuals may have behaved more like individuals from Lokomotiv and Ust-Ida than others.

While the results suggest some differences in behavior prior to 16 years of age, one must not lose sight of the substantial similarities. The ranges of shape and size-standardized area and SMAs for all groups overlap heavily throughout development. Such evidence of strong commonalities in behavior proves unsurprising, because juveniles learned to forage in a similar environment. Indeed, under such circumstances, it is unlikely that juveniles in any group practiced behaviors that others did not. This concords with prior interpretations of CSG, which concluded that "on a broad level... there was considerable homogeneity in the habitual behavior of Cis-Baikal hunter-gatherers throughout the Holocene" (Stock and Macintosh, 2016, p. 1). All Middle Holocene hunter-gatherer groups exhibited the same basic subsistence pattern. The extent to which foraging strategies could differ was limited, since the two major food resources were ungulate meat and fish (Weber and Bettinger, 2010; Weber et al., 2011).

Adolescents and young adults were analyzed to ascertain if the sexual dimorphism and chronological changes in CSG seen in prior studies of adults were present by the end of adolescence. Previous studies showed sexual dimorphism in the EN and the LN/EBA for bone robusticity and lower limb shape. The same patterning emerges in the evaluation of adolescents and young adults. Males have more robust bones and less circular lower limbs than females from the same archaeological period. In addition, this study is the first to detect sexual differentiation in upper limb shape. Females have less circular humeri than males, indicating repetitive unidirectional loading. Sexual dimorphism in area and SMA measures may partially reflect the differential effect of sex hormones on bones' response to loading. However, hormonal differences cannot also account for differences in shape. These provide strong indications for sexual division of labor by the end of adolescence, with females focused more on processing, manufacturing, and localized foraging, while male adolescents learned to hunt. As a result, they traveled farther and employed different tools (spears, bows, harpoons).

While sexual dimorphism is evident for both robusticity and shape by the end of adolescence, it remains unclear if chronological differences emerged by this point in development. A tendency for EN individuals to show greater robusticity is only evident in females. While small sample size makes interpretations provisional, the results suggest that females assume adult behaviors earlier than males, and female behavior also underwent more chronological change than male behavior. Ethnographic studies support this interpretation. Females mature earlier than males, and, as they age, female juveniles devote increasing amounts of time to behaviors characteristic of adult females. In contrast, particularly with regards to hunting, young males do not behave like older adult males until the end of young adulthood.

#### **10.3 Future Directions in Bioarchaeological Research**

To close, I focus on the larger relevance of this study to bioarchaeological analysis of juvenile postcranial robusticity and Cis-Baikal archaeology, placing emphasis on future research directions.

This study was unique in that few prior studies have considered how prehistoric juvenile robusticity changed over time within a single region (Cowgill, 2014a). Most studies of juvenile biomechanics have instead focused on how behavior varies between groups inhabiting different environments and practicing different modes of subsistence (*e.g.* Cowgill, 2010; Cowgill, 2014b; Osipov et al., 2016). The only prior published study on chronological change in juvenile robusticity within the same region considered individuals from successive occupations of Point Hope, Alaska (Cowgill, 2014a). That study did not find many significant differences, despite archaeological evidence for substantial change in subsistence practices from a greater focus on caribou hunting to whaling. As a result, Cowgill (2014a) suggested that biomechanics is best suited for the detection of broad differences in juvenile behavior. At finer grades of resolution, noise from "nutritional status, genetic background, population structure and maternal health swamp the signal of activity patterns" (Cowgill, 2014a, p.227).

The results of the Cis-Baikal study somewhat contradict this conclusion, indicating that juvenile robusticity can provide indications of behavioral differences, even when the magnitude of behavioral change is limited. However, the fact remains that multiple factors (genetics, diet, activity, illness) influence robusticity levels. An inability to account for juvenile body mass differences with a high degree of confidence poses an especially large problem for biomechanical reconstruction of chronological and regional variation in juvenile behavior and workloads (Cowgill, 2010; Ruff et al., 2013; Osipov et al., 2016). Critically, it also remains unclear just how much do activity, genetics, and health have to differ in order to produce a difference in bone size and shape? Biomechanical analysis of skeletal remains has predominantly focused on detecting differences in ranges of postcranial robusticity between groups. However, there are no clear standards for translating these relative differences in bone robusticity into a measure of the actual difference in the magnitude or frequency of limb loading. More work on both modern and prehistoric human populations, as well as animal models, can address this crucial issue. Such studies will prove particularly beneficial if contextualized with information on genetic history, health status, and behavioral repertories. Conducting such foundational work will amplify the analytical power of both juvenile and adult studies of bone robusticity.

The current study has made significant contributions to the understanding of chronological and geographic variation in Middle Holocene Cis-Baikal juvenile behavior and developmental stress. Still, much work remains to be done. This study analyzed development and behavior specifically in EN and LN juveniles from only two microregions of the Cis-Baikal, the Angara River Valley and the South Baikal lakeshore. Individuals in these groups show differentiation in mobility levels and upper limb loading prior to 16 years of age. Sexual dimorphism in activity types and robusticity emerges in adolescence, and chronological differences in female behavior are evident by young adulthood. Developmental stress also decreased from the EN to the LN, and EN juveniles buried at Lokomotiv may have experienced the highest levels of developmental stress.

A lack of skeletal material sufficiently preserved for biomechanical analysis precludes similar study of EBA juveniles or juveniles from the Little Sea and Upper Lena micro-regions. Four juveniles from Ust-Ida and Shamanka date to the Early Bronze Age, two perinates, one older child, and one adolescent. This sample proves insufficient for the construction of a skeletal growth profile or comparisons to the larger EN and LN datasets. The Khuzhir-Nuge XIV cemetery in the Little Sea microregion contains a sizeable number of juveniles, but diaphyses are highly fragmented. Reconstructions of developmental stress for other micro-regions and the EBA period have only been carried out using enamel defects, since teeth preserve better than bone and adult dentition can be used (Lieverse et al., 2007a; Waters-Rist, 2011). Levels of mechanical loading and differences in body mass during growth cannot be directly addressed for these individuals.

The question of how much the behavior and developmental stress levels of juveniles examined in his investigation resembled that of individuals from the EBA and other microregions is a complicated one. The answer depends on what environmental and archaeological evidence one emphasizes. A few potential scenarios provide heuristic examples. For instance, if one focuses on freshwater resource abundance as a determinant of behavior, it would be important that such resources are least abundant in the Upper Lena (Weber and Bettinger, 2010; Weber et al., 2011; Losey et al., 2012). For this reason, juveniles in this microregion may have devoted less time to fishing than individuals from the Angara and South Baikal. Little Sea juveniles may have behaved similarly to South Baikal juveniles, since individuals from both microregions utilized lakeshore resources. However, aquatic resource abundance also differs between these regions. Most noticeably, some Shamanka groups likely included the abundant Angara River Valley fishery in their foraging rounds (Weber et al., 2011; Losey et al., 2012).

If the proportion of aquatic resources in the diet influences juvenile behavior, it is also possible that Upper Lena and Little Sea juvenile behavior may have undergone less chronological change than in the Angara and South Baikal microregions. Little Sea and Upper Lena EN population do not appear to have been more reliant on aquatic resources in the EN than in the LN and EBA periods (Weber and Bettinger, 2010). Analysis of the Freshwater Reservoir Effect also suggests chronological increases in aquatic resource consumption throughout the EBA in the Little Sea, but increased migration into the region may also account for this trend (Weber et al., 2016a). Issues such as chronological fluctuations in population size also matter, because the population of the Little Sea and Upper Lena increased from the EN to the LN/EBA (Weber and Bettinger, 2010). If increased population size and density depletes local terrestrial resources, LN/EBA juveniles from the Little Sea and Upper Lena may have exhibited levels of developmental stress and workloads more similar to that of EN than LN juveniles in the current sample (Waters-Rist, 2011).

The above discussion does not aim to exhaustively analyze every potential reason that the developmental health and behavior of EBA, Upper Lena, and Little Sea juveniles may have

differed from or resembled that of the EN and LN individuals considered in this study. Instead, it demonstrates that application of the findings derived in this study to the EBA and other microregions is possible. However, this would require a careful consideration of how multiple factors, including resource abundance and population size, would affect juvenile behavior and developmental stress. The work of the Baikal Hokkaido Archaeology Project has illustrated substantial chronological and geographic variation in behavior and health (Weber and Bettinger, 2010). Comparisons of CSG in EN and LN juveniles from the Angara River Valley and South Baikal echo this general trend. It is therefore reasonable to suspect that significant temporal and geographic variation also existed in the growth and behavior of Upper Lena and Little Sea juveniles.

Future analysis can utilize other lines of evidence to expand reconstructions of juvenile behavior and health. Studies of enamel defects have already been carried out to analyze developmental stress (Lieverse et al., 2007a; Lieverse, 2010; Waters-Rist, 2011). Additional studies of stable isotopes that track changes in diet and foraging range throughout growth are ongoing. These will add a powerful new dataset relevant to addressing age-related variation in behavior and health (Haverkort et al., 2010; Lieverse et al., 2011; Waters-Rist et al., 2011; Weber et al., 2011; Weber and Goriunova, 2013). For the Angara River Valley and South Baikal individuals, it will prove particularly interesting to see how the biomechanical differences detected between juveniles from different archaeological periods and cemeteries correlate with age-related change in diet and foraging location. Furthermore, as dependence on aquatic resources increased throughout the EN, comparisons of individuals dated to different portions of the EN may reveal further chronological variation in developmental stress and behavior. As discussed above, additional studies of bone micro-architecture can offer additional insights into functional adaptation and health.

During ontogeny, behavior, health, and genetics influence the accrual of bone robusticity and shape. However, more work must be done to ascertain the extent to which these various signals can be teased apart from each other in bioarchaeological studies. Applied to Middle Holocene Cis-Baikal juveniles, study of bone robusticity ontogeny improved understanding of chronological and regional variation in juvenile behavior and health. While a lack of preserved skeletal material precludes the expansion of biomechanical analyses to other portions of the CisBaikal, the findings can inform reconstructions of behavior and health in these regions, if variations in resource abundance, population size, and foraging strategies are taken into account. Future work on the current sample will consider how juvenile behavior and health changed throughout the EN. In addition, comparison of Cis-Baikal ontogenetic patterns to that of hunter-gatherer juveniles from different archaeological contexts can produce a better understanding of hunter-gatherer childhoods in the past. Comparative studies have already begun, and they address how differences in environment and subsistence strategies affect juvenile behavior and growth (Osipov et al., 2016). Continued work on bone robusticity ontogeny can develop new methodologies that offer novel insights into the growth and behavior of past populations.

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IND*	Age (years) <sup>a</sup>	Ageing Method <sup>b</sup>	Sex Estimate	Body Mass (kg)	BM method <sup>c</sup>	Archaeological Period <sup>d</sup>
LOR.5.1	0	Fusion	Indeterminate	6.65	BM regressed on age	EN
UID.40.2 .1	0	Fusion	Indeterminate	6.65	BM regressed on age	EBA
UID.46.1	0	Fusion	Indeterminate	6.65	BM regressed on age	EBA
SHA.27. 4	0.5	Fusion	Indeterminate	6.46	1 yo DF	EN
SHA.61. 3	0.5	Fusion	Indeterminate	7.21	BM regressed on age	EN
LOK.3.1.	0.88	DD	Indeterminate	7.65	BM regressed on age	EN
SHA.80. 1	0.88	DD	Indeterminate	7.65	BM regressed on age	EN
UID.26.2	0.88	DD	Indeterminate	7.55	1 yo DF regressed on femur distal epiphysis	LN
SHA.87. 1	1.0	Fusion	Indeterminate	7.09	1 yo DF regressed on clavicle maximum length	EN
SHA.91. 1	1.0	Fusion	Indeterminate	7.8	BM regressed on age	EN
SHA.27. 3	1.5	DD	Indeterminate	9.26	1 yo DF	EN
SHA.66. 2	1.5	DD	Indeterminate	8.56	1 yo DF	EN
SHA.69. 3	1.5	DD	Indeterminate	8.18	1 yo DF	EN
USB.6.1	1.5	DD	Indeterminate	8.06	1 yo DF	EN
UID.4.1	2.0	Ulna diaphysis length	Indeterminate	9.14	2 yo DF regressed on femur proximal metaphysis	LN
LOR.10. 1	2.5	DD	Indeterminate	8.46	2 yo DF regressed on femur proximal metaphysis	EN
SHA.28. 1	2.5	DD	Indeterminate	10.04	2 yo DF	EN
SHA.38. 1	2.5	DD	Indeterminate	8.31	2 yo DF regressed on tibia proximal metaphysis	EN
SHA.72.	2.5	DD	Indeterminate	9.06	2 yo DF	EN
SHA.82.	2.5	DD	Indeterminate	10.06	2 yo DF regressed on tibia proximal metaphysis	EN
SHA.95. 1	2.5	DD	Indeterminate	9.51	2 yo DF regressed on ulna maximum length	EN
UID.21.1	2.5	DD	Indeterminate	9.76	BM regressed on age	LN
UID.36.1	2.5	DD	Indeterminate	10.13	2 yo DF regressed on femur proximal metaphysis	LN
UID.55.1	2.5	DD	Indeterminate	11.87	2 yo DF	LN
LOR.7.3	2.6	Femur Diaphysis Length	Indeterminate	9.61	3 yo DF	EN
SHA.89. 1	3.2	Tibia Diaphysis Length	Indeterminate	11.39	3 yo DF regressed on tibia proximal metaphysis	EN
SHA.48. 2	3.5	DD	Indeterminate	11.23	BM regressed on age	EN
UID.17.1	3.5	DD	Indeterminate	10.56	3 yo DF regressed on femur diaphysis length	LN
UID.25.1	3.5	DD	Indeterminate	11.16	3 yo DF regressed on clavilce maximum length	LN
LOK 14.4.3	4.2	Femur Diaphysis Length	Indeterminate	11.17	4 yo DF	EN
SHA.56. 1	4.5	DD	Indeterminate	12.4	4 yo DF	EN
UID.26.3	4.5	DD	Indeterminate	14.22	4 yo DF	LN

**Appendix 1: List of Age and Body Mass Estimates** 

SHA.94.	5.3	Femur Diaphysis Length	Indeterminate	12.61	5 yo DF	EN
SHA.31.	5.5	DD	Indeterminate	14.36	5 yo DF	EN
UID.53.2	5.5	DD	Indeterminate	16.91	5 yo DF regressed on tibia proximal metaphysis	LN
LOK.41. 2	6.5	DD	Indeterminate	15.97	6 yo DF regressed on clavicle maximum length	EN
LOR.13. 1	6.5	DD	Indeterminate	16.46	6 yo DF	EN
UID.8.1	6.5	DD	Indeterminate	17.28	6 yo DF regressed on femur proximal metaphysis	LN
UID.15.1	6.5	DD	Indeterminate	16.99	6 yo DF	LN
UID.21.2	6.5	DD	Indeterminate	16.27	6 yo DF regressed on femur proximal metaphysis	LN
UID.26.5	6.5	DD	Indeterminate	18.27	6 yo DF	LN
UID.44.2	6.5	DD	Indeterminate	15.03	6 yo DF	LN
LOK.24. 3	7.5	DD	Indeterminate	13.83	7 yo FH	EN
LOR.9.1	7.5	DD	Indeterminate	21.51	7 yo FH	EN
SHA.55. 2	7.5	DD	Indeterminate	21.64	7 yo FH	EN
SHA.67. 1	7.5	DD	Indeterminate	21.87	7 yo FH	EN
SHA.88. 1	7.5	DD	Indeterminate	17.45	7 yo DF	EN
SHA.103 .2	7.5	DD	Indeterminate	17.96	7 yo DF	EBA
UID.9.1	7.5	DD	Indeterminate	23.27	7 yo FH	LN
LOK 14.2.2	7.8	Femur Diaphysis Length	Indeterminate	21.84	8 yo FH	EN
SHA.26.	8.5	DD	Indeterminate	29.02	8 yo FH	EN
UID.25.2	8.5	DD	Indeterminate	25.17	8 yo FH regressed on femur proximal metaphysis	LN
LOK.18. 1.3	9.3	Femur Diaphysis Length	Indeterminate	22.65	9 yo FH	EN
LOK.24. 4	9.5	DD	Indeterminate	29.78	9 yo FH	EN
UID.32.1	9.5	DD	Indeterminate	30.9	9 yo FH	LN
UID.44.1	9.5	DD	Indeterminate	27.52	9 yo FH	LN
LOK 14.3	10.5	DD	Indeterminate	28.23	10 yo FH regressed on femur proximal metaphysis	EN
LOR.12. 1	10.5	DD	Indeterminate	35.41	10 yo FH	EN
SHA.92. 1	10.5	DD	Indeterminate	32.37	10 yo FH	EN
UID.5.1	10.5	DD	Indeterminate	27.72	10 yo FH	LN
UID.10.1	10.5	DD	Indeterminate	35.35	10 yo FH	LN
UID.25.3	10.5	DD	Indeterminate	31.65	10 yo FH	LN
UID.31.1	10.5	DD	Indeterminate	39.38	10 yo FH	LN
UID.56.2	10.5	DD	Indeterminate	32.26	BM regressed on age	LN
LOR.13. 2	11.1	Femur Diaphysis Length	Indeterminate	32.55	11 yo FH	EN
UID.18.1	11.5	DD	Indeterminate	42.18	11 yo FH	LN
UID.26.4	11.5	DD	Indeterminate	41.88	11 yo FH	LN
UID.44.3	11.5	DD	Indeterminate	28.48	11 yo FH	LN

SHA.56.	12.0	Femur Diaphysis	Indeterminate	36.67	12 yo FH	EN
LOK.41.	14.0	DD	Female	48.76	14yo FH regressed on clavicle max	EN
SHA.24.	14.0	DD	Indeterminate	43.34	14 yo FH regressed on tibia proximal epiphysis	EN
UID.33.2	14.2	Tibia Diaphysis Length	Indeterminate	47.12	14 yo FH	LN
SHA.103	14.5	DD	Indeterminate	46.93	14 yo FH	EBA
UID.26.1	14.5	DD	Indeterminate	45.26	14 yo FH	LN
UID.33.1	14.9	Tibia Diaphysis Length	Indeterminate	60.45	14 yo-YA FH BM regressed on age	LN
LOK.27. 1	15.0	DD	Male	63.51	14yo- YA FH interpolated	EN
SHA.21. 3	15.0	DD	Indeterminate	53.47	14yo- YA FH interpolated	EN
LOK.24. 1	15.7	Femur Diaphysis Length	Indeterminate	50.24	14 yo-YA FH BM regressed on age	EN
LOR.7.2	15.9	Humerus Diaphysis Length	Female	67.95	14yo- YA FH interpolated	EN
UID.55.2	16.4	Humerus Diaphysis Length	Male	66.81	14 yo-YA FH BM regressed on age	LN
SHA.9.1	17.5	DD	Male	68.37	YA PT	EBA
UID.24.1	18.0	Ulna diaphysis length	Female	48.64	YA FH	EBA
SHA.59. 2	18.0	Humerus Diaphysis Length	Female	62.46	YA PT	EN
UID.22.1	18.5	DD	Female	54.49	YA FH	LN
SHA.73.	19.5	DD	Female	49.82	YA FH	EN
SHA.90.	19.5	DD	Male	57.87	YA FH	EN
LOK 2.1	YA	Fusion	Indeterminate	65.50 6	YA FH	EN
LOK.10. 1	YA	DD and Fusion	Male		no measures- BM not estimated	EN
LOK 10.2	YA	Fusion	Male	68.73	YA PT	EN
LOK 12.1	YA	Fusion	Female	52.46	YA FH	EN
LOK.14. 4.4	YA	Fusion	Female	57.76	YA FH	EN
LOK.23.	YA	Fusion	Male	69.9	YA PT	EN
LOK.25. 2	YA	Fusion	Female	49.6	YA FH	EN
LOK.36. 1	YA	Fusion	Female		no measures-BM not estimated	EN
LOK.39.	YA	DD and Fusion	Female	53.11	YA FH	EN
LOR.13.	YA	Fusion	Female	63.2	YA PT	EN
SHA.5.1	YA	DD and Fusion	Male	68.63	YA PT	EBA
SHA.11.	YA	DD and Fusion	Female	61.7	YA FH	EN
SHA.17.	YA	Fusion	Male	55.6	YA FH	EN
SHA.22.	YA	DD and Fusion	Male	55.18	YA FH	EN
SHA.47.	YA	DD and Fusion	Female	48.29	YA FH	EN
SHA.49.	YA	DD and Fusion	Male	58.31	YA FH	EN
SHA.51.	YA	Fusion	Male	56.64	YA FH	EN

SHA.53. 1	YA	DD and Fusion	Male	42.05	YA FH	EN
SHA.54. 1	YA	DD and Fusion	Female	57.47	YA FH	EN
SHA.83. 1	YA	DD and Fusion	Male	65.76	YA FH	EN
SHA.111 .1	YA	DD and Fusion	Male	62.38	YA FH	EBA
UID.14.1	YA	Fusion	Male	65.8	YA FH	LN
UID.20.1	YA	Fusion	Male	59.52	YA FH	LN
UID.43.1	YA	Fusion	Male	68.71	YA FH	LN
SHA.25. 2	YA	Fusion	Indeterminate		no measures-BM not estimated	EN

\*LOK= Lokomotiv, LOR= Lokomotiv-Raisovet, SHA= Shamanka II, UID= Ust-Ida I

a YA= Young Adult

b DD= Dental Development; Fusion= Skeletal Fusion

c DF= Distal Femur Metaphysis; FH= Femoral Head, PT= Proximal Tibia Epiphysis

d EN= Early Neolithic; LN= Late Neolithic; EBA= Early Bronze Age