RECONSTRUCTING ACTIVITY PATTERNS IN PREHISTORIC JOMON PEOPLE
USING LONG BONE CROSS-SECTIONAL GEOMETRY

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by
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The undersigned, appointed by the Dean of the Graduate School, have examined the thesis entitled

RECONSTRUCTING ACTIVITY PATTERNS IN PREHISTORIC JOMON PEOPLE
USING LONG BONE CROSS-SECTIONAL GEOMETRY

Presented by Sharon Knobbe

A candidate for the degree of Master of Arts

And hereby certify that in their opinion it is worthy of acceptance.

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Professor Daniel Temple

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Professor Carol Ward

Dedicated to my parents, Dennis and Marcella

For all your support and love

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CHAPTER 1: INTRODUCTION

This thesis documents and interprets prehistoric Jomon long bone diaphyseal structure within the context of its mechanical environment. The primary goal is to help reconstruct activity patterns of the prehistoric Jomon hunter-gatherers of Japan within an archaeological framework. By using archaeological knowledge and the principles of bone functional adaptation, long bone cross-sectional geometric analysis will be applied to infer Jomon subsistence behavior and related activities.

In this thesis I use engineering beam theory to analyze bending rigidity to specifically compare mid-distal humeral and midshaft femoral diaphyseal cross-sectional properties (cortical area, second moments of area, and polar second moments of area) of Jomon long bones from Yoshigo to the long bones of coastal hunter-gatherers from Alaska, California, and Georgia. The purpose is to gain a better understanding of prehistoric Jomon activity patterns, including mobility and sexual division of labor, along the coast of Japan. I expect that the Jomon from Yoshigo will have similar long bone morphology as other coastal, marine hunter-gatherers, especially Aleuts, and will exhibit: 1) similar robusticity[1] of femoral diaphyses in terms of the polar second moment of area (J) as the Aleut, 2) more robust humeral diaphyses in terms of the polar second moments of area (J) compared to the California and Georgia coastal hunter-gatherers, 3) similar femoral and humeral diaphyseal shape ratio (I_x/I_y) compared to other coastal hunter-

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[1] Robusticity is utilized in the present study as defined by Ruff et al. (1993: 25): "strength or rigidity of a structure relative to the mechanically relevant measure of body size."

gatherers, and 4) similar levels of sexual dimorphism in diaphyseal shape (I_x/I_y), and overall robusticity (J) in the femora and humeri compared to the coastal hunter-gatherers of Alaska, California, and Georgia. Testing these hypotheses provide insight on Jomon mobility patterns, marine activities and differences in male and female activities.

I. BONE BIOMECHANICS & ANTHROPOLOGICAL APPLICATIONS

Bone Biology and Bone Functional Adaptation

Bone is a dynamic, integrated tissue that serves a role in maintaining functional homeostasis of the human body (Currey, 2002). Bone functions in both a metabolic and structural capacity, which is closely tied to its composition. Organic and inorganic compounds make up the structural composition of bone. In particular, collagen, proteoglycans and glycoproteins form the organic osteoid matrix of bone, while hydroxyapatate—crystalline calcium phosphate—forms the inorganic portion. The body utilizes inorganic bone metabolically as a mineral reservoir. Production of erythrocytes in hematopoietic marrow within the medullary cavity of long bones is also an important function especially during growth and development.

Bone serves as an attachment site for tendons, ligaments and muscles, houses organs and acts as a lever in movement (Currey, 2002). Additionally, bone also serves a primary structural role in responding to mechanical loading of the skeleton. Together the organic and inorganic components of bone provide the skeleton with the flexibility and strength to adapt to its external and internal mechanical environment.

Previously, "Wolff's Law" was utilized to explain the relationship between

mechanical loading and bone morphology, specifically stating that during growth and development trabecular bone orients itself in the direction of primary mechanical loading (Roux, 1881; Wolff, 1892; Martin et al., 1998). However, the "law" is limited in that it refers only to trabecular bone and adheres to strict mathematical rules to explain the mechanical response. As a result, the term bone functional adaptation is applied to describe the general premise that bone tissue and structure adapts to mechanical stimuli and focuses on cortical bone architecture (Ruff et al., 2006).

Modeling and remodeling are the processes by which bone responds to its mechanical environment. Both processes involve bone formation and bone resorption, but in different contexts and with different outcomes. Modeling is mainly the process used when the skeleton is growing and generates changes in bone size and shape (Martin et al., 1998). After the skeleton reaches maturity, modeling decreases to a trivial level. It persists in adults only when drastic mechanical loads are applied (Ruff et al., 1994; Frost, 1997; Robling et al., 2002).

Through the independent activities of osteoblasts and osteoclasts, shaping and alteration of bone occurs during modeling (Martin et al., 1998). Osteoblasts build bone through production of the organic osteoid matrix, which subsequently becomes mineralized. Osteoclasts, on the other hand, work to break down bone through utilization of enzymes and acids that dissolve the mineral and organic components of bone. When long bone diaphyses are modeled to increase bone diameter during growth, for instance, formation drift occurs in the form of periosteal deposition via osteoblastic activity and resorption drift takes place on the endosteal surface through osteoclastic activity.

Remodeling is the coupling of osteoblastic and osteoclastic activity at the same

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location for bone repair and maintenance (Martin et al., 1998). Like modeling,

remodeling occurs throughout skeletal growth and maturity, but does not result in the net

gain of bone. The collaboration of osteoblasts and osteoclasts occurs in a basic

multicellular unit (BMU) made up of approximately ten osteoclasts and several hundred

osteoblasts. The BMU acts in the sequential pattern of activation, resorption and

formation. During activation bone lining cells and osteocytes signal osteoclasts when

fluid fills the canaliculi in response to microstrain, which then commences the osteoclasts

to resorb the bone tissue (Martin et al., 1998; Cowin et al., 1991). Osteoblasts are

subsequently formed from osteoclasts and work to replace the resorbed bone.

The mechanostat model hypothesizes when modeling and remodeling occur in the

skeleton in the context of mechanical loading (Frost, 1983, 2003). Mechanical loads

affect bone in terms of strain. In other words, forces applied to bone in the form of

mechanical loads produce stress—force per unit area—which in turn generate strain, a

physical deformation of bone. The mechanostat model is a type of feedback model,

similar to a home thermostat, whereby certain magnitudes of strain will either activate or

inhibit modeling and remodeling (Frost, 1983, 2003). It further relates these processes to

the resulting effects of bone structure and strength in adults and subadults.

Modeling and remodeling have opposite responses to the magnitude of strains

produced by mechanical loading under the mechanostat model (Frost, 1997, 2003). The

threshold range at which modeling is activated is termed the "minimally effective strains

of modeling" and occurs when mechanical loads produce stress at 2000 microstrains and

above. Specifically, this occurs between about 2000 and 3000 microstrains and results in

an increase in bone deposition. As a primary phenomenon of growth, modeling affects

subadults almost exclusively. Modeling affects subadults by increasing bone strength, mass, external diameter, cortical area, trabecular density and longitudinal growth (Frost, 1983) and has an associated decrease in the medullary cavity up until about mid-adolescence (Ruff et al., 1994). In both adults and subadults, when mechanical loads exceed the production of 3000 microstrains bone becomes microscopically damaged leading to eventual bone failure (Frost, 1983, 1997, 2003).

Remodeling is activated within the disuse window, when mechanical loads generate "minimally effective strains" at 100 microstrains or below (Frost, 1983, 1997, 2003). Bone resorption is then triggered, which results in a decrease in bone strength and bone mass in both adults and subadults. Subadults, in particular, acquire less gain in bone mass and additionally demonstrate decreases in their bone external diameters, cortical area, trabecular density and growth in bone length (Frost, 1983). At the threshold range between 100 and 2000 microstrains, termed the adaptive window, bone achieves a biomechanically adapted state (Frost, 1983, 1997, 2003). Within this state, bone strength and bone mass are maintained through inhibition of bone resorption. Remodeling in this situation works to repair bone microdamage from mechanical usage in subadults and adults, rather than undergoing bone resorption from disuse.

Bone Biomechanics and Long Bone Cross-sectional Geometry

To understand long bone morphology within the context of its mechanical environment, a bone biomechanical model is used. In general, biomechanics applies engineering principles to biologically dynamic tissues that are altered by a variety of mechanical loading forces and loading magnitudes. With the bone biomechanical model,

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a long bone diaphysis is modeled as a hollow beam that responds to mechanical loads (Huiskes, 1982). It is the cross-sectional distribution of bone, rather than any other material property, that responds most to increased mechanical loading (Larsen, 1997; Ruff, 2008). Thus, differing mechanical loads and magnitudes are reflected in long bone cross-sectional diameter, area, and overall shape.

Five primary loading forces affect long bones—tension, compression, shear, bending, and torsion (Larsen 1997). Tensile loading occurs outwardly along the long axis of the bone, pulling the components apart. Compressive loading is the reverse, with the force applied towards the long axis of the bone pushing components together. When forces are applied perpendicular and opposite to the direction of the long axis of a long bone, shear loading is taking place. A combination of tensile and compressive loading produces bending. Where a long bone is loaded by bending forces, tension will occur on the convex side and compression on the concave side. Torsion is produced by the combination of tension, compression and shear loads with the resulting force in the form of twisting perpendicular to the long axis.

Resistance to mechanical loads in long bone cross-sections is more accurately designated as bone strength and bone rigidity (Ruff, 2008). Bone strength is the property of bone indicating the ability to resist breaking (fracture), while bone rigidity is the resistance to bending, before the point of fracture. Bending and torsion are the two mechanical loads that are most important to understanding the structure of human long bones since they are the most common and largest loads placed on the skeleton (Larsen, 1997). In a cross-section of a long bone, taken perpendicular to its long axis, the magnitude of these mechanical loads is proportional to the distance from the neutral axis.

Specifically, the neutral axis indicates the bending plane or torsional axis where stress is zero. Thus, theoretically, the long bone cross-section that is more resistant to bending or torsion has the distribution of bone oriented further away from the neutral axis.

Long bone cross-sectional geometric properties measure both the amount and distribution of bone in a cross-section and, consequently, aid in the determination of bone strength and rigidity in relation to mechanical loads (Ruff, 2008; Larsen, 1997) (Figure 1). Bending and torsional rigidity is estimated using the geometric properties of second moments of area. The bending second moment of area (I) estimates bending rigidity and is calculated by multiplying small unit areas of bone within a cross-section by the squared distances of these areas to the bending axis. It is customary to calculate this second moment of area in relation to its anatomical axes, including anteroposterior (I_y) and mediolateral (I_x) axes, along with the minimum (I_{min}) and maximum (I_{max}) axes.

In contrast, the polar second moment of area (J) is proportional to both torsional rigidity and twice the average bending rigidity. This indicates that the polar second moment of area provides a useful indication of overall rigidity (Ruff, 2008). The polar second moment of area is calculated in a similar manner as the bending second moment of area, but with the exception that the squared distance is calculated from the torsional centroid. This property may also be calculated by summing any two perpendicular values of the bending second moment area (Ruff, 2008; Larsen, 1997). Lieberman and colleagues (2004) contend that J is the best parameter to use in cross-sectional geometric analyses of long bones based on the absence of experimental data on limb loading. Thus, this property is most relevant in assessing long bone functional adaptation in past populations.

Pure compressive and tensile loading of long bones are measured by the amount of cortical bone in cross-section, known as cortical area (CA) (Larsen, 19997; Ruff, 2008). Cortical area is calculated by taking the difference between the endosteal and periosteal surfaces, represented by the medullary area (MA) and the total subperiosteal area (TA). It must be noted that pure compressive or tensile loading is rare, however, and thus second moments of area are more accurate for the estimation of resistance to different loading magnitudes.

To estimate bone strength section moduli are used (Larsen, 1997; Ruff, 2008). Section moduli (Z) use second moments of area in their estimation of bone strength (Ruff, 2008). Since the outermost surface of a cross-section has the most stress under bending or torsion, second moments of area are divided by the distance from this surface to the bending axis or torsional centroid to determine the section moduli. Like second moments of area, bending section moduli are calculated in reference to anteroposterior (Z_y) and mediolateral (Z_x) axes and the minimum (Z_{min}) and maximum (Z_{max}) axes. Also, the torsional section modulus is referred to as the polar section modulus (Z_p) and measures both torsional strength and twice the average bending strength.

$$I = \int_A y^2 dA$$

$$J = \int_A r^2 dA$$
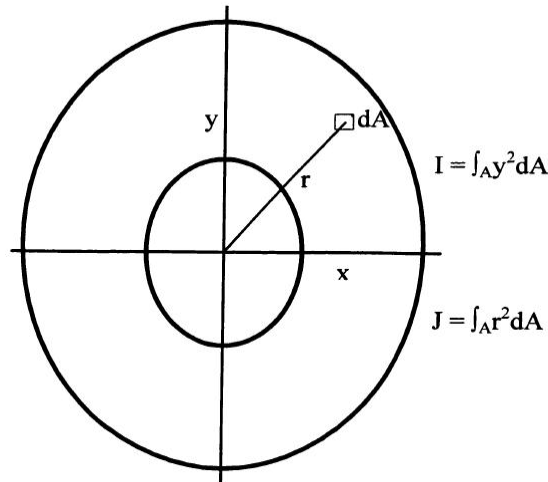
Figure 1. Measurements of cross-sectional properties (I) and (J). From Wescott (2001).

Methods for Obtaining Cross-Sectional Geometric Properties

Various methods are used to obtain cross-sectional geometric properties from

long bone diaphyses. Methods are categorized into invasive and non-invasive types.

Invasive techniques include direct sectioning of long bone diaphyses, while non-invasive

techniques include the use of computed tomographic (CT) scanning, radiography,

molding of long bone sections and radiography, and external dimension estimation.

While direct sectioning of long bone diaphyses is the most straightforward

technique for quantifying cross-sectional properties, it is destructive and thus not

recommended for most situations. A better alternative is the non-invasive technique of

CT scanning. With this method, whole bones are used and scanned at the desired

anatomical location. With correct calibration of image display parameters, the result is

an accurate two-dimensional image of the periosteal and endosteal contours of the section

(Ruff and Leo, 1986). It is important to correctly determine these contours due to the fact

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that cross-sectional properties are dependent upon these reference outlines for accurate measurement (Stock and Shaw, 2007). Cross-sectional properties from direct sectioning and CT scanned section images are derived by utilizing an image macro such as SLICE (Nagurka and Hayes, 1980) or in image analysis software such as NIH Image and Image J (Ruff, 2008).

When CT scanning of long bone sections is not available, biplanar radiographic techniques are used to obtain cross-sectional properties. Alternative radiographic methods include a latex cast method (LCM), an eccentric elliptical method (EEM) and an ellipse model method (EMM) (Stock, 2002; O'Neill and Ruff, 2004). To approximate section contours, the LCM uses a combination of molding of the periosteal contour along with measurement of cortical thickness from radiographic breadths to estimate the endosteal contour. In the EEM and EMM methods, biplanar radiography alone is utilized. Contours are obtained by estimating radiographic breadths in the AP and ML planes and modeling them as ellipses. While the EMM assumes the ellipses have the same centers, the EEM uses a formula that places the centroid of the internal ellipse within the external ellipse.

Comparisons of the cross-sectional properties derived from LCM, EEM and EMM methods with true cross-sectional properties have been conducted by Stock (2002) and O'Neill and Ruff (2004). Both studies found that the LCM provides reasonable estimates of cross-sectional properties and are accurate within 5% of direct measurements. On the other hand, when compared with true cross-sectional property values, EEM and EMM both overestimate second moments of area while reasonably estimating cross-sectional areas (Stock, 2002; O'Neill and Ruff, 2004). Thus, caution

should be used when comparing cross-sectional properties obtained from EEM or EMM methods with data compared from different methods.

The final non-invasive technique involves measuring external dimensions of long bone diaphyses. With this method the internal contour, and thus cortical bone thickness and medullary shape, is not factored into derivations of cross-sectional properties. Rather, external long bone dimensions measured at the desired location are utilized in conjunction with appropriate formulae to approximate cross-sectional robusticity and shape (Wescott, 2006, 2008). A study by Wescott (2001) supports the validity of using external dimensions to estimate cross-sectional properties. Furthermore a study by Stock and Shaw (2009) emphasize that externally derived cross-sectional properties reasonably correlate with true cross-sectional values, but demonstrate considerably high prediction errors. Again, like the elliptical radiograph methods, caution must be exercised when comparing externally derived cross-sectional properties with data obtained from other methods.

Challenges and Limitations of Using Cross-Sectional Geometry

The application of cross-sectional geometry—wherein long bone cross-sectional shape reflects habitual activity—to estimate loading experienced during life is a contentious approach to inferring the behavior of past populations. Although the use of the principal of bone functional adaptation is supported by experimental research (Lanyon et al., 1975; Lanyon and Baggott, 1976; Churches et al., 1979; Woo et al., 1981; Biewener, 1983; Umemura et al., 1997; Robling et al., 2002), the relationship between bone functional adaptation and cross-sectional geometry is not without complication

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(Judex et al., 1997; Demes et al., 1998, 2001; Lieberman et al., 2003; Lieberman and Pearson, 2001; Lieberman et al., 2004). Discussion of the issues that researchers call into question has been laid out clearly in recent reviews (Pearson and Lieberman, 2004; Ruff et al., 2006). These issues include the validity of the approach, and the effect of age and other factors on bone functional adaptation.

The validity of the relationship between bone functional adaptation and cross-sectional geometric properties is called into question. In particular, experimental evidence is not straightforward in relating *in vivo* strains in long bones to the resulting cross-sectional properties and their interpretations. For instance, in a study of *in vivo* loading of sheep tibial and metatarsal midshafts, Lieberman and colleagues (2004) tested hypotheses on the correspondence of cross-sectional properties derived from experimentally determined neutral axes (NA) and properties derived from neutral axes running through the section centroid axes (SCA), the latter of which is utilized in cross-sectional geometric analyses. The researchers found that there were significant differences in cross-sectional properties calculated from the NA versus the SCA. Also, the orientation of principle bending determined from the NA did not match the orientation of principle bending from the SCA, suggesting that with use of the SCA the plane of bending where resistance should be reinforced does not correspond to the direction of maximum strains (Lieberman et al., 2004). Demes and colleagues (1998; 2001) also demonstrated similar findings by *in vivo* experiments with macaque tibiae and ulnae.

It can be argued that if bone is adapted to the strain environment established from previous habitual loading, such as in the plane of bending assessed in these studies, then

the measurement of maximum strain would not be within this plane of bending. Therefore, the results of these experiments fit the expected outcome that maximum strains are measured from loading experienced in the plane of bending not customary to the animals. Ruff and colleagues (2006) also recognize that although there are complications in correspondence between experimentally derived cross-sectional properties and properties determined from the SCA, the approach is still useful. Ruff and colleagues (2006: 495) state:

> "The *in vivo* strain environment that drives bone functional adaptation is complex and variable. Given this variability and the fact that we do not (and probably will not) have direct strain data available for a broad, representative array of activities, species and skeletal locations, it is advisable to continue to use 'idealized' geometric section properties in functional analyses, with the understanding that correspondence of these with actual strain distributions will only be approximate."

Despite research that calls into questions the assumptions of the cross-sectional geometric approach, there is research that supports its utility. For instance, Robling and colleagues (2002) studied the effect of discrete bouts of compressive loading on adult rat ulnae over a period of 16 weeks. Due to the curved ulnar diaphyses of the rats, the compressive loading translated into mediolateral bending especially at the midshaft and mid-distal diaphyses. Results showed that bone was added in the ML plane where strain was highest, which was revealed in the higher second moment of area in the ML plane than in the AP plane (Robling et al., 2002). A general conclusion of Robling and colleagues' study (2002) is that bone functional adaptation was clearly operating in the adult rats' ulnae. This is interesting to note since another point of contention for researchers is the effect of age on bone functional response to loading (Pearson and Lieberman, 2004). Researchers demonstrate that bone modeling and remodeling have a

greater response to loading in subadults than adults (Lieberman et al., 2003; Turner and Robling, 2003). The issue then is how to interpret adult cross-sectional geometric properties.

Although the response of the skeleton to mechanical loading is more pronounced in subadults, research shows that an effect is still present in adults, which is exemplified in Robling and colleagues' study (2002). Adult skeletal response is also indicated by bone maintenance through activation of the remodeling process, which can be detected through secondary osteons counts in adult long bone cross-sections (Robling and Stout, 2003). Ruff and colleagues (1994) observed that the difference in adult and subadult modeling response is in part due to differences in bone envelope sensitivity. In particular, before mid-adolescence, bone is added to the periosteal surface in response to loading, while after this period bone is added to the endosteal surface (Ruff et al., 1994; Bass et al., 2002). Thus, cross-sectional geometry of adult long bones can be interpreted as a reflection of adult behavior with activities before adulthood having an impact on adult long bone morphology. Pearson and Lieberman (2004: 89) assert that

> "it is likely that adolescents in most [preindustrial] societies begin to engage intensively in the strenuous activities typical of adults during their adolescent growth spurts and thus adult morphology and cross-sectional geometry of their long bones probably would reflect those activities."

Also, while modeling may be reduced in adults, bone is not a static entity and still needs to be maintained through the remodeling process. As a result, behavioral inferences from adult long bone morphology are possible.

Another point of contention is the effect of genetic and systemic factors on bone morphology and the response of bones to mechanical loading. For instance, Lovejoy and

coworkers (2003) contend that some aspects of bone morphology are determined much more by genetic mechanisms than by bone functional adaptation. Research by Cowgill (2010) on subadult groups from the Late Pleistocene and Holocene demonstrate that variation in humeral and femoral strength between groups is established as early as one year of age and is maintained throughout development. This suggests that a combination of genetic, systemic and mechanical factors influence postcranial morphology and strength which are established during ontogeny and maintained in adulthood. As Ruff and colleagues (2006) point out, past research clearly shows the influence of mechanical stimuli on bone morphology, and as a result, emphasize that it is likely the interaction of both genetics and environment that should be considered when understanding bone morphology.

Researchers also assert that modeling and remodeling are affected by other systemic factors such as health, nutrition and hormonal status (Frost, 1987; Pearson and Lieberman, 2004). For example, Cowgill's research (2010) also revealed that the nutritionally stressed Kulubnarti sample consistently demonstrated the lowest level of postcranial robusticity compared to the other subadult groups. This suggested that the Kulubnarti subadults were influenced by reduced bone mass and lower levels of activity due to nutritional stress in addition to the impact of maternal malnourishment, which produced small infants.

Although debate exists, when cautiously approached with the limitations and challenges in mind, cross-sectional geometry can be useful in making behavioral inferences. One must account for the limitations by designing studies that control for the confounding factors. For example, an effective cross-sectional analysis limits

comparisons to similar skeletal locations and species and furthermore compares similar age categories (subadult versus adult) and controls for systemic factors such as genetic background, health status, diet and body physique.

Anthropological Applications of Long Bone Cross-sectional Geometry

To explain variation in skeletal morphology in past and present populations, specifically in long bone diaphyses, anthropologists utilize the bone biomechanical model (Ruff, 2008; Larsen, 1997). Application of this model, specifically in terms of cross-sectional geometric analysis, aids in the interpretation and reconstruction of activity patterns in past populations. Over the past several decades, physical anthropologists have investigated long-term evolutionary trends in long bone diaphyseal structure as well as long bone structural variation within populations and individuals. In particular, this research helps to understand patterns of behavior related to subsistence strategy, including mobility and sexual dimorphism, and ecological context, such as environmental terrain, within past populations. Also, studies of long bone structural variation within individuals helps in understanding patterns of ontogenetic change in response to mechanical loading.

Previous investigations have focused much attention on the behavioral patterns associated with subsistence strategy. Bone biomechanical research within this area typically characterizes groups as either possessing hunter-gatherer, agricultural or industrial subsistence economies. Associated with these strategies is mobility pattern, activity level and the degree of sexual dimorphism in mobility, activity type, and activity level. In general, on a continuum from hunting and gathering to industrial groups—with

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agricultural groups in between—mobility and sexual dimorphism decreases (Ruff, 1987; Ruff, 2005). Examination of the effects of these subsistence behaviors on long bone diaphyseal structure have largely been between hunter-gatherer and agricultural groups, especially within the transition to agriculture in the same region (Ruff et al., 1984; Bridges, 1989; Wescott and Cunningham, 2006; Wescott, 2008.). Shape differences in femoral midshaft and sexual dimorphism in shape and robusticity (strength/size) are the most consistent effects associated with subsistence (Wescott, 2001).

Ruff and colleagues (1984), for example, studied the long bone diaphyseal structural differences between the prehistoric preagricultural and agricultural groups from the Georgia coast of the United States. The femoral diaphyses of the agricultural group demonstrated a general decline in bone rigidity compared to hunter-gatherers, in particular in male subtrochantric maximum bending rigidity (I_{max}) and torsional rigidity (J). Agricultural males also showed a significant decline in cross-sectional "shape index" (I_{max}/I_{min}) at the femoral subtrochantric region and in the "mobility index" (I_x/I_y) at the femoral midshaft compared to hunter-gatherers. This indicates that the agricultural group, at least within the males, had a relatively more circular cross-sectional shape and a relative reduction in the anteroposterior bending rigidity compared to the preagricultural group. These results support the interpretation that the agricultural group experienced an increase in sedentism and a decreased workload, leading to participation in less intensive subsistence activities (Ruff et al., 1984). A similar trend within the cross-sectional properties of humeri was also observed (Ruff and Larsen, 1990).

Bridges (1989) conducted a similar study of long bone structural variation during the transition to agriculture in the southeastern United States, specifically within the

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northwest region of Alabama (Bridges, 1995). In contrast to the transition in the Georgia coast, Bridges found that the long bone structural variation between the Archaic hunter-gatherers and Mississippian agriculturalist did not demonstrate a trend of decreasing workload (1989). Rather, the adoption of maize agriculture by the Mississippian group was interpreted by Bridges as more intensive than hunting and gathering and manifested skeletally in terms of larger and stronger femoral midshafts, tibiae, humeri, radii, and ulnae. The pattern of structural change between the sexes illustrates that a change in the division of labor occurred.

Previous research has also examined the differences in long bone diaphyseal structure based on sex. Sexual dimorphism in this regard is attributed to differences in mechanical loadings associated typically with different workload activities and thus with the sexual division of labor. For instance, Ruff (1987) observed that sexual dimorphism was different in femoral midshaft cross-sectional shape across the continuum of subsistence strategies studied. Hunter-gatherers demonstrated the greatest sexual dimorphism, as measured by the difference in the ratio of anteroposterior to mediolateral bending rigidity (I_x/I_y), while agriculturalists displayed less and industrialists only showed minimal sexual dimorphism (Ruff, 1987; Ruff, 2005). This trend is most likely correlated with the tendency for male hunter-gatherers to be more mobile than females within the same group (Ruff, 1987). In Bridges (1989) study, however, compared with the Archaic males and females, Mississippian males had a greater increase in bone strength in the lower limbs, while females were similar in strength in both the upper and lower limbs in the two populations. Bridges (1989) suggests that this increased disparity between the sexes could possibly be due to an increase in the variety of activities taken

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on by females with the shift to agriculture. Bilateral asymmetry of the Mississippian female distal humeri indicates that maize processing utilizing mortars and pestles likely contributed to their morphology (Bridges, 1989).

Other recent studies also illustrate the conflicting effect of subsistence on femoral cross-sectional properties. A study conducted by Wescott (2006) on North American hunter-gatherers, horticulturalists, and industrialists with varying levels of mobility—the daily distance traveled by an individual or group from the residence and back (Kelly, 1983, 1992)—supports the pattern of sexual dimorphism observed by Ruff (1987), but only within highly mobile groups. As a result, the investigation highlights the issue in using mobility pattern in relation to subsistence strategy. Many researchers argue that mobility pattern can be estimated using the "mobility index"—the ratio of anteroposterior to mediolateral second moments of area (I_x/I_y) of the femur midshaft (Ruff, 1987; Larsen, 1997; Stock and Pfeiffer, 2001). However, others criticize the complexity of teasing out mobility from other factors that also affect long bone diaphyseal morphology, but which are unrelated to mechanical loading. Wescott (2006: 205) provides further support for these criticisms and concludes that the "morphological differences [in femora midshaft diaphyseal structure] were not found consistently in all populations, suggesting that the effect of mobility on femur midshaft structure may not be universal".

The physical environment or terrain in which a particular group lives also has an impact on mechanical loading of the skeleton, and thus affects lower limb long bone diaphyseal morphology. A study by Ruff (1999) compared Amerindian preagricultural and agricultural groups with varying types of terrain. Amerindians preagricultural and

agricultural groups from Georgia were associated with the coastal terrain, preagricultural

and agricultural groups from South Dakota were associated with a plains environment,

and the preagricultural Great Basin and New Mexican agriculturalist groups were

categorized as mountainous. Results demonstrated that femoral midshaft bending and

torsional rigidity (J) was significantly greater for rugged, mountainous samples when

compared to groups from lower relief areas such as the plains and coast. Differences

between the plains and coastal regions were not significant. Also, this pattern was not

demonstrated in the humerus (Ruff, 1999).

Climate additionally influences the structure of long bone diaphyses. Previous

research demonstrates that climate has an effect on both long bone robusticity and shape.

For instance, Pearson (2000) conducted a study that analyzed modern hunter-gatherer and

sedentary groups from different regions with cold and hot climates. Results generally

showed that groups within the colder environment had more robust upper and lower limb

diaphyses than groups from warmer environments. Pearson (2000) attributed this

outcome to the effect of limb length on robusticity—as defined by biomechanical

strength relative limb length—whereby cold-adapted groups possessing shorter limbs are

more robust than warm-adapted groups that have longer limbs. A more recent study by

Stock (2006) also found the negative correlation of climate to robusticity in the upper and

lower limbs.

Weaver (2003) additionally demonstrated the impact of climate on long bone

diaphyseal shape. The study revealed that in cold-adapted individuals femoral midshaft

shape is more circular than in warm-adapted individuals. Weaver (2003) attributed this

difference to the variation of body proportions generated by climatic adaptation. Thus,

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the more circular femoral midshaft shape of cold-adapted groups is understood as resulting from a wider body shape that is influenced more by mediolateral loading.

Overall, these studies demonstrate that by utilizing cross-sectional geometric analysis the variation observed in long bone diaphyseal structure can be understood in terms of the mechanical loadings applied during life. In general, research shows that hunter-gatherer groups are expected—due to high levels of mobility, sex differences in workload and a generally high level of activity—to exhibit more robust long bones, more pronounced differences in long bone structure between the sexes, and to display a less circular femoral midshaft shape. However, reconstructing the activity patterns of these past populations is not always consistent. For instance, trends in long bone structural changes during the agricultural transition are inconsistent when relating groups across regions. The effects of terrain relief and climate also vary by group. Therefore, when interpreting long bone structure in terms of activity patterns, these inconsistencies must be kept in mind.

II. BIOCULTURAL CONTEXT OF JOMON PERIOD JAPAN

The following discussion explores issues of Jomon origins, geography, environmental variability, subsistence economy, diet and morphology to establish a biocultural context for Jomon people. This will aid in the development of hypotheses regarding Jomon cross-sectional diaphyseal morphology. In particular, Jomon people from the Yoshigo site in the Tokai coastal region of eastern Honshu will be investigated to assess this issue.

Origins of the Jomon People

The Jomon were a prehistoric group of hunter-gatherers that inhabited the Japanese archipelago beginning around 14,500 through 2300 BP (Hanihara, 1991; Habu, 2004). The manufacture and use of pottery characterizes the Jomon culture and, in fact, the term Jomon means "cord-marked", which refers to the type of cord impressed decoration used extensively in Jomon pottery (Kobayashi, 2005). The Jomon people show no evidence of adoption of an agricultural subsistence strategy (Akazawa, 1999). Rather, the Jomon are recognized as sedentary hunter-fisher-gatherers that exploited all regions of the Japanese archipelago. Today, the Ainu—the indigenous population of Hokkaido—are identified as the direct descendents of Jomon people (Adachi et al., 2009).

The Japanese archipelago was initially populated by a group of Late Pleistocene migrants that developed a culture represented in the archaeological record by a knife-blade tool kit (Kobayashi, 2005). Around 20,000 BP the ancestors of the Jomon migrated into Hokkaido displacing and absorbing this earlier culture. It was from these Pleistocene nomads, which were associated with a microlithic technology similar to the Yubetsu culture of Siberia, and their expansion within the Japanese Islands that the Jomon ceramic culture developed at approximately 13,000 BP (Imamura, 1996; Kobayahsi, 2005; Hanihara and Ishida, 2009). Several hypotheses attempt to clarify the geographical point of origin for Pleistocene microlithic and Jomon cultures of Japan.

Research based on a dental morphological complex suggests that the ancestors of Jomon people originated in Southeast Asia (Turner, 1990). Utilizing Asian and Pacific dental morphological variation, Turner (1990) determined that the variation separated

into two distinct patterns known as sundadonty and sinodonty based of frequencies of crown and root features. Sundadonty is the dental pattern associated with people of Southeast Asian origin, while sinodonty is the more complex pattern associated with the inhabitants of Northeast Asia and derived from sundadont morphology. Analysis shows that unlike other inhabitants of Japan, the Jomon and some Ainu possess a sundadont pattern similar to Southeast Asian populations. Thus, Turner's conclusion points to Jomon ancestral origins in Sundaland (1990). Similarity in cranial and dental metrics between the Jomon and the inhabitants of modern Southeast Asia support Turner's (1990) conclusions (Hanihara, 1991; Matsumura, 2007).

Another set of hypotheses predict Jomon ancestral origins in Northeast or Central Asia. Evidence for this conclusion stems from research on cranial metrics, modern and ancient DNA, and body size estimates. In a comparison of craniometric variation between Jomon crania and a series of samples from Eurasia, Africa and Australia, Hanihara and Ishida (2009) demonstrate that the Jomon were most similar to the Northeast Asian sample. In addition, intraregional variation was highest within Hokkaido, indicating this region as the initial source of ancestral occupation (Hanihara and Ishida, 2009). Furthermore, in a study comparing mtDNA haplogroups from Hokkaido Jomon and modern East Asian and Siberian samples, the Jomon exhibited a strong genetic relationship with southeastern Siberians (Adachi et al., 2009). However, analysis of Y-chromosome haplogroups between modern Japanese, Ainu and Central, Southeastern, and Northeastern Asian samples suggests that Paleolithic founders contributed to two lineages founded in Central Asia. These data also indicate that the Paleolithic male lineages entered Japan around 20,000 years ago (Hammer et al., 2006).

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Enlarged relative body size retained in Late/Final Jomon people further suggest long term evolution in a cold environment before migration to Japan by ancestors of the Jomon people (Temple et al., 2008; Temple and Matsumura, 2010).

Environmental Variation and Jomon Dietary Pattern

Jomon people occupied the main islands of Hokkaido, Honshu, Shikoku, and Kyushu. It is customary to identify the geographic areas of western Japan as the southwestern regions of Honshu, the Kinki and Chugoku districts, and the islands of Shikoku and Kyushu. The eastern regions of Japan refer to southern Tohoku, Kanto, Chubu, Hokuriku, and Tokai regions of Honshu, while the northern regions references northern Tohoku and the island of Hokkaido (Habu, 2004) (Figure 2).

Through discriminant function analysis of lithic and marine tools from approximately 200 Final Jomon sites, Akazawa (1986) demonstrated that specific tool kits developed in different environments. The Jomon sites discriminated into eastern and western regions with further distinction of western sites within a forest-freshwater transitional zone and eastern sites occupying three geographically distinct resource exploitation regions: 1) the inland and coastal area of the Sea of Japan, 2) the coastal area of Tokai and Kanto districts (coastal lowlands), and 3) and the coastal area of Tohoku and Hokkaido districts (northern coast). The tool kits of the eastern sites functioned for marine and terrestrial use, while the western tool kit was for terrestrial plant exploitation, suggesting resource procurement adaptations to regional ecology.

Figure 2. Map of the regions of Japan. Modified from d-maps.com, Daniel Dalet (2007).

Stable isotope analyses support the impact of environmental variability of the archipelago on Jomon dietary patterns. Interregional variation in Jomon diet is recognized in the eastern regions of Japan at coastal sites in Hokkaido and coastal and inland sites within northeastern Honshu. Between the Honshu and Hokkaido samples studied by Minagawa and Akazawa (1992), more dietary variation was found within the Honshu sample. The Honshu sites had proportional mixing of terrestrial and marine foods with coastal sites showing more dependence on marine foods than the inland site studied. The Hokkaido sample, in contrast, showed more consumption of large marine animals and with little C_4 plant consumption. However, eastern and western regions demonstrated similarity in reliance on plants.

Analysis of carbon and nitrogen isotopes taken from Jomon skeletal samples from Honshu and Hokkaido by Chisholm and Koike (1999) demonstrate a disparity between

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eastern and western sites. The relative proportion of dietary protein from marine resources was more prevalent in eastern Japan at 40-80%, with sites from Hokkaido slightly more marine based than central Honshu sites. Western Honshu marine protein was at less than 50% of dietary intake. Further study indicates that interregional variation in diet existed between coastal and inland sites, as shown in Minagawa and Akazawa's study (1992). As would be expected, coastal sites were more marine oriented than the inland sites. In Honshu, the coast had proportional mixing of terrestrial and marine resources, while inland resources were more terrestrial based. In terms of the actual food sources in each sample, Honshu reflected consumption of C_3 plants, terrestrial herbivores, shellfish, fish and possibly C_4 plants (Chisholm and Koike, 1999).

A recent carbon and nitrogen stable isotope analysis further reveals the similarity in diet at coastal sites between eastern and western Honshu dating from the Middle to Final Jomon period (Kusaka et al., 2010). The isotopic analysis revealed that coastal sites from both regions consumed a wide range of marine and terrestrial foods. In particular, each region was consuming a mixed diet of marine protein based on shellfish and fish and terrestrial protein from C_3 plants and terrestrial mammals.

From these studies it is clear that similar amounts of plant food and marine food were consumed between regions. Differences in resource availability based on environmental variability are likely. In the west, during the Jomon period, broadleaf evergreen forests dominated while in the eastern half of the archipelago deciduous forests were prominent (Akazawa 1999). Tsukada describes western postglacial forests as "dense with broad, shiny-leaved evergreen species of oaks and other laurel trees" while the eastern forests had "predominantly deciduous broadleaf species" (1986: 11). The

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eastern forests were much richer in the natural resources available for use by hunter-gatherers (Tsukada, 1986).

Skeletal evidence supports this difference in resource availability between regions. A study of Middle to Final Jomon period remains conducted by Temple (2007a) compared frequencies of stress indicators—linear enamel hypoplasia (LEH) and carious teeth—between eastern and western/inland regions. The results reveal that the frequencies of LEH were greater in the western/inland sample than the eastern sample. This is expected given that the western/inland region was located within an area where resources were less available. Caries frequency was similar between the regional groups demonstrating similarity in plant intake. Despite variation in stress, Jomon in different regions were the same height indicating that minimal caloric intake between the two groups was similar enough to sustain normal longitudinal growth (Temple, 2008).

In contrast, carious teeth were more prevalent in the Late/Final Jomon period (Temple, 2007a). Temple (2007a) suggests that, as a result, a subsistence shift may have occurred between the Middle and Final Jomon period. This work is further supported by isotope analysis (Kusaka et al., 2010). Combined with other research that demonstrates a temporal increase in stress in the form of greater frequencies of periostitis and decreasing stature in western Jomon, an increase in chronic infection via increased pathogen load was also suggested (Temple, 2007b; Temple, 2008). Overall, these results are consistent with the consequences of a population aggregation and weakened immune systems via nutritional stress (Temple, 2008).

Although plants played a significant role in the Jomon diet, Jomon subsistence practices do not suggest a level of food production consistent with an agricultural strategy

(Temple, 2007b; Temple and Larsen, 2007; Tsude, 2001). Rindos (1984) defines agriculture on the basis of a co-evolved mutual dependence between humans and plants with much human energy expended on plant cultivation. However, a high level of energy was not spent towards plant cultivation by the Jomon. Paleobotantical evidence does demonstrate that the Jomon participated in some plant cultivation and domestication (Hudson, 1999). This is reflected in the botanical remains of such plants as bottle gourds, barnyard millet, azuki and mung beans, Perilla herbs, great burdock, paper mulberry, lacquer tree, hemp, barley, and buckwheat. Other possible cultigens include peaches, broomcorn millet, foxtail millet, melons and Chinese cabbage (Crawford, 1992a, 1992b). It should be emphasized, however, that it was not until the Yayoi period that agriculture, in the form of wet rice farming, appeared in Japan (Hudson, 1999).

Morphological Analyses of Jomon Postcranial Skeletons

Previous bioarchaeological research has utilized skeletal remains to reconstruct the biocultural context of the prehistoric Jomon. For example, examination of variation in limb proportions between prehistoric Jomon, Yayoi agriculturalists and modern Japanese provides evidence for ecogeographical adaptation in the Jomon. The relative length of Jomon limbs follows a pattern of distal relative to proximal elongation, which contributes to the high crural and brachial indices of the Jomon (Kato and Ogata, 1989; Yamaguchi, 1989; Temple et al., 2008). It is hypothesized that this pattern is either a retention of an ancestral trait in the Jomon, representing the temperate/tropical limb proportions of their ancestors, or it corresponds to a morphological change after colonization of the archipelago from a colder climate (Temple et al., 2008). An

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alternative hypothesis suggests that Jomon limb proportions are an adaptation to "life-mode" or locomotion during hunting activities (Kato and Ogata, 1989: 19). However, little evidence for a relationship between locomotion and intralimb indices is observed in modern humans (Holliday and Falsetti, 1995; Holliday, 1999). Temple and colleagues (2008), suggest that this morphology represents changes following migration into the Japanese Islands by Pleistocene ancestors of the Jomon people. Specifically, the Jomon are viewed as a "transitional variant" with retention of shorter proximal elements adapted to their ancestral cold environment, while their distally elongated limbs are an indication of adaptation to a warmer, contemporary environment (Temple et al., 2008: 171). It is also possible that these proportions are associated with founder effect and some selection (Temple and Matsumura, 2010).

Previous research on Jomon long bone cross-sectional geometry is used to aid in the reconstruction of activities of the prehistoric Jomon. Analyses on humeri, femora, tibiae and fibulae demonstrate that the Jomon express robust long bones consistent with a hunting and gathering subsistence behavior (Kimura and Takahashi, 1982; Nakatsukasa, 1990; Kimura, 2006; Sakaue, 1998). For example, when compared to modern Japanese samples, larger second moments of area at the long bone midshafts indicate that the Jomon—from Middle to Late and Late to Final periods in the Kanto and Setouchi and Toukai districts, respectively—have stronger resistance against bending and torsion, particularly in the antero-posterior direction, in both femora and tibiae (Kimura and Takahashi, 1982; Nakatsukasa, 1990; Kimura, 2006). This is visually apparent in the Jomon femora, which often manifest a developed linea aspera—identified externally as pilastering (Kimura, 2006). Based on analysis of external cross-sections in subadults,

Okazaki (2007) demonstrated that pilastering of the Jomon femora develops in early adolescence, which suggests that Jomon subadults participated in hunting and gathering activities by adolescence. However, the impact of developmental genetic adaptation cannot be excluded.

A significant sex difference in the mechanical resistance to bending in the antero-posterior direction has also been found in Jomon femora. In particular, male Jomon femora demonstrate stronger resistance to mechanical loads (anteroposterior bending), and thus pilastering, than Jomon females (Kimura, 2006; Nakatsukasa, 1990). This suggests that Jomon men were doing activities that placed a higher load on their lower limbs. The degree of sexual dimorphism is highlighted further when Jomon and modern Japanese femora are compared. Modern samples show no significant sex difference, while Jomon samples clearly do (Nakatsukasa, 1990). Both Kimura (2006) and Nakatsukasa (1990) observed this sexual dimorphism in femoral structure and suggested the disparity stems from a sexual division of labor among the Jomon.

Research has also been conducted on the upper limbs of the Jomon. A study carried out by Sakaue (1998) on Jomon humeri from Middle to Late shell mound sites from the reveal similar patterns as in Jomon femora. First, Jomon humeri demonstrate a higher resistance to mechanical loading than modern Japanese humeri, and a similar level of sexual dimorphism as other hunter-gatherer groups. This serves as another indication that a sexual division of labor existed in Jomon society. However, the Jomon display no difference in cross-sectional properties between the right and left humeri, suggesting that both sexes were involved in activities that placed bilateral loads on the upper limbs (Sakaue, 1998). Okazaki (2007) found that the infants (1-3 years of age) also display

robust humeri, which he argued is indicative of early participation in habitual activities perhaps related to subsistence. However, this may also be an indicator of a genetic potential for bone robustness.

As described, previous research using cross-sectional geometric analyses of Jomon long bones has focused on making comparisons with modern samples. Inferring activity patterns through the use of this method has thus been limited. By comparing Jomon long bones with other hunter-gatherers from similar environments and with generally similar subsistence activities, Jomon long bone structure can be appropriately evaluated. As a result, the present study compares Jomon femora and humeri with femora and humeri from other coastal hunter-gatherer groups to more clearly assess Jomon long bone structure and activity patterns.

IV. BACKGROUND: STUDY SAMPLES

To set up the background for the hypotheses that are tested, descriptions of the study samples are provided. In particular, to understand the context of the Yoshigo skeletal sample, the Yoshigo site is first described. The contexts of the skeletal samples that serve as comparisons in hypothesis testing are also offered. These samples include the skeletal remains of coastal hunter-gatherers from Alaska, California, and the Georgia Coast.
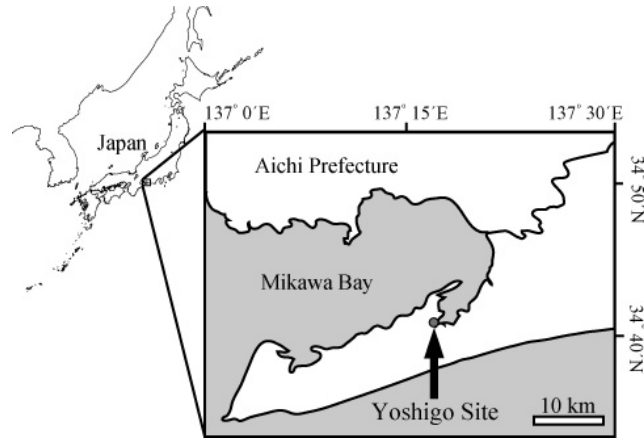
Figure 3. Location of Yoshigo site. Modified from Temple and Matsumura (2010).

Yoshigo site: An Overview

Yoshigo is a Late to Final Jomon period shell mound site located on the Bay of

Mikawa in Aichi Prefecture, Tokai district, along the coast of eastern Honshu, Japan

(Figure 3.). Excavations of the site occurred in 1922 and 1923 led by Dr. Kiyono and

later in 1951 by the Commission for the Protection of Cultural Properties in conjunction

with the Aichi Prefectural Educational Committee. These excavations yielded the

skeletal remains of over 300 individuals, some with associated burial goods, and

numerous lithic and ceramic artifacts (Saito et al., 1952; Harunari, 1986). Artifacts at

Yoshigo include "earthenware, pieces of stone artifacts such as stone axes, stone

arrowheads, stone weights and aliening stones; bone and horn pieces such as shell

bracelets, bone arrowheads and bone needles; pieces made of shell; and other such

artificial objects" (Saito et al., 1952: xii). Radiocarbon analysis of human bone collagen

at Yoshigo date the site at 3200 to 2800 cal BP (Kusaka et al., 2009).

The cemetery within the site has been the focus of much research (Harunari,

1986; Kusaka et al., 2008; Temple and Sciulli, 2005; Temple, 2007a; Temple, 2010;

Temple et al., 2010). The remains of over 300 individuals are located within two circular, banded areas. Each area is divided into smaller segments, generating eight burial sectors within each circular area (Harunari, 1986). Grave goods found associated with the burials reflect the achieved social identities of the individuals. Ritual tooth ablation is also present and research has determined that these social markers were not related to patterns of postmarital residence, but rather to age (Temple et al., 2010). Further study has determined that the group identities associated with different forms of ritual tooth ablation may relate to kin-based social units with age or achievement acting as the basis for group membership (Temple et al., 2010; Kusaka et al., 2008).

Diet and subsistence in the Yoshigo site follows the pattern of regional variation discussed previously. In particular, as an eastern coastal site, Yoshigo shows a larger portion of dietary protein derived from marine sources than terrestrial sources. Stable isotope analysis suggests that marine resources contributed between 40% and 80% to the diet of Yoshigo's inhabitants (Chisholm and Koike, 1999). Further analysis by Kusaka and colleagues (2008) supports this conclusion and points to finfish and shellfish as the main sources of marine protein and C_3 plants and terrestrial mammals as their source of terrestrial protein. It was also noted that in comparison with other Jomon sites, Yoshigo had a greater degree of dietary variability. This was indicated by large variation in the standard deviations of δC^{13} and, particularly, δN^{15} values of the sample. The dietary variability was further distinguished by sex with males having a more variable diet than females. This likely reflects both a sexual division of labor and occupational differentiation in males from Yoshigo (Kusaka et al., 2008).

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Comparative Samples

Aleuts

The Alaskan group is derived from several sites within the Aleutian Islands, mainly from Kagamil, Ship Rock and Umnak, and has a temporal range from late prehistoric to historic. Although spatially and temporally broad, the Aleut sample exhibits both biological and cultural homogeneity (McCartney, 1984; Smith et al., 2009). Archaeological remains and ethnographic accounts provide evidence for the types of subsistence activities performed by the Aleuts. The ocean provided these hunter-gatherers with much of their subsistence base. Sea mammals such as sea otters, seals, sea lions and whales were captured on kayaks and open skin boats by way of harpoons (Hrdlicka, 1945; Laughlin, 1970, 1975). Fishing was also important and was accomplished through the use of hooks and lines, nets and weirs (Hrdlicka, 1945). Terrestrial hunting was limited to capture of caribou and deer on Aleutian Islands, and Hrdlicka (1945) emphasizes that there was no land hunting except near the Alaskan Peninsula and the island of Unimak. While males mainly hunted on the open ocean and fished, female Aleuts collected seaweed, roots and shellfish in addition to creating clothing, mats, baskets and cordage (Osborn, 1990; Hrdlicka, 1945).

California Amerinds

The California group is derived from the Ryan Mound shell mound site (CA-Ala-329) located on the eastern shore of the San Francisco Bay area (Coberly, 1973; Leventhal, 1993). Radiocarbon dating places the specimens in a temporal range of 2180 - 250 BP and prior to European contact (Leventhal, 1993; Weiss, 2009). Archaeological

evidence demonstrates that hunting, fishing and gathering were occurring at this site as evinced by obsidian points, hooks, harpoons and mortars and pestles. Furthermore, analysis of burial good associations suggests that males were clearly hunting and fishing while females were gathering (Leventhal, 1993). Specifically the group hunted deer, birds and other small game, in addition to fishing, and collection of shellfish, nuts and seeds (Coberly, 1973; Leventhal, 1993). Weiss (2009) emphasizes that compared to ocean-rowing British Columbian Amerinds, the California group traveled by canoe and used marine resources less extensively.

Georgia Coast Precontact Preagriculturalists

The Georgia coast preagriculturalists represent a biologically and culturally homogenous group that relied upon a hunting, fishing and gathering subsistence economy. Faunal and plant remains provide evidence for the dependence on riverine, estuarine and marsh resources within the group. In particular, the preagriculturalists collected several types of mollusks, such as clams, oysters and mussels, and fished for several species of fish such as trout, bass, ray and flounder. Sea mammals, including otters, seals and whales have also been found among faunal remains at Georgia coast sites, but not consistently across the temporal periods. There is also evidence for abundant hunting of deer and other land mammals like raccoons and rabbits. Acorns and hickory nuts were the main plant resources utilized across the preagricultural period (Larsen, 1982). The group also relied upon marine travel using tule reed boats to access food resources in rivers and marshes (Hudson, 1976; Weiss, 2003). As in other hunter-gatherer groups males were the predominant hunters while females gathered plants and

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shellfish (Hudson, 1976; Larsen, 1982).

III. HYPOTHESES ON JOMON LONG BONE STRUCTURE AND ACTIVITY PATTERNS

Archaeological and bioarchaeological evidence indicate that the Jomon were residentially sedentary hunter-gatherers that subsisted on both terrestrial and marine food resources in varying proportions, and were likely logistically mobile (Habu, 2001, 2004; Imamura, 1996). In particular, the Jomon used both forest and coastal environments and, based on environmental variability, consumed more marine protein and terrestrial foods in the coastal regions than in the inland regions of Japan. Given this information, the premises of bone functional adaptation and the biomechanical model, and based on the previously described biomechanical analyses of archaeological groups, three research hypotheses are developed.

Hypothesis I: Robusticity and shape of femoral diaphyses at Yoshigo will not significantly differ from Aleut hunter-gatherers.

Mobility is a defining characteristic of hunter-gatherer groups (Kelly, 1992). Past research (Holt, 2003; Ruff, 1987; Ruff and Larsen, 1990; Ruff et al., 1993; Stock and Pfeiffer, 2001, 2004; Marchi, 2008) suggests that the structure of the femoral and tibial midshaft corresponds with terrestrial logistic mobility—the daily distance traveled by an individual or group from the residence and back (Kelly, 1992; Kelly, 1983). Archaeological evidence indicates that the Jomon people were residentially sedentary

hunter-gatherers that remained at year round settlements (Watanabe, 1986; Pearson, 2006), but likely sent coordinated hunting parties to procure resources (Habu, 2001, 2004). The Aleuts were also a residentially stable group which made, on average, only one residential move per year (Coxe, 1894; Kelly, 1983). It is predicted that the Jomon people at the Yoshigo site will demonstrate comparable levels and patterns of mobility when compared to other hunter-gatherers from similar environments and with similar residential mobility. This will be indicated in the cross-sectional properties of CA, I, J, and the I_x/I_y ratio between the lower limb of Jomon and Aleut groups. Specifically, it is predicted that the Jomon and Aleut will have similar robusticity (J), and shape (I_x/I_y).

Hypothesis II: Robusticity and shape of humeral diaphyses at the Yoshigo site will not significantly differ from hunter-gatherers that participated in ocean rowing (Aleut) and will significantly differ from those hunter-gatherers that did not row upon the ocean (California and Georgia coast hunter-gatherers) in terms of robusticity, but not shape.

Previous research indicates that upper limb structural variation, in particular diaphyseal robusticity and shape, correlates with marine mobility (Stock and Pfeiffer, 2001; Weiss 2003; Stock, 2006). Bioarchaeological evidence demonstrates that the Jomon people hunted terrestrially and fished in both inland and coastal regions (Akazawa, 1988). It is specifically predicted that the Jomon humeri will be similar in robusticity (J) and shape (I_x/I_y) as the Aleut humeri, and will be larger in robusticity than the California and Georgia coast hunter-gatherers, but similar in shape.

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Hypothesis III: No significant difference in sexual dimorphism in robusticity and shape of femora and humeri will be observed between the Jomon at Yoshigo compared to the Aleut, California and Georgia coast hunter-gatherers.

Sexual dimorphism in long bone structure, due to differences in mechanical loading between the sexes, relates to the sexual division of labor associated with subsistence strategy. In particular, previous research reveals a decreasing trend from hunting and gathering to agricultural and industrial societies especially in the reduction of robusticity and shape in males (Ruff, 1987). Additionally, it has been shown that sexual dimorphism in long bone diaphyseal shape and robusticity are the most consistent effects associated with subsistence (Wescott, 2001). As the Jomon people relied upon a hunting and gathering subsistence, it is expected that there will be differences in the values of CA, I, J and I_x/I_y between the males and females in both femora and humeri between groups. It is predicted that the Jomon will be similar in terms of sexual dimorphism in robusticity (J) and shape (I_x/I_y) as all the comparative groups.

To summarize, it is expected that the Jomon from Yoshigo will demonstrate similar long bone morphology as other coastal, marine hunter-gatherers. As a result, through cross-sectional geometric analysis, the Jomon are expected to exhibit: 1) robusticity of femoral and humeral diaphyses in terms of the polar second moment of area (J) which is indicative of average bending rigidity, 2) greater femoral and humeral A-P bending rigidity of the diaphyses as measured by the shape ratio (I_x/I_y), and 3) sex differences in diaphyseal shape (I_x/I_y), and overall robusticity (J) in the femora and humeri similar to the coastal hunter-gatherers of Alaska, California, and Georgia. Testing these hypotheses will provide insight on Jomon mobility patterns, marine

activities and differences in male and female activities.

CHAPTER 2: MATERIALS & METHODS

The following chapter introduces the reader to the materials from which data were collected, including the Jomon sample from the Yoshigo site and the comparative samples derived from Alaska, California and the Georgia Coast. The methods used in data collection and hypothesis testing are also provided. Additionally, the methods used in obtaining the cross-sectional geometric properties are explained in detail. Finally, the statistical methods used to test the hypotheses in relation to the Yoshigo sample are explained.

I. MATERIALS

Yoshigo Sample

A skeletal sample comprised of femora and humeri acquired from 23 individuals ($N_{\male}$ = 12, $N_{\female}$ = 11) from the Kiyono collection curated at the Laboratory of Physical Anthropology, University of Kyoto was used in this study. Femora and humeri were selected by Dr. Daniel Temple based on adult estimated age and a lack of active skeletal indicators of stress including cribra orbitalia and periostitis. Individuals with linear enamel hypoplasia defects were included since these lesions are indicative of past events. While age was analyzed based on the morphology of the pubic symphysis and auricular surface of the pelvis, epiphyseal fusion, and mandibular dental wear, sex was determined

by assessment of the pelvis, particularly through analysis of the morphological variation

within the pubic bone and greater sciatic notch (Temple, 2007b). In total, computed

tomographic (CT) scans were collected by Dr. Temple from 20 femora ($N_\male = 9$, $N_\female = 11$)

and 10 humeri ($N_\male = 6$, $N_\female = 4$) with left sides preferentially used unless prevented by

poor preservation (Appendix 2). A CT scanner housed at the Laboratory of Physical

Anthropology, University of Kyoto was used to obtain CT images. Methods for

assessment of age, sex, pathological lesions and bone measurement are presented in

Temple (2007b). The cross-sectional properties from the CT images were calculated and

analyzed by the present author.

Comparative samples

Aleuts

The Aleut sample consists of 38 femora ($N_\male = 20$, $N_\female = 18$) and 29 humeri ($N_\male = 17$, $N_\female = 12$) aged 17-50. Dr. Daniel Wescott scanned the humeri and femora using a CT

scanner at the Smithsonian National Museum of Natural History. Age and sex of the

individuals were estimated by Wescott previously. Also, Wescott provided cross-

sectional properties of the femora, while raw CT scans of the humeri were supplied from

which I calculated cross-sectional properties.

California Amerinds

Humeral cross-sections of California hunter-gatherers were provided by Dr.

Elizabeth Weiss and consist of 107 humeri ($N_\male = 45$, $N_\female = 62$) of individuals aged

between 16 to 50 years. Sex and age were previously assessed by Jurmain (1990), while

cross-sectional data was obtained from radiographs by Weiss (2009) (note: see General Considerations section for discussion of using x-ray data). Left sides were preferentially used over rights.

<div align="center">Georgia Coast Precontact Preagriculturalists</div>

The Georgia coast sample was supplied by Dr. Christopher Ruff and consists of 27 humeri ($N_\male = 15$, $N_\female = 12$) from individuals aged 16-50 years. The sample originates from several precontact sites along the coast of Georgia dated 2200 BC to 1150 AD (Larsen, 1982; Ruff et al., 1984; Ruff and Larsen, 1990). Cross-sectional properties were obtained by direct sectioning of humeri and then quantified from photographs using the program SLICE. After cross-sectional properties were obtained the values were side averaged to control for bilateral asymmetry (Ruff and Larsen, 1990). Sex and age of the sample remains were previously evaluated by Larsen (1982).

<div align="center">II. METHODS</div>

<div align="center">*Preparation of Cross-sections*</div>

In terms of the Yoshigo sample, computed tomographic scans of femora and humeri were taken at 50% and 35% of bone length, respectively, by Dr. Temple. These cross-sectional locations were chosen based on standard use in cross-sectional geometric analyses and their avoidance of many muscle attachment sites, for example with the deltoid tuberosity of the humerus. Bone lengths and femoral head diameter were obtained to control for body size. Femoral length is the maximum bone length defined as the distance from the most distal edge of the condyles to the superior or proximal edge of

the femoral neck. Femoral head diameter or femoral head breadth (FHB) was measured along the superior-inferior plane. Humeral length is defined as the distance from the distal edge of the lateral lip of the trochlea to the proximal edge of the humeral head (Ruff and Larsen, 1990).

Before scanning, each long bone was positioned in relation to the sagittal and coronal planes. The femora were oriented in accordance with Ruff and Hayes (1983), while the humeri were positioned as described by Ruff (2002). In general, each bone was initially laid posterior side down and leveled. For the femur leveling the coronal plane was established by placing a support under the proximal end until the anteroposterior (AP) midpoints, taken distal to the lesser trochanter, until it was equidistant from the surface to the midpoint of the proximal condyles. The sagittal plane was determined as passing through the mediolateral (ML) midpoints, which were located just distal to the lesser trochanter proximally and at the deepest point of the intercondylar notch distally (Ruff and Hayes, 1983; Ruff, 2002).

A similar method was used to establish the planes in the humerus. After leveling, with a support placed under the distal end of the humerus, the coronal plane was established. The plane was determined to be parallel to the surface passing through the AP midpoints of the shaft distal to the head and the lesser tubercle and proximal edge of the olecranon fossa. The ML midpoints oriented the sagittal plane with reference to the surgical neck and lateral lip of the trochlea (Ruff, 2002).

Once each bone was positioned the cross-sectional locations were marked and CT images were then taken perpendicular to the sagittal and coronal planes. Each femur and humerus was scanned and provided a 1-2 mm thick slice with a pixel size of 0.5 mm.

Determination of Cross-sectional Properties

Cross-sectional properties were determined from CT images, which were first converted to TIFF files, and then imported into Image J (http://rsb.info.nih.gov/ij/) and analyzed using Moment Macro (http://www.hpkinsmedicine.org/FAE/mmacro.htm). Moment Macro works by calculating cross-sectional properties based on the density of pixels in a given area of an image under the assumption of an elliptical cross-sectional shape. Prior to analysis trabecular bone was removed from any problematic images using Image J's drawing tools.

The principal properties calculated by Moment Macro included cross-sectional areas, such as total subperiosteal area (TA) and cortical area (CA), second moments of area in relation to the ML (I_x) and AP planes (I_y), and maximum and minimum second moments of area (I_{max} and I_{min}). These properties represent measures of pure compressive and tensile strength (CA) and bending rigidity (I). From these values, the polar second moment of area (J: $I_{max} + I_{min}$) and the ratio of I_x/Iy were calculated. Torsional rigidity and average bending rigidity is represented by J, while I_x/Iy indicates diaphyseal shape and AP/ML bending rigidity.

Size Standardization

To control for body size variation between individuals within the Yoshigo sample and between individuals from the Yoshigo sample and samples from the Georgia coast, California and Alaska, cross-sectional properties were size standardized. Body size must be accounted for given that it inherently creates a mechanical load that impacts long bone structure (Ruff, 2008). Therefore, by controlling for variation in body size within and

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between samples, the long bone structure influenced by external loading can be analyzed. Estimates of body size were used to standardize both the femora and humeri based on FHB, and bone length and powers of bone lengths, respectively (Ruff et al, 1991; Ruff et al., 1993; Ruff, 2000; Auerbach and Ruff, 2004).

Femoral head breadth is utilized in estimating body mass based on the fact that articular size correlates with body weight. In particular, the femoral head does not change in external size, but rather is affected internally by trabecular remodeling, thus limiting body weight changes to changes in internal articular structure (Ruff et al., 1991). To estimate body mass the equations formulated by Ruff and colleagues (1991) were utilized: $BM_{\male}= (2.741 \times FHB -54.9) \times 0.9$ and $BM_{\female}= (2.426 \times FHB -35.1) \times 0.9$. These were used instead of those reported by McHenry (1992) and Grine et al. (1995) because the Jomon are not exceptionally large or small in body size (Temple and Matsumura, 2010). These formulae were also applied to the Aleut sample. The product of body mass and bone length were used to standardize second moments of area (I and J) of the femora, while body mass alone was used to standardize cross sectional area (CA) of the femora (Ruff, 2000; Holt, 2003; Stock and Pfeiffer, 2001; 2004; Carlson et al., 2007).

Powers of bone length were applied to size standardize cross-sectional properties of the humeri of all samples. This method was used based on absence of FHB measurements for estimating body mass for all individuals. As a result, powers of bone length, as described by Ruff and colleagues (1993), were appropriately applied. Specifically humeral cross-sectional areas (CA) were standardized by diving by bone length^3 and cross-sectional moments of area (I and J) were divided by bone length$^{5.33}$ (Ruff et al, 1993; Stock and Pfeiffer, 2001; Weiss, 2003).

Data were analyzed using the statistical software programs SAS 9.1 and SYSTAT 12.0. T-tests were used to compare differences in mean cross-sectional properties in the evaluation of terrestrial mobility between the Jomon and Aleut samples. Equality of variance between all groups was examined using a folded F-statistic due to differences in sample size. Where equality of variance was observed, pooled t-tests were used to evaluate the significance of difference in cross-sectional properties related to mobility. Where equality of variance was not observed, Cochran's and Satterwaite's t-statistic were used to evaluate significance of difference in these properties.

The second hypothesis addressing marine mobility was tested by comparing the Jomon sample to the Aleut, California and Georgia samples using a two-factor analysis of variance (ANOVA). In this case, the independent factors were group and sex, while the dependent factor was cross-sectional property. Interactions between independent factors were additionally examined. Tukey's HSD studentized range test was then utilized to investigate the differences in cross-sectional properties between the samples.

Differences in the expression of sexual dimorphism in terms of the cross-sectional properties of I_x/I_y and J were tested between Jomon, Aleut, California and Georgia femora and humeri. Previous studies compare sexual dimorphism, often expressed as the ratio [(male mean-female mean)/female mean]*100 (Ruff, 1987; Ruff and Larsen, 1990; Stock and Pfeiffer, 2004; Marchi, 2008; Wescott, 2008), between males and females of a particular group, but do not always compare the difference in sexual dimorphism between samples. This study, therefore, employs a test statistic that clarifies significance of difference in sexual dimorphism between two samples using mean values (Relethford and

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Hodges, 1985) to explore variability in sexual dimorphism between the Jomon and comparative samples in terms of the cross-sectional properties I_x/I_y and J. This calculation is based on an extension of the t-statistic that tests the equality of slopes males and females of the two samples in the calculation of differences in sexual dimorphism, which is based on a linear regression model (Relethford and Hodges, 1985). T is defined as $(b_1 - b_2) / \sqrt{AB/df}$ where $(b_1 - b_2) = (\overline{Y}_{m1} - \overline{Y}_{f1}) - (\overline{Y}_{m2} - \overline{Y}_{f2})$, $A = [M_1 + F_1/M_1F_1] + [M_2 + F_2/M_2F_2]$, $B = (M_1 - 1)s_{m1}^2 + (F_1 - 1)s_{f1}^2 + (M_2 - 1)s_{m2}^2 + (F_2 - 1)s_{f2}^2$ and $df = M_1 + F_1 + M_2 + F_2 - 4$ (Relethford and Hodges, 1985).

Sexual dimorphism was further explored through the use of t-tests that compared the degree of dimorphism between males and females in terms of I_x/I_y and J after removing individuals with overlapping I_x/I_y and J values within the area of the normal curves shared by both sexes. Thus, this method estimates the difference between the sexes for I_x/I_y and J by eliminating male-female overlap (Bennett, 1981). This is done by first deleting the proportion of males contained within the female distribution curve for the sample. First the point of intersection of the male and female curves is calculated as x $= (\mu_m + \mu_f)/2$. Then the difference between the point of intersection and the male mean is calculated and converted into one standard deviate, which provides the area between the male mean and one standard deviation. By adding 0.5 to this value, the result is the proportion of males that classify as male according to the morphological trait of interest. The procedure is then performed for the females of the sample. To compare if the overlap is similar between two between groups, the proportions are converted into a variable by the use of an arcsine transformation and then applied to t-tests (Bennett,

1981). Here t is defined as $(\arcsin \sqrt{p_1} - \arcsin \sqrt{p_2}) / \sqrt{820.8(\frac{1}{n_1} + \frac{1}{n_2})}$ where p is the

proportion of males or females and n is the sample size.

CHAPTER 3: RESULTS

This chapter presents the results of the statistical tests performed between the Jomon sample from the Yoshigo site and other coastal hunter-gatherers from Alaska, California and Georgia. To help infer mobility in the Jomon sample from Yoshigo femoral cross-sectional properties were compared with the Aleut sample. Next, cross-sectional properties of the humeri were compared between the Jomon sample and the Aleut, California and Georgia samples to aid in understanding marine mobility in the Jomon sample. Finally, differences in sexual dimorphism in the femora and humeri were tested among the samples.

I. FEMORAL COMPARISONS

Summary statistics for the cross-sectional properties of femora from Jomon and Aleut groups are provided in Table 1 with plots of robusticity (J) and shape (Ix/Iy) visible in Figures 4 and 5. Independent group t-test results are given for each sex in Tables 2 and 3. Between Jomon and Aleut samples, CA is larger for both males and females in the Jomon sample. In both sexes the difference is statistically significant (males: $t = 2.11$, $df = 23.8$, $p = 0.0452$; females: $t = 3.4$, $df = 26.4$, $p = 0.0067$).

There are few differences between the Jomon and Aleut in femoral cross-sections. In terms of the second moments of area, I_x and Iy are smaller in the Jomon

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sample compared to the Aleut sample. Between males I_x is not statistically significant (t = -0.98, df = 25.8, p = 0.3368) but I_y is significant (t = -2.15, df = 21.1, p = 0.0429). Jomon and Aleut females demonstrate a statistically significant difference for I_x (t= -2.29, df = 23.3, p = 0.0316) but not in I_y (t = -1.03, df = 27, p = 0.3121).

The shape ratio I_x/I_y between males is larger for the Jomon sample than the Aleut, while the female femoral shape ratio is smaller in the Jomon sample than the Aleut sample. However, in both sexes the difference is not statistically significant (males: t = 1.72, df = 27, p = 0.0972; females: t = -1.4, df =27, p = 0.1732).

The polar second moment of area, J, is smaller in the Jomon sample compared to the Aleut sample, but the difference is not significant for either sex (males: t = -1.5, df = 23, p = 0.1472; females: t = -1.84, df = 24.7, p = 0.0781).

These results provide support for Hypothesis I: Robusticity and shape of femoral diaphyses at Yoshigo will not significantly differ from the Aleut hunter-gatherers. The Jomon do not differ significantly from the Aleuts in J or the ratio of I_x/I_y in either sex. I_x in males and I_y in females are not significantly different between groups, which is likely contributing to the similarity in robusticity and shape in the Jomon and Aleut. CA and I_y, however, are significantly different in males, and CA and I_x significantly differ in females between the Jomon and Aleut samples.

Table 1. Summary statistics by group and sex for femoral cross-sectional properties[1,2].

Cross-sectional property	Statistic	Jomon		Aleut	
		M (n = 9)	F (n = 11)	M (n = 20)	F (n = 18)
CA mm^2	mean	724.371	609.829	622.697	505.639
	SD	51.559	55.293	200.914	108.915
I_x mm^4	mean	11424.234	6697.924	13043.9	8241.19
	SD	2200.1	940.684	6633.94	2596.986
I_y mm^4	mean	8201.39	6616.669	10620.76	7368.031
	SD	789.63	1246.276	4882.803	2203.433
(I_x/I_y)	mean	1.389	1.032	1.245	1.126
	SD	0.221	0.178	0.203	0.174
J mm^4	mean	19625.624	13314.593	23664.66	15609.22
	SD	2762.649	1960.65	11316.93	4665.978

[1]Cross-sectional properties size standardized and with area multiplied by 10^2 and second moments of area multiplied by 10^4.

Table 2. Comparison of femoral cross-sectional properties of Jomon and Aleut males[1,2].

MALES	Jomon (n = 9)		Aleut (n = 20)				
	Mean	SD	Mean	SD	t	df	p-value
CA	**724.371**	**51.559**	**622.697**	**200.914**	**2.11**	**23.8**	**0.0452**
Ix	11424.234	2200.1	13043.898	6633.94	-0.98	25.8	0.3368
Iy	**8201.39**	**789.63**	**10620.761**	**4882.803**	**-2.15**	**21.1**	**0.0429**
(Ix/Iy)	1.389	0.221	1.245	0.203	1.72	27	0.0972
J	19625.624	2762.649	23664.658	11316.932	-1.500	23	0.1472

[1]Cross-sectional properties size standardized and with area multiplied by 10^2 and second moments of area multiplied by 10^4.
[2]Bold values are significant at p ≤ 0.05 based on independent t-tests.

Table 3. Comparison of femoral cross-sectional properties of Jomon and Aleut females[1,2].

FEMALES	Jomon (n = 11)		Aleut (n = 18)				
	Mean	SD	Mean	SD	t	df	p-value
CA	**609.829**	**55.293**	**505.639**	**108.915**	**3.4**	**26.4**	**0.0067**
Ix	**6697.924**	**940.684**	**8241.19**	**2596.986**	**-2.29**	**23.3**	**0.0316**
Iy	6616.669	1246.276	7368.031	2203.433	-1.03	27	0.3121
(Ix/Iy)	1.032	0.178	1.126	0.174	-1.4	27	0.1732
J	13314.593	1960.65	15609.22	4665.978	-1.84	24.7	0.0781

[1]Cross-sectional properties size standardized and with area multiplied by 10^2 and second moments of area multiplied by 10^4.
[2]Bold values are significant at $p \leq 0.05$ based on independent t-tests.
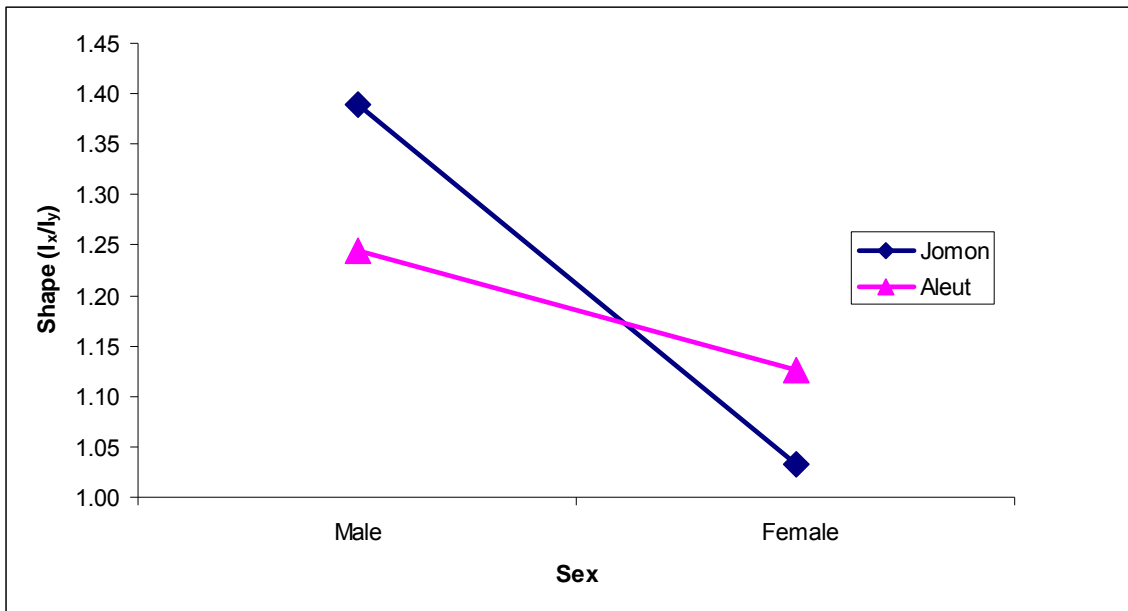
Figure 4. Plot of Jomon and Aleut femoral shape (I_x/I_y) by sex.
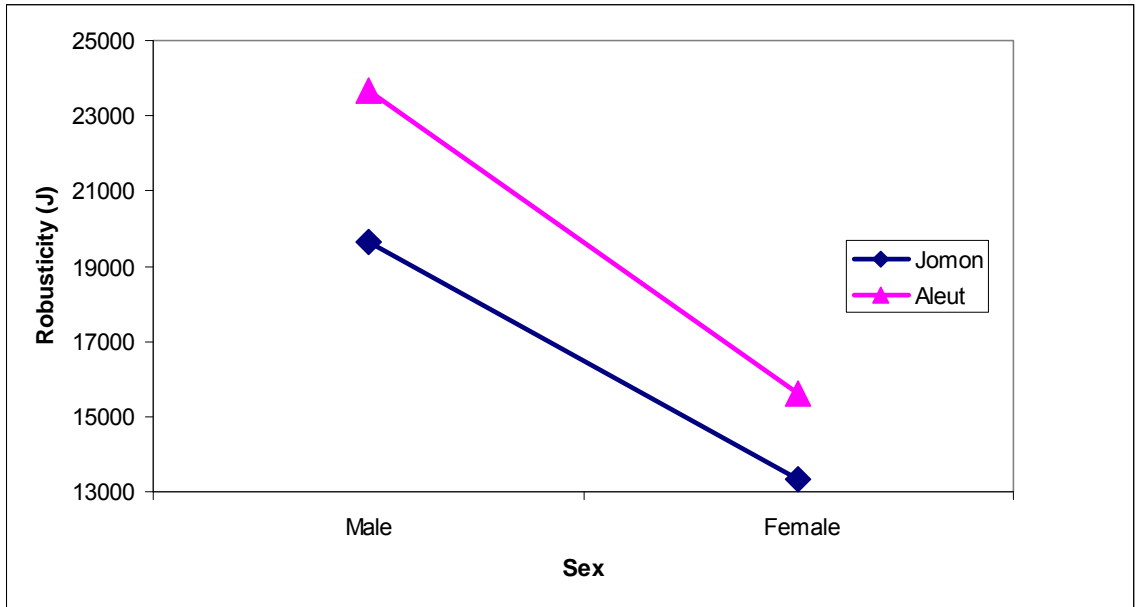
Figure 5. Plot of Jomon and Aleut femoral robusticity (J) by sex.

II. HUMERAL COMPARISONS

Summary statistics for cross-sectional properties of humeri from Jomon, Aleut, California and Georgia groups are provided in Table 4. Table 5 lists the results from the two-way ANOVA. The results of Tukey's HSD tests by group and sex are illustrated in Tables 6 and 7. Plots of the comparison of shape and robusticity between Jomon and comparative groups are visible in Figures 6 and 7. In general, in comparison with the other groups, the Jomon sample demonstrates larger cross-sectional properties (CA, I_x, I_y, and J). The only property that deviates from this trend is the humeral shape ratio, I_x/I_y in which the Jomon have the smallest shape ratios.

The Jomon sample exhibits a larger CA value compared to the other groups. This trend is observed even when comparing Jomon females to males in other groups. The

results from the two-way ANOVA demonstrate that between the groups the difference is statistically significant (F = 17.3, df = 3, p ≤ 0.0001). Between the sexes within groups the difference is also significant (F = 18.58, df = 1, p ≤ 0.0001). There is no significant group and sex interaction for this property (F = 0.27, df = 3, p = 0.8457). Tukey's HSD tests show that Jomon males are significantly larger than males from the comparative samples. Jomon females, however, are only significantly larger than the Aleut and California females. Jomon females and Georgia coast females are similar in terms of CA.

The Jomon demonstrate a larger mean I_x value compared to the Aleut, California and Georgia groups with significant differences, both between the groups (F = 41.4, df = 3, p ≤ 0.0001) and between the sexes (F = 21.39, df =1, p ≤ 0.0001). No significant interaction effect is observed by group and sex (F = 1.29, df =3, p = 0.2781). According to Tukey's HSD tests, Jomon males are significantly larger than males in all comparative groups, while Jomon females are only significantly larger than the California group.

For I_y, as with CA and I_x, the Jomon sample has a larger mean value when compared with the other groups. The two-way ANOVA demonstrates that there is a significant difference between groups (F = 27.45, df = 3, p ≤ 0.0001) and between sexes (F = 15.44, df = 1, p ≤ 0.0001), and there is a significant interaction between group and sex (F = 2.89, df =3, p = 0.0372). Examination of the difference in means between the sexes within each groups shows that the Jomon have the largest mean difference (1534.688), with the difference in means decreasing from the Aleut sample (1180.9) to the Georgia sample (1020.6), with the smallest difference in the California sample (273.909). Results from Tukey's HSD tests demonstrate that Jomon males and females are significantly larger than all the comparative groups.

Jomon males have the most round humeri (smallest I_x/I_y ratio) of all groups. Jomon females also exhibit this trend, except when compared to the California females. However, the difference between the sexes for this ratio is not significant (F = 1.31, df =1, p = 0.2541). In general, this indicates that although the Jomon sample differs from the Aleut, California and Georgia samples (F = 27.13, df = 3, p ≤ 0.001), within each sample there is no significant difference between males and females. In addition, there is a significant interaction between the effects of group and sex (F = 6.45, df =3, p = 0.0004), indicating that the little sexual dimorphism present differs among groups. For the Jomon (-0.011), Aleut (- 0.046) and Georgia (-0.148) samples, females have a larger I_x/I_y ratio. Within the California sample, males have a larger ratio than females have a mean positive difference (0.0895). According to Tukey's HSD tests, Jomon males and females are not statistically significant compared to the Aleut, California or Georgia groups.

Finally, J follows the same trend as CA, I_x and I_y. The Jomon have greater torsional rigidity (J) than any other group for both sexes. Two-way ANOVA results indicate that both between the groups (F = 34.52, df = 3, p ≤ 0.0001) and between the sexes (F = 19.66, df =1, p ≤ 0.0001) the difference in J is statistically significant. There is a lack of significant interaction effect by group and sex (F = 2.03, df =3, p = 0.1123). Jomon males have significantly larger mean J values than males in the comparative samples. Female Jomon have significantly larger mean values of J than California and Georgia coast females, but not Aleut females based on with Tukey's HSD tests.

Overall, these results partially support the predictions made under Hypothesis II, which state that the Jomon sample will be similar in robusticity (J) and shape (I_x/I_y) as the

Aleut humeri, and will be larger in robusticity than the California and Georgia coast hunter-gatherers, but similar in shape. Jomon male humeri have significantly larger J values than the Aleut, California and Georgia groups but are similar in terms of the I_x/I_y ratio. Jomon females, on the other hand, are more variable (Table 7), but are similar in J as Aleut females, but larger than the California and Georgia groups. The female humeral shape ratio is similar across all groups.

Table 4. Summary statistics by group and sex for humeral cross-sectional properties[1].

Cross-sectional property	Statistic	Jomon		Aleut		California		Georgia	
		M (n = 6)	F (n = 4)	M (n = 17)	F (n = 12)	M (n = 45)	F (n = 62)	M (n = 15)	F (n = 12)
CA mm^2	mean	966.113	814.049	667.28	576.437	655.859	578.587	682.261	599.053
	SD	132.822	29.393	167.783	145.37	110.621	95.417	167.441	162.918
I_x mm^4	mean	5506.234	4190.413	4174.995	3084.35	2548.185	2067.956	3173.203	2583.145
	SD	1485.665	731.429	1518.202	1067.847	764.791	572.997	1131.468	973.597
I_y mm^4	mean	5920.648	4385.963	3787.791	2606.922	2650.874	2376.965	3286.926	2266.348
	SD	2126.245	861.575	1620.408	846.302	804.067	673.724	1271.225	776.609
(I_x/I_y)	mean	0.953	0.965	1.14	1.186	0.971	0.881	0.982	1.13
	SD	0.121	0.131	0.158	0.209	0.125	0.121	0.107	0.139
J mm^4	mean	11426.882	8576.376	7962.786	5691.272	5199.059	4444.921	6460.36	4846.576
	SD	3567.751	1498.178	3100.411	1849.739	1523.109	1206.339	2371.457	1723.22

[1]Cross-sectional properties size standardized and with area multiplied by 10^8 and second moments of area multiplied by 10^{13}.

Table 5. Results from two-way ANOVA for humeral cross-sectional properties in Jomon, Aleut, California and Georgia groups[1].

Cross-sectional property	Source	F	df	p-value
CA	**group**	**17.13**	**3**	**<0.0001**
	sex	**18.58**	**1**	**<0.0001**
	group*sex	0.27	3	0.8457
Ix	**group**	**41.4**	**3**	**<0.0001**
	sex	**21.39**	**1**	**<0.0001**
	group*sex	1.29	3	0.2781
Iy	**group**	**27.45**	**3**	**<0.0001**
	sex	**16.44**	**1**	**<0.0001**
	group*sex	**2.89**	**3**	**0.0372**
Ix/Iy	**group**	**27.13**	**3**	**<0.0001**
	sex	1.31	1	0.2541
	group*sex	**6.45**	**3**	**0.0004**
J	**group**	**34.52**	**3**	**<0.0001**
	sex	**19.66**	**1**	**<0.0001**
	group*sex	2.03	3	0.1123

[1]Bold values are significant at $p \leq 0.05$.

Table 6. Comparison of males by group[1,2].

Cross-sectional property	Jomon (n = 6)	Aleut (n = 17)	California (n = 45)	Georgia (n = 15)	Paired Group Difference
CA mm^2	966.113 132.822	667.28 167.783	655.859 110.621	682.261 167.441	J>A>G>C
Ix mm^4	5506.234 1485.665	4174.995 1518.202	2548.185 764.791	3173.203 1131.468	J>A>G>C
Iy mm^4	5920.648 2126.245	3787.791 1620.408	2650.874 804.067	3286.926 1271.225	J>A>G>C
(Ix/Iy)	0.953 0.121	1.14 0.158	0.971 0.125	0.982 0.107	A>G>C>J
J mm^4	11426.882 3567.751	7962.786 3100.411	5199.059 1523.109	6460.36 2371.457	J>A>G>C

[1] Results of Tukey's HSD tests: highlighted terms demonstrate significant difference between Jomon males and comparative group males at $p \leq 0.05$.
[2] Groups ordered sequentially from largest to smallest mean.

Table 7. Comparison of females by group[1,2].

Cross-sectional property	Jomon (n = 4)	Aleut (n = 12)	California (n = 62)	Georgia (n = 12)	Paired Group Difference
CA mm^2	814.049	576.437	578.587	599.053	J>G>C>A
	29.393	145.37	95.417	162.918	
Ix mm^4	4190.413	3084.35	2067.956	2583.145	J>A>G>C
	731.429	1067.847	572.997	973.597	
Iy mm^4	4385.963	2606.922	2376.965	2266.348	J>A>C>G
	861.575	846.302	673.724	776.609	
(Ix/Iy)	0.965	1.186	0.881	1.13	A>G>J>C
	0.131	0.209	0.121	0.139	
J mm^4	8576.376	5691.272	4444.921	4846.576	J>A>G>C
	1498.178	1849.739	1206.339	1723.22	

[1] Results of Tukey's HSD tests: highlighted terms demonstrate significant difference between Jomon males and comparative group males at $p \leq 0.05$.
[2] Groups ordered sequentially from largest to smallest mean.

Figure 6. Plot of Jomon, Aleut, California and Georgia Coast humeral shape (I_x/I_y) by sex.
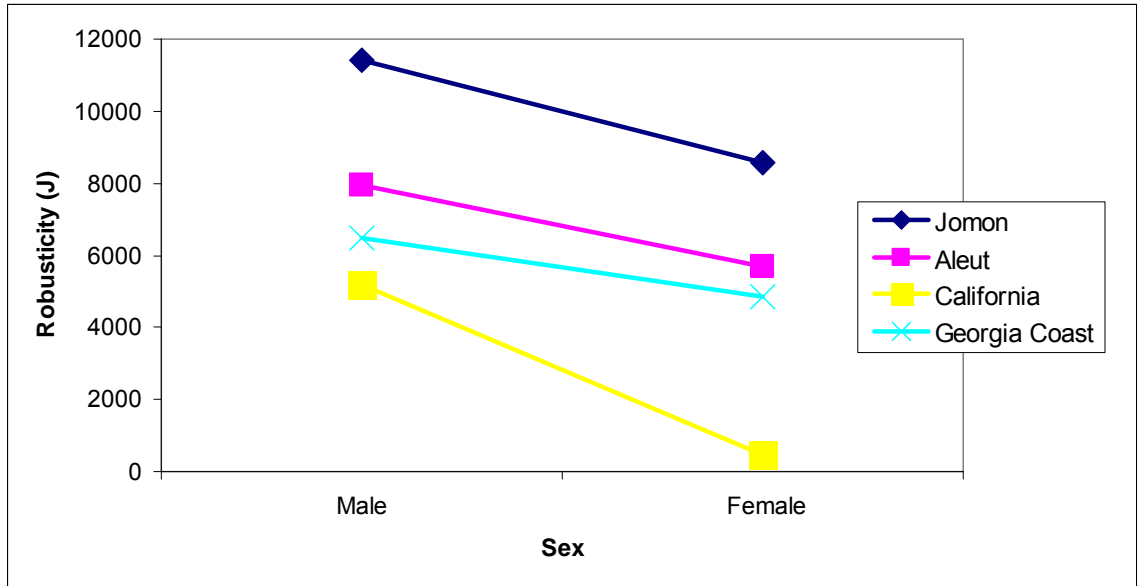
Figure 7. Plot of Jomon, Aleut, California and Georgia Coast humeral robusticity (J) by sex.

III. SEXUAL DIMORPHISM IN FEMORA & HUMERI

Femora

Results from the t-test for the difference in sexual dimorphism in femora between Jomon and Aleut groups are provided in Table 8. The ratio of difference in sexual dimorphism (SDD) is included to help clarify the comparisons. Recall that this test utilizes mean male and female property values to determine if sexual dimorphism differs between samples (Relethford and Hodges, 1985). According to the t-tests, I_x/I_y is statistically significant between Jomon and Aleut samples with Jomon more dimorphic than the Aleut (t = 2.227, df = 54, p = 0.0301). For J sexual dimorphism within the Jomon is smaller than that observed in the Aleut group, though not significantly so (t = -0.429, df = 54, p = 0.0.6696).

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Table 8. Comparison of difference in sexual dimorphism for femoral I_x/I_y and J between Jomon and Aleut samples[1,2].

	SDD Jomon	SDD Aleut	Jomon male	Jomon female	Aleut male	Aleut female	t	df	P
Ix/Iy	34.59	10.57	**1.389**	**1.032**	**1.245**	**1.126**	**2.227**	**54**	**0.03**
J	47.40	51.61	19625.624	13314.593	23664.658	15609.22	-0.43	54	0.67

[1]SDD is the value of percent difference in sexual dimorphism [(male mean-female mean)/female mean]*100.
[2]Bold values are significant at p ≤ 0.05.

Table 9 provides the results from the t-test for differences in male and female overlap between Jomon and Aleut femora. There is less overlap between males and females in I_x/I_y ratio and in J among the Jomon compared to the Aleut. The difference is not, however, significant for either variable (I_x/I_y: t = 0.0102, df = 57, = 0.9919; J: t = 0.0128, df = 57, p = 0.9898). This result is the same between Jomon and Aleut females (t = 0.0117, df = 57, p = 0.9907). Between the females, the Jomon have a smaller proportion of females that do not overlap with male variation for the property of J, but it is not significantly different (t = 0.0084, df = 57, p = 0.9933).

Table 9. Proportion of males and females within sex-specific distribution for femoral I_x/I_y and J between Jomon and Aleut samples.

MALES	Jomon	Aleut	t	df	p
Ix/Iy	79.1	61.41	0.0102	57	0.9919
J	87.29	64.06	0.0128	57	0.9898
FEMALES					
Ix/Iy	84.13	63.31	0.0117	57	0.9907
J	65.54	80.51	-0.0084	57	0.9933

These results partially support the predictions made under Hypothesis III, which states that the difference in sexual dimorphism in femoral cross-sectional properties will not significantly differ between the Jomon and Aleuts. This prediction is rejected for the ratio of I_x/I_y, but not J. Also supporting Hypothesis III are the results from the tests of

differences in the proportion of males and females within sex-specific ranges for both robusticity and shape.

Humeri

Results from the t-test for the difference in sexual dimorphism in humeri between Jomon and Aleut, California and Georgia groups are provided in Tables 10 and 11. The ratio of I_x/I_y is less sexually dimorphic within the Jomon sample compared to the Aleut, California and Georgia samples. Interestingly, Jomon females have a greater I_x/I_y ratio than Jomon males. This pattern is similar to the Aleut and Georgia samples with the Aleut as the most similar group to the Jomon. The Jomon sample, however, shows the opposite pattern as the California sample with females exhibiting a larger I_x/I_y ratio than males. The difference in sexual dimorphism for I_x/I_y is not statistically significant between the Jomon and Aleut (t = 0.268, df = 35, p = 0.7899), the Jomon and California (df = 113, t = -1.321, p = 0.2209) or the Jomon and Georgia samples (t = 1.471, df = 33, p = 0.1508).

Table 10. Comparison of differences in sexual dimorphism for humeral I_x/I_y between groups[1].

Ix/Iy	SDD	Male	Female	t	df	p
Jomon	-1.24	0.953	0.965			
Aleut	-3.88	1.14	1.186	0.268	35	0.7899
Cal	10.22	0.971	0.881	-1.231	113	0.2209
Georgia	-13.1	0.982	1.13	1.471	33	0.1508

[1]SDD is the value of percent difference in sexual dimorphism [(male mean-female mean)/female mean]*100.

In terms of J, the Jomon sample shows a larger difference in sexual dimorphism than the California and Georgia samples with the Georgia sample most similar to the

Jomon. Compared to the Aleut, the Jomon have less sexual dimorphism in J. In each

instance, males are larger than females. The difference between the Jomon and Aleut (t =

0.283, df = 35, p = 0.7787) and Jomon and Georgia (t = 0.699, df = 33, p = 0.4895)

samples is not statistically significant. However, the Jomon significantly differ from the

California samples in sexual dimorphism of J (t = 2.044, df = 113, p = 0.0433).

Table 11. Comparison of differences in sexual dimorphism for humeral J between groups[1,2].

J	SDD	Male	Female	t	df	p
Jomon	33.24	11426.882	8576.376			
Aleut	39.91	7962.786	5691.272	0.283	35	0.7787
Cal	16.97	**5199.059**	**4444.921**	**2.044**	**113**	**0.0433**
Georgia	33.3	6460.36	4846.576	0.699	33	0.4895

[1]SDD is the value of percent difference in sexual dimorphism [(male mean-female mean)/female mean]*100.
[2]Bold values are significant at $p \leq 0.05$.

Results for the tests of differences in the proportion of males and females within

sex-specific distributions for each group are provided in Table 12 and 13. For males, in

terms of I_x/I_y, the Jomon sample has a smaller proportion of males that do not overlap

with the female distribution than each of the comparative groups. The difference is not

significant for the Aleut (t = - 0.00207, df = 38, p = 0.9984), the California group (df

=116, t = -0.00667, p = 0.9947), or the Georgia coast sample (t = -0.01187, df = 36, p =

0.9906). With J, the Jomon sample has a larger proportion of males that do not overlap

with the female distribution than each of the comparative groups. There is no statistical

difference when compared to the Aleut (t = 0.00051, df = 38, p = 0.9996), the California

Amerinds (t = 0.00296, df = 116, p = 0.9976) or the Georgia coast group (t = 0.00102, df

= 36, p = 0.9992).

Table 12. Proportion of males within male distribution for humeral I_x/I_y and J.

MALES	Ix/Iy	t	df	p
Jomon	51.99			
Aleut	55.96	-0.00207	38	0.9984
Cal	64.06	-0.00667	116	0.9947
Georgia	75.49	-0.01187	36	0.9906
	J	t	df	p
Jomon	65.54			
Aleut	64.43	0.00051	38	0.9996
Cal	59.87	0.00296	116	0.9976
Georgia	63.31	0.00102	36	0.9992

For females, in terms of I_x/I_y, the Jomon sample has a smaller proportion of females that do not overlap with the male distribution than each of the comparative groups. The difference is not significant with the Aleut (t = - 0.0013, df = 38, p = 0.9990), the California group (t = -0.0069, df =116, p = 0.9945), or the Georgia coast sample (t = -0.0146, df = 36, p = 0.9884). With J the Jomon sample has a larger proportion of females that do not overlap with the male distribution than each of the comparative groups. There is no statistical difference when compared to the Aleut (t = 0.00404, df = 38, p = 0.9968), the California Amerinds (t = 0.00981, df = 116, p = 0.9922) or the Georgia coast group (t = 0.00608, df = 36, p = 0.9952).

Table 13. Proportion of females within female distribution for humeral I_x/I_y and J.

FEMALES	Ix/Iy	t	df	p
Jomon	51.99			
Aleut	54.38	-0.0013	38	0.9990
Cal	64.43	-0.0069	116	0.9945
Georgia	70.19	-0.0146	36	0.9884
	J	t	df	p
Jomon	82.89			
Aleut	72.91	0.00404	38	0.9968
Cal	62.17	0.00981	116	0.9922
Georgia	68.08	0.00608	36	0.9952

Based on these results, Hypothesis III is partially supported when observing the non-significant differences in sexual dimorphism between Jomon and comparative

groups based the ratio of I_x/I_y for the humeri. However, the difference in sexual dimorphism for the cross-sectional property J provides a different conclusion. Hypothesis III is supported between the Jomon sample and the Aleut and Georgia samples. The difference between the Jomon and California sample is statistically significant, which fails to support this particular prediction of Hypothesis III. However, when considering the results from the tests of differences in the proportion of males and females within sex-specific distributions between the Jomon and the comparative samples Hypothesis III is supported.

CHAPTER 4: DISCUSSION

I. TERRESTRIAL MOBILITY

Jomon Femoral Midshaft Structure and Mechanical Interpretation

In general, Jomon femora demonstrate a reduced level of postcranial robusticity—as observed in I_x, I_y, I_x/I_y and J—when compared to the Aleut. CA is the only property that exhibits a greater level of robusticity within the Jomon compared to the Aleut group. However, statistically significant differences are only found for CA and I_y in males. Females only exhibit significant differences in relation to CA and I_x.

In males, overall robusticity is comparable between the Jomon and Aleut groups. In conjunction with femoral cross-sectional shape, both groups of males demonstrate an elliptical midshaft as indicated by a higher value of I_x to I_y. It is interesting to note that although the Jomon males have a significantly larger amount of cortical area, it is distributed significantly less in the ML plane compared to the Aleut. The Aleut males, in contrast, have less cortical bone but it is distributed farther from the ML plane. Thus, the similarity of overall robusticity in the males, as indicated by J, is accounted for.

For females, overall robusticity is similar between the Jomon and Aleut groups. The female shape ratio indicates a similarity in elliptical shape. However, Jomon females have a slightly more circular midshaft shape than Aleut females since the ratio is closer to 1.0, which is more indicative of torsional rigidity. As in Jomon males, it is interesting to note that although the Jomon females have a significantly larger cortical area, the

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distribution of the cortical bone is significantly less in the AP plane compared to Aleut females, contributing to the similarity in J values. These trends in Jomon femoral midshaft robusticity and shape in males and females are supported by previous cross-sectional studies on Jomon femora (Kimura and Takahashi, 1982; Nakatsukasa, 1990; Kimura, 2006).

In the context of mechanical loading it can be concluded that the Jomon and Aleut groups have similar overall robusticity. That is, the average bending rigidity between the groups is comparable. This similarity is further exemplified by the shared elliptical midshaft shape. In both sexes, AP bending rigidity is larger than ML bending rigidity. As a result, both groups experienced greater mechanical loads in the AP compared to ML plane.

Taking into consideration the primacy of J as an indicator of overall robusticity, in addition to the shape ratio, the results support the prediction that Jomon and Aleut groups shared a similar level and pattern of mechanical loading history. Furthermore, this relationship can be correlated to a similar level and pattern of mobility between the groups.

The elliptical shaped femoral midshaft in both groups reveals the dominance of AP oriented forces compared to ML oriented forces that acted upon the femora. Researchers have attributed this pattern of bending to locomotion, particularly to activities such as running and climbing (Morrison, 1968, 1969, 1970) and as a result to terrestrial mobility (Ruff, 1987). Specifically, AP elongation is associated with the effects of hamstring and quadriceps contraction, which in turn causes modeling of the basic circular femoral midshaft (Wescott, 2006). Previous research shows that the

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elliptical shape exhibited in both the Jomon and Aleut groups, particularly in males, is typical of hunter-gatherer groups when compared to more sedentary agriculturalists (Ruff et al., 1984; Ruff, 1987; Ruff and Larsen, 1990).

For instance, Ruff and colleagues (1984) studied the temporal changes in femoral midshaft robusticity and shape between two groups from the Georgia coast, a terrestrially mobile prehistoric preagricultural group and a more sedentary agricultural group. Between these groups the shape ratio of the femur declined with the hunter-gatherer group exhibiting a higher shape ratio (1.28 in males and 1.16 in females), while the agricultural group shifted to a smaller shape ratio (1.08 in males and 1.03 in females) (Table 14). The change to a more circular midshaft shape is statistically significant between the males, but not the females. Overall this change is attributed to a shift in subsistence from hunting and gathering to agriculture, and thus to a more sedentary lifestyle for the males (Ruff et al., 1984).

In a study of European Upper Paleolithic (UP) and Mesolithic hunter-gatherers, Holt (2003) found that femoral midshaft robusticity and shape, and thus mobility, declined over time between groups. This finding corroborates with the archaeological record for these groups: That is, sedentism increased over time between the Early to Late UP and to the Mesolithic groups. In the context of these highly mobile hunter-gatherers (Table 14), the Jomon males are similar in midshaft shape to the Late UP group. In comparison with Holocene populations from North America, the Late UP group is similar in femoral midshaft shape as Great Basin hunter-gatherers (Ruff, 1999; Holt, 2003). Jomon females, on the other hand, have femoral midshaft shape ratios that resemble the Mesolithic group. These groups, when compared to Holocene populations from North

America, are more similar to agricultural and mixed hunter-gatherer and agricultural groups (Holt, 2003; Ruff, 1994). Since the Mesolithic group was not practicing an agricultural subsistence, Holt (2003) attributes this similarity to increased exploitation of coastal resources and dependence on semi-sedentary settlements.

Table 14. Comparison of mean femoral midshaft I_x/I_y between Jomon, Georgia coast, Upper Paleolithic, Mesolithic, Great Basin and Plains samples.

Sample	Male	Female
Jomon	1.389	1.032
Georgia coast[1a]	1.28	1.16
Georgia coast[1b]	1.08	1.03
Early UP[2]	1.53	1.54
Late UP[2]	1.39	1.23
Mesolithic[2]	1.13	1.11
Great Salt Lake[3]	1.37	1.08
Stillwater[3]	1.26	0.98
Middle Missouri[4a]	1.11	0.98
Southern Plains[4b]	1.74	1.29

[1a] Data from Ruff et al. (1984): hunter-gatherers.
[1b] Data from Ruff et al. (1984): agriculturalists.
[2] Data from Holt (2003).
[3] Data from Ruff (1999): Great basin hunter-gatherers.
[4a] Data from Ruff (1994): mixed hunting-gathering and agriculture.
[4b] Data from Ruff (1994): agriculture.

Direct evidence of terrestrial logistic mobility in the Jomon is not available, but indirect lines of support based on the archaeological record and ethnographic accounts provide insight into the habitual activities that influenced Jomon femoral architecture. It is plausible that the similarity of Jomon and Aleut femoral midshaft robusticity is due to similarity in residential mobility patterns. As a residentially stable group the Aleuts made, on average, only one residential move per year (Coxe, 1894; Kelly, 1983). Osborn (1990) describes Aleut settlements as including a permanent winter village and a temporary summer settlement. Settlements were located near the shore and consisted of

several semi-subterranean houses (McCartney and Veltre, 1999). The location of settlements was often positioned based on several factors, including availability of fresh water, protection from the ocean, access to beaches that allowed for launching of watercraft, and proximity to observation points (Frohlich, 2002). Temporary sites were also utilized for seasonal or specialized tasks (McCartney and Veltre, 1999).

Mounting evidence suggests that the Jomon were also residentially sedentary hunter-gatherers with seasonal procurement of food resources away from the home base. Watanabe (1986) illustrated that residential stability is functionally correlated to such factors as the 1) manufacture and use of pottery, 2) size and weight of stone implements and the scale of stone structures, 3) presence of burials or cemeteries, and 4) the permanence of dwellings represented by construction features.

Watanabe (1986) indicated that the above mentioned factors, represented by material remains, were not conducive to a nomadic lifestyle in the prehistoric Jomon. In other words, Jomon material remains were not for temporary use or portable transport. The archaeological record points to large scale production by the Jomon of fragile ceramics that varied in size, function and decoration. Also, the Jomon manufactured heavy stone tools, such as batons and mortars, and constructed stone paved dwellings and stone circles. In addition, Jomon burials have been found in concentrations near settlements, often in cemeteries, rather than disposed randomly across the landscape. Finally, the Jomon had permanent dwellings represented by large, deep post holes that show evidence of alteration, either by repair, enlargement or rebuilding.

Research conducted by Pearson (2006) on the southwestern island of Kyushu also supports the conclusion that the Jomon were residentially sedentary hunter-gatherers.

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The pattern observed over 5,000 years during the Incipient (14,000 to 9250 cal. BC) to Early (9,250 to 5,300 cal. BC) Jomon periods was one of increasing residential stability and a shift towards increased storage economy. This was evinced by the development of large multifunctional villages with many storage pits, an abundance of decorated ceramic vessels and other lasting site features. Earlier sites in this region showed evidence of smaller scale groupings of permanent house structures (Pearson, 2006). For example, Pearson (2006: 254) notes that "the pit houses of Incipient Jomon lack internal hearths, seem to have few recognizable supporting posts and their average size is smaller than that of later Jomon house sites."

In the context of Binford's (1980) forager/collector model of hunter-gatherer subsistence-settlement patterns, the Jomon are expected to have a high logistic mobility pattern based on their high residential stability when compared to foragers (Habu, 2001, 2004). Foragers are those hunter-gatherer groups that have high residential mobility and tend to acquire food on a daily basis near their home base. Often these groups are in environments that have temporally (seasonally) or spatially homogenous food resources. In contrast, collectors have low residential mobility, provision their food resources logistically away from the residential base, and are usually found in environments that have critical resources that are spatially and temporally uneven (Binford, 1980; Habu, 2001).

Habu (2001, 2004) tested this model based on intersite variability of lithic assemblages and site size on Early Jomon sites in the Kanto and Chubu regions. Based on large lithic variability, large size site variability and a clustered distribution pattern between the sites within each region, Habu (2001, 2004) concluded that the Jomon were

sedentary collectors rather than foragers. However, Habu (2001) considers that the Jomon were semi-sedentary collectors that moved across the landscape in a seasonal manner rather than occupying a year-round residence.

Ethnoarchaeological studies may provide an important perspective that unifies both perspectives regarding Jomon mobility. By looking at contemporary hunter-gatherers, including the modern descendents of the Jomon, the Ainu, Watanabe (1986) demonstrates that based on similarities in food gathering and the spatial distribution of food resources the Ainu are the best model to draw analogies on Jomon residential shifts. Watanabe (1972, 1986) describes the Ainu as residentially stable with permanent, year-round settlements. Throughout the year, coordinated groups of Ainu migrate in search of resources including forays into mountainous terrain. For example, Ainu people travel to hunting huts to procure deer and bear (Watanabe, 1972; 1986). Thus, although residentially stable, the Ainu sent out specialized task groups to procure seasonal food resources, while the majority remained at year round settlements. In light of these findings, the similarity in femoral robusticity between Aleut and Jomon may represent similar degrees of mobility.

Previous research shows that other factors may also influence femoral robusticity. For instance, geographic terrain is shown to impact J when comparing groups from rugged and non-rugged terrain relief (Ruff, 1999). Specifically, groups that traveled over mountainous terrain had higher femoral robusticity than groups from lower relief terrain such as the plains and coast (Ruff, 1999). Although both the Jomon and Aleut samples are derived from coastal locations, it is possible that similarity in femoral robusticity was associated with physical terrain, rather than, or in addition to similarity in mobility

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patterns. For instance, Aleutian coasts are predominately rugged with steep headlands (Veltre, 1998).

The particular terrain of the coast on the Atsumi Peninsula, in which the Yoshigo site is located, is non-rugged. However, the area northeast of Yoshigo around Mikawa Bay has rugged terrain. In particular Yoshigo is located within the Toyohasi plain, but the area immediately northeast of the site is classified as encompassing low relief mountains and hills to medial relief mountains (Chirriin, 1990). Specifically, from east to northeast of Yoshigo are the mountain ranges of Akaisi and Kiso, and further northeast the Minomikawa plateau. The mountains are within 160 km of Yoshigo—with such peaks as Mt. Akiha, Mt. Hongu, and Mt. Dando within 65 km of the site—and reach elevations of about 1000 m (Google Earth). If the rugged area surrounding Yoshigo was utilized by the Jomon for resource procurement, then the similarity between Jomon and Aleut femoral robusticity could be explained by terrain.

If terrain is influencing Jomon femoral robusticity, then the disparity between terrestrial exploitation of resources between the Jomon and Aleut may explain similarity in J. The Jomon people spent time hunting terrestrial animals such as deer and boar and collecting plants in addition to fishing and shellfish collecting (Akazawa, 1986). In contrast, the Aleut almost exclusively exploited marine resources (Hrdlicka, 1945), but experienced travel over mountainous terrain. Thus, similarity in femoral robusticity between Aleut and Jomon groups may be explained by seasonal forays into regions with rugged terrain in the Jomon, while the Aleut femoral robusticity may be explained by exposure to rugged terrain in daily life.

II. MARINE MOBILITY

Jomon Humeral Mid-Distal Structure and Mechanical Interpretation

Overall, both male and female Jomon humeri display a greater mean value of the cross-sectional properties—CA, I_x, I_y, and J—in comparison to the Aleut, California and Georgia coast groups. In Jomon males this trend is consistently significantly different across all comparisons. For Jomon females, a consistent statistically greater difference across all comparisons is only observed in I_y. Jomon females lack a significant difference with 1) the Georgia females for CA, 2) Aleut and Georgia females for I_x, and 3) Aleut females for J.

In the case of the shape ratio I_x/I_y the Jomon demonstrate one of the smallest mean values, although for both sexes there is a lack of significant difference with the comparative samples. For males the Jomon have the smallest shape ratio than all the comparative samples, while female Jomon only have a greater mean shape ratio than the California females. It is important to observe that the Jomon humeral shape does fall within the range of variation for all groups. Specifically, Jomon humeri have a circular shape, which is consistent with the relatively round humeri of the comparative groups.

In males, Jomon overall humeral robusticity, J, is greater compared to all other groups. The shape ratio indicates that Jomon males have a relatively round humeral diaphyseal shape. Together these properties indicate that male Jomon not only experienced high average bending rigidity, but also high torsional rigidity. This indicates that Jomon males experienced more average bending and torsional loads than males in other groups.

This trend is also observed in Jomon females. In particular, Jomon females have

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a greater overall humeral robusticity compared to the California and Georgia coast groups. However, Jomon females are similar in robusticity as Aleut females. The humeral diaphyseal shape ratio indicates that, like the males, Jomon females are relatively round. This indicates that Jomon females also experienced high average bending and torsional rigidity. These trends in Jomon humeral robusticity and shape in males and females have also been observed by Sakaue (1998).

Evidence for Open-Ocean Rowing

Previous studies correlate humeral robusticity to marine mobility, particularly to rowing of watercraft. Although the upper limbs are used in multiple activities, findings by Weiss (2003) and Stock and Pfeiffer (2001) suggest the strong influence of marine habitual activities such as rowing on humeral robusticity. Weiss (2003) demonstrated that humeral robusticity is greater in ocean-rowing groups compared to river-rowing and non-rowing groups. Using an aggregate robusticity score, which takes into account TA, CA, I_x, I_y, and J, ocean-rowing groups such as Aleut and British Columbian hunter-gatherers had greater overall humeral robusticity than riverine-rowing Georgia coast hunter-gatherers and agriculturalists. Additionally, these rowing groups had greater humeral robusticity than non-rowing, terrestrial control samples (Weiss, 2003). As expected, a similar pattern was revealed in the current study with the ocean-rowing Aleut demonstrating greater robusticity than river-rowing Georgia coast hunter-gatherers and the California group. Surprisingly, humeral robusticity in Jomon males also far exceeded values observed in Aleut ocean rowers.

Evidence of marine mobility in the Jomon is not directly observable, but the

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archeological record provides indirect evidence that the Jomon accessed marine resources through the use of ocean watercraft. Remains of dugout canoes, or logboats, have been found throughout Japan associated with the Jomon period (Miyashita, 2006). Most logboats were discovered at inland and coastal sites around Honshu within the regions of Kanto, Chubu, Kansai, Chogoku and Kyushu, with most found within the Kanto and Kansai regions. Additionally, paddles were often found in association with the remains of the watercraft. In total, eight logboats have been excavated in association with the Early Jomon period, while five logboats from Middle Jomon sites have been located. The discovery of watercraft remains from the Late/Final Jomon period increase substantially with 66 logboat remains associated with the Late and Final periods.

Indirect evidence of the exploitation of marine resources also comes from stable isotope analysis of human bone collagen from the Yoshigo site. In particular, as an eastern coastal site, Yoshigo shows a larger portion of dietary protein derived from marine sources than terrestrial sources. Stable isotope analysis suggests that marine resources contributed between 40% and 80% to the diet of Yoshigo's inhabitants (Chisholm and Koike, 1999). Further analysis by Kusaka and colleagues (2008) supports this conclusion and points to greater intake of high trophic fish among the Yoshigo people compared to regional satellite sites such as Inariyama. Higher trophic fish consumed by the Jomon include tuna and bonito, both available in offshore contexts (Kobayashi, 2005). Thus accentuated levels of Jomon humeral robusticity compared to groups from California and the Georgia coast is attributed to open ocean rowing.

While the robusticity of Jomon humeri provides evidence for a high level of marine mobility, with Jomon males significantly more robust than Aleut males, humeral

shape can be indicative of the pattern of activity experienced by the Jomon. In both males and females humeral diaphyseal shape is relatively round with AP and ML loading nearly equal. Due to the fact that Jomon male humeral shape fits within the range demonstrated by the ocean rowing Aleut, humeral diaphyseal shape likely reflects this activity. However, additional activities contributing to the greater robusticity and circular shape of the Jomon upper limb should be discussed.

Evidence for Additional Manual Activities

A study by Shaw and Stock (2009) comparing humeral robusticity and shape in modern-day swimmers, cricketers and a sedentary control group demonstrated that the dominant arm of the cricketers was more robust and relatively circular compared to the control group. The researchers attributed this shape to habitual throwing caused by torsional stress (Shaw and Stock, 2009). This conclusion was made based on previous studies that observed circular humeral diaphyses in Late Upper Paleolithic humans that habitually threw spears (Churchill et al., 1996). Also, experimental evidence suggests that a throwing motion produces humeral torque through the coupled rotation of the proximal and distal ends of the humerus (Sabick et al., 2004) and with enough intensity spiral fractures in baseball pitchers, which are indicative of humeral torsion (Ogawa and Yoshida, 1998). In contrast, more elliptically shaped humeral diaphyses, strengthened in the AP plane, have been attributed to such motions as thrusting as observed in the humeral diaphyses of Neanderthals (Schmitt et al., 2003).

Shaw and Stock (2009) also demonstrated that the humeri of swimmers were more robust than humeri of the control group, with shape similar between both groups.

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Additionally, both the dominant and non-dominant humeri of the swimming group were similarly robust. This pattern of approximate bilateral symmetry was not significantly different compared to the sedentary control group. The authors attributed the symmetric humeral robusticity pattern of these groups to bilateral loading in the swimmers and low loading levels in the sedentary control group (Shaw and Stock, 2009).

In the context of hunter-gatherer marine mobility, Stock and Pfeiffer (2001) revealed that swimming, in addition to rowing, is detected through humeral robusticity. In the study, the researchers compared marine mobile Andaman Island hunter-gatherers, who gathered off-shore resources through swimming and rowing of watercraft, to terrestrial mobile Later Stone Age hunter-gatherers. When comparing the humeral robusticity of these two groups, Stock and Pfeiffer (2001) demonstrated that the Andamanese had significantly greater overall robusticity in the humerus compared to the Later Stone Age group. Furthermore, this trend was displayed in both males and females between the groups.

From these studies by Shaw and Stock (2009) and Stock and Pfeiffer (2001), it is plausible that the Jomon, in addition to rowing on the open ocean, were habitually loading their humeri due to throwing and swimming activities. Specifically, it is plausible that the high humeral robusticity and the circular shape of the Yoshigo inhabitants were acquired through habitual loading due to throwing. Jomon tool assemblages studied by Akazawa (1986, 1988) indicate that spear points, harpoons and net sinkers were used in food procurement activities, each of which could be thrown in hunting and fishing activities. The fact that Aleut males also have a relatively circular, though slightly more AP elongated, humeral diaphysis also supports this idea since

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throwing of harpoons and bolas was practiced during food procurement activities (Osborn, 1990). This is also apparent in the difference in robusticity between right and left humeri in Aleut males, which exhibits 16.4% asymmetry (Churchill, et al., 1996) Given the little asymmetry reported in Jomon humeri, unilateral throwing seems unlikely (Sakaue, 1998; Churchill et al., 1996). It may be that bimanual activities, such as throwing and lifting of nets during fishing, are differentiating the Jomon from the Aleut. Additional factors such as swimming should also be considered as contributing to differences in the Jomon and Aleut.

Archaeological remains provide evidence for the dependence upon marine activities, especially at coastal sites, and the particular tool kits utilized by the Jomon. Based on discriminant function analysis of artifact assemblages, different fishing gear types of the eastern coast clustered by Pacific shelf littoral, estuarine, and freshwater environments (Akazawa, 1988). The tool types used to discriminate between sites included toggle harpoons, one-piece fish hooks, composite fish hooks, stone sinkers and ceramic sinkers. While the Pacific shelf littoral region is distinguished by harpoons and fish hooks, the freshwater type is predominated by notched stone sinkers and the estuarine environment is discriminated by reused ceramic sinkers, both of which were used for net-fishing. Watanabe (1973) hypothesized that reused ceramic sinkers were used for net-fishing in shallow waters. Thus it is likely that the Jomon in embayment areas were utilizing the shallow waters of the bay for net fishing activities. Exploitation of embayment areas is further supported by zooarchaeological remains. For example, Akazawa (1980) noted that high frequencies of brackish water fish species were found at the embayment site of Nittano in Kanto.

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Auditory exostoses are hyperplastic bony lesions that form in the external auditory canal as a response to habitual contact with water below body temperature, in particular through swimming and diving (Kennedy, 1986). Kennedy (1986) demonstrated that a high frequency of the lesion correlates to the middle latitudes (30 - 45° N and S) where aquatic exploitation is evident. High and low latitudes (0 - 30°N and S and above 45°) show little to no cases of auditory exostoses. It is likely that in the tropical and subtropical latitudes terrestrial resources were exploited more heavily, while cold water was more of a deterrent to swimming and diving in the polar and subpolar regions.

Katayama (1998) conducted a study of the frequency of auditory exostoses in 24 prehistoric groups from around the Pacific Ocean, including Jomon from sites within Honshu and Kyushu dated from the Initial to Final Jomon periods. In comparison with the other samples, the Jomon had one of the highest frequencies of auditory exostoses with 23.9% incidence in Jomon males and 13.9% incidence in Jomon females. Furthermore the Jomon sample grouped with other samples with a high incidence of auditory exostoses from the middle latitudes (Katayama, 1998). It is likely that frigid temperatures of the arctic waters would have deterred the Aleuts from habitually pursuing this activity. Therefore, swimming, as an intense bimanual activity, may be responsible for differences between the Aleut and Jomon. It is also plausible that lifting of heavy fishing nets, if a bilateral activity, could further differentiate the Jomon from the Aleut.

III. SEXUAL DIMORPHISM

Jomon Sexual Dimorphism at the Femoral Midshaft

Results of the comparison of differences in sexual dimorphism at the femoral

midshaft between the Jomon and Aleut groups demonstrate that the Jomon show a similar

difference between the sexes for J, but not for I_x/I_y, as the Aleut. While in both groups

males are larger than females for these properties, the Jomon are more sexually

dimorphic in terms of the shape ratio I_x/I_y. Furthermore, the results support the prediction

that the Jomon have similar differences in the degree of dimorphism between males and

females as the Aleut. Previous studies have observed the difference between male and

female femoral midshaft robusticity and shape in the Jomon (Kimura and Takahashi,

1982; Nakatsukasa, 1990; Kimura, 2006). This may be associated with the sexual

division of labor.

The sexual division of labor is a general framework that describes the economic

roles of the sexes—the specific activities allocated to males and females—within a

particular subsistence group from the past and present (Murdock and Provost, 1973). A

cross-cultural study by Murdock and Provost (1973) illustrates the general pattern of

activities performed by the sexes across hunter-gatherer, horticultural and agricultural

subsistence strategies. By analyzing the sex assignments of fifty technological activities

of 185 ethnographic cases the researchers established this general pattern (Murdock and

Provost, 1973).

In particular, the study showed that males almost exclusively take up tasks that

require both a high level of strength and travel away from the home base, including

hunting of large aquatic animals and large land fauna, fowling, trapping, boatbuilding,

stoneworking and working of bone, horn and shell. No technological activities were assigned as strictly female activities, but activities that were most often correlated with females include vegetal food gathering and preparation, cooking and other activities that do not require traveling long distances from the home base. This is closely attributed to the constraint on females due to pregnancy, lactation and general child care efforts (Brown, 1970). Furthermore it is hypothesized that this is an evolutionary stable strategy for mitigating the impact of environmental stress on children (Hurtado et al., 1992). The researchers noted that this general pattern holds best with hunter-gatherer and nomadic pastoralist societies (Murdock and Provost, 1973). A more recent cross-cultural study by Marlowe (2007) supports this trend in hunter-gatherers and emphasizes male optimal foraging of food resources and cooperation in conjunction with the constraint on female tasks. Murdock and Provost (1973) further emphasized that as craft specialization and sedentism increase, as within agricultural societies, males tend to take on more tasks that in hunter-gatherer societies are assigned typically to females. Thus, the authors suggest that as greater technological complexity increases, a shift occurs in sexual allocation of more complex activities from females to males (Murdock and Provost, 1973).

Sexual dimorphism of diaphyseal robusticity and shape is useful in elucidating the sex-specific behaviors of a group. However, difficulties in interpreting the disparity between male and female diaphyseal robusticity and shape do exist. Stock and Pfeiffer (2004: 1010) clarify this and state: "Patterns of sexual dimorphism are difficult to interpret directly, as differences in both skeleton design and hormonal substrate may affect the norm of biomechanical response to loading. Despite this problem, comparisons of sexual dimorphism between groups can inform us about relative differences in the

gender-based division of labour." Thus, as a localized rather than systemic

biomechanical response of the long bones, it is productive to look at the differences in

male and female diaphyseal robusticity as a reflection of differences in activities and

furthermore, as indicative of the sexual division of labor.

In terms of long bone cross-sectional geometry, research conducted by Ruff

(1987) supports the application of variation in sexual dimorphism in the lower limbs to

the sexual division of labor, particularly to differences in mobility between the sexes.

Ruff (1987) examined sexual dimorphism in lower limb shape in groups associated with

hunting and gathering, agriculture and industrial subsistence strategies. Ruff (1987)

found that sexual dimorphism, in particular, in femoral midshaft shape was greatest in the

hunting and gathering societies (8-36%), intermediate in the agricultural groups (2-9%),

and the least dimorphic in the industrial societies (0-2%). Taking into consideration the

higher levels of mobility in males than females in both the hunter-gatherer and

agricultural groups, with mobility similar in the industrial groups, Ruff (1987) concluded

that the sex differences in relative mobility reflect real differences in activities between

the sexes.

The results of the current study fit those established by Ruff (1987). Sexual

dimorphism in femoral midshaft shape for the Jomon (34.59%) is at the upper range

documented by Ruff (1987) for hunter-gatherers. A study by Stock and Pfeiffer (2004)

also supports the finding that sexual dimorphism, particularly in femoral robusticity, is

due to differences in terrestrial mobility between the sexes. Stock and Pfeiffer (2004)

studied Late Stone Age hunter-gatherers of South Africa from two different ecological

biomes, a forest and fynbos environment. In both groups males were allocated the role of

hunters while females did the gathering. Males in both biomes had a larger robusticity level at the femoral midshaft compared to females, which the authors attributed to a higher level of terrestrial mobility. Sexual dimorphism in the fynbos group was 23.8% while the forest group had 12.8% difference (Stock and Pfeiffer, 2004). This disparity in femoral robusticity between the sexes is considerably lower than expressed in the Jomon (47.4%). These studies suggest that sexual dimorphism of femoral robusticity are attributed to differences in hunter-gatherer terrestrial mobility, specifically with males traveling more across the landscape than females.

The Ainu are again helpful in elucidating Jomon behavior. In this case, as an ethnographic model, the Ainu serve to represent the type of sexual division of labor that the Jomon may have applied within their society. Therefore, indirect evidence for Jomon differences in male and female activities related to terrestrial mobility can be drawn from the Ainu, and supported with the archaeological record. Watanabe (1977a) describes the Ainu division of labor as a clear cut disparity between men hunting deer, and to a lesser extent bear, and women gathering plants. Fishing, however, was a task that both males and females participated, but with males using spears and women utilizing bag-net and basket traps. Watanabe (1972) also explains that Ainu males participated in activities for the construction and manufacture of fishing and hunting devices. Females, on the other hand, participated more in collecting plants and raw materials, and processing of fish, animals and plants.

Watanabe (1977b) further attests that the activity fields—the area of land covered by each sex—of Ainu males and females was clearly differentiated. Females were limited to activities near the base camp while men ventured beyond the home area due to

hunting activities. In particular, males traveled to hunting huts located in the mountains and hillsides and moved along the rivers where they fished in the spring, autumn and winter. Females remained near the home settlement and along the river terraces and river banks throughout the seasons. Overlap of activity areas occurred near the home settlement for fishing activities where both males and females traversed the river and its tributaries in the spring, summer and autumn (Watanabe, 1977b). In total, Ainu males spent about two to three months of the year hunting, Ainu females devoted five to six months to plant collection and both sexes pursued fishing activities for eight to nine months (Watanabe, 1977a). These observations imply greater mobility and contact with rugged terrain among male Ainu.

Archaeological evidence demonstrates that many Jomon non-dwelling sites—sites with no evidence of pit dwellings—have been excavated in conjunction with large dwelling sites (Habu, 2004). While Habu (2001, 2004) suggests that these sites are indicative of residential bases in a system of seasonally moving Jomon residence, it is however much more likely based on the ethnoarchaeological evidence that these sites were special purpose campsites for food procurement activities (Watanabe, 1972; 1986; Imamura, 2006; Pearson, 2006). The disbursement of these sites is associated with logistical mobility and may represent locations for male hunting bases (see previous comments).

Archaeological evidence based on stable isotopic analysis of human bone collagen at the Yoshigo site supports dietary distinctions between male and females, and likely a sexual division of labor. In most hunter-gatherer societies food sharing is standard between the sexes and as a consequence the dietary differences between males

and females is not large (Bird, 1999). Research by Kusaka and colleagues (2008) found that although there was no difference in carbon and nitrogen isotopic mean values between the sexes at Yoshigo, there was a difference in the variation of nitrogen values between males and females. The variation of nitrogen values for males was much more widespread than female values, indicating that Jomon males at the Yoshigo site had a wider dietary breadth of terrestrial and marine food consumed. The researchers suggest that this trend may be due to both differential access to food related to the sexual division of labor and occupational differentiation in males. Specifically the wider variation in male diet may be due to male hunting and fishing away from the home settlement and consumption of acquired foods (Kusaka et al., 2008).

In sum, Jomon sex differences in the femur demonstrate a pattern whereby males have a larger overall robusticity and more AP elongated femoral midshaft than females. This feature is associated with a pattern of sexual dimorphism where Jomon are at the upper range of hunter-gatherers. In general it is possible to designate the difference between the sexes as due to differences in terrestrial mobility, likely stemming from the sexual division of labor. Jomon males were traveling across the landscape differently than females. Specifically, Jomon males were likely experiencing higher levels of mechanical loading contributing to higher overall bending rigidity from traveling on longer forays outside the permanent residential base to procure food resources at seasonal hunting camps. These camps were likely located in areas of more rugged terrain (see Discussion p 66).

Jomon Sexual Dimorphism at the Mid-Distal Humerus

Results of the comparison of differences in sexual dimorphism at the mid-distal humerus illustrate that the Jomon show a similar difference between the sexes in I_x/I_y and J as the comparative groups. However, J is significantly different between the Jomon and California group, with the Jomon more sexually dimorphic. The results also demonstrate that the degree of dimorphism between Jomon males and females is similar to the comparative groups.

As in the femora, Jomon males have a greater overall bending rigidity than Jomon females. Although humeral robusticity is greater in males than females in all samples, the Jomon demonstrate a greater average bending rigidity difference between the sexes than the California group. In accordance with the shape index, Jomon males are more elliptical in the ML direction than Jomon females. As a result, Jomon females have a rounder humeral mid-shaft than Jomon males. Previous research by Sakaue (1998) on Jomon humeri support the results presented here for the presence of Jomon sexual dimorphism in humeral robusticity and shape.

Sexual dimorphism in the upper limbs has also been studied in terms of long bone cross-sectional geometry. In the upper limbs, analysis of sexual dimorphism in humeral robusticity and shape can help clarify the manual activities that each sex engaged in. For instance, Ruff and Larsen (1990) examined sexual dimorphism in humeral robusticity in Georgia coast groups associated with the sexual division of labor of hunting and gathering and agriculture subsistence strategies. The researchers found that from the preagricultural to agricultural periods the sexual dimorphism in humeral robusticity declined, although the pattern of greater robusticity in males than females was

maintained. While the Georgia coast preagriculturalists males and females differed by

42.7% in robusticity, the agriculturalists demonstrated a disparity of 25.1%. This overall

decrease is attributed to increases in sedentism and the decline in sex-based task

differentiation among the agriculturalists (Ruff and Larsen, 1990).

Additionally, a biomechanical analysis of hunter-gatherers from the Great Basin

at Stillwater Marsh exhibited a difference of 33.7% in humeral mid-distal robusticity

between males and females (Larsen et al., 1995). Also, Stock and Pfeiffer (2004) showed

that sexual dimorphism of humeral robusticity of Late Stone Age hunter-gatherers

differed between males and females in the fynbos biome by 24.9% in the right humerus,

while the sexes differed by 32.2% in the right humerus in the forest biome. Thus, in the

context of these studies, the sexual dimorphism of humeral mid-distal robusticity of the

Jomon (33.24%) fits within the hunter-gatherer pattern.

Sexual dimorphism of humeral robusticity can help reveal particular activities of

the sexes. For example, Weiss' (2003) study on rowing activity, as previously described,

illustrates that rowing is detectable in males based on humeral robusticity. In each of the

rowing groups, rowing was a principally male activity and this was reflected in the

greater male aggregate robusticity scores compared to females within the ocean-rowing

and riverine-rowing groups. Weiss (2003) further noted that the humeral robusticity of

both male and female ocean-rowers was greater than river-rowers and non-rowers. In

particular, female Aleuts were observed to be more robust than females of the groups that

did not row upon the ocean, despite the fact that female Aleuts rarely rowed watercraft

(Hrdlicka, 1945). Weiss (2003) attributed this to a generally higher level of activity in

the Aleuts to meet the demands of living in a harsher environment. It is also possible that

the higher level of cross-sectional robusticity is due to Bergmann's rule (1847), which predicts higher muscle mass, and thus, larger long bone cross-sections, in northern latitude groups (Weiss, 2003).

In the current study, sexual dimorphism in robusticity at the humeral mid-distal shaft between the Aleut (39.91%) and Jomon (33.24%) are similar, with males more robust than females. Furthermore, Jomon males demonstrate a higher level of robusticity compared to the Aleut. Thus, if the robusticity of these groups is a reflection of marine mobility, then this trend suggests that the sexual division of labor within the Jomon parallels that of the Aleuts, with males expressing greater robusticity with rowing ocean watercraft. It also indicates that Jomon females had a similar level of manual loading in the humerus as Aleut females based on similarity in robusticity, which suggests that Jomon females were similarly using upper limbs in manual activities. These parallels in activity are also supported by similarity in shape between the Jomon and Aleut.

Yet again, the division of labor in Ainu society provides an interpretive framework for the Jomon sexual division of labor, particularly pertaining to the use of upper limbs between the sexes. As previously illustrated, Ainu males pursued hunting activities while females practiced gathering and processing of plants and raw materials. Additionally, both sexes cooperated in fishing activities at inland and coastal regions (Watanabe, 1972; 1977b). Furthermore, Ainu males at coastal sites fished using large nets and hunted sea mammals and large fish utilizing modified dugouts and sailing vessels to travel the open sea to harpoon large fish, sea otters, seals, sea lions and whales (Watanabe, 1972; Ölschleger, 1999; Iwasaki-Goodman and Nomoto, 1999). Ainu

females, on the other hand, were limited to bag net and basket trap fishing (Watanabe, 1972).

As previously described, the range of nitrogen values between males and females at the Yoshigo site suggest that differences in procurement activities existed between males and females. Kusaka and colleagues (2008) suggest that the wider dietary breadth of males may be due to both differential access to food related to the sexual division of labor and occupational differentiation in males. Specifically applied to the use of the upper limbs, the wider variation in male diet may be due to male participation in marine activities such as rowing and fishing, and consumption of the marine foods obtained (Kusaka et al., 2008). Swimming, although not directly analyzed at Yoshigo, may also be contributing to differences in humeral robusticity. Previous research shows that Jomon are bilaterally symmetrical in the humerus and share a high frequency of auditory exostoses with middle latitude groups, with 23.9% incidence in males and 13.9% incidence in Jomon females (Sakaue, 1998; Katayama, 1998). Therefore, it is plausible that swimming was pursued by both sexes, but moreso in males.

While the level of humeral robusticity in the Jomon is informative of marine activities in males, the humeral shape can also provide insight into the other manual activities that males and females participated in. For example, Stock and Pfeiffer (2004) showed that Late Stone Age hunter-gatherers of South Africa in both forest and fynbos environments were sexually dimorphic in humeral robusticity and shape. While males were more robust than females, the humeral shape of males was more circular indicating loading patterns that were primarily torsional. Females, in contrast, had a more elliptical humeral mid-distal shape that was strengthened in the AP plane. From the archaeological

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evidence of these hunter-gatherers and in conjunction with the sexual division of labor, the authors inferred specific activities that each sex pursued. The authors contend that the elongated AP humeral morphology in females was associated with harvesting shellfish using digging sticks, digging for tubers and processing plants with mortars and pestles. It is plausible that the male circular humeral morphology was caused by throwing activities, specifically with the use of spears during hunting of large game (Stock and Pfeiffer, 2004).

As described in the previous section, Jomon males and females demonstrate little difference in humeral mid-distal shape. Both sexes have circular humeral diaphyses, which is similar to the comparative samples of coastal hunter-gatherers of this study. The overall similarity in shape between the sexes indicates that habitual loading of the humeri was influenced more by activities that placed torsional stress on the humerus, rather than any activity that would result in significant loading in a single plane.

Again the Ainu sexual division of labor can provide insight into the specific manual activities performed by male and female Jomon. While Ainu males hunted, females practiced gathering and processing of plants and raw materials. Additionally, both sexes cooperated in fishing activities at inland and coastal sites (Watanabe, 1972; 1977b). With these activities, Ainu males and females utilized different implements for sex-specific tasks. For instance, for hunting and fishing Ainu males utilized bows and arrows, spears and nets, and at coastal sites, harpoons and paddles for rowing watercraft. In Ainu society socially imposed rules were in place that made it taboo for females to use fish spears and bow and arrows (Watanabe, 1972). Thus, Ainu females were limited to

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basket trap and bag net fishing, using wooden picks for collecting wild plants, nuts and roots, and using the tools associated with processing fish, deer, and raw materials.

Archaeological evidence of plant and animal remains support the occurrence of similar activities in the Jomon people. For example, faunal analysis suggests that terrestrial animals such as deer and wild boar were hunted and shellfish collected at Jomon sites (Akazawa, 1986). Archaeological remains also suggest that nuts, such as chestnuts, acorns and walnuts were collected and stored in pits, while tubers were likely collected by digging with chipped stone axes (Habu, 2004; Imamura, 1996). Fishing is evident from zooarchaeological analysis of fish remains. For instance, in a study of nine shell midden sites from the Middle and Late Jomon period on the eastern Kanto coast, Komiya (2005) demonstrated that fishing activities in the inner bay area exhibited high frequencies of coastal small fish species. In contrast, the inland sites had a higher frequency of freshwater fish while areas between the bay and inland sites showed higher frequencies of brackish water fish.

Archaeological evidence of Jomon tool-kits can help further elucidate the specific manual activities of Jomon males and females. The tool kits found in the coastal area of the Tokai and Kanto districts, from which the Yoshigo site Jomon derive are useful here. Artifacts found within this region in high frequency and within the lithic assemblage include: projectile points and polished stone axes, and to a lesser extent stemmed scrapers, awls, flake scrapers, stone querns, grinding stones, grinding slabs and both chipped and polished stone axes. The fishing assemblages included in high frequency spear points and ceramic sinkers and to a lesser extent one-piece fishhooks. Although of negligible frequency, other artifacts belonging to the fishing tool kit include: harpoons,

composite and anchor type fishhooks, and stone sinkers (Akazawa, 1986). Many of these types of artifacts were excavated at Yoshigo. They include "earthenware, pieces of stone artifacts such as stone axes, stone arrowheads, stone weights and aliening stones; bone and horn pieces such as shell bracelets, bone arrowheads and bone needles; pieces made of shell; and other such artificial objects" (Saito et al., 1952: xii). At the very least, these results suggest tools associated with food processing, possible hunting and fishing with spears, hunting with bows, and fishing with nets**.**

Although bilateral asymmetry could not be analyzed in the current study, past studies have demonstrated that Jomon humeral bilateral asymmetry in robusticity and shape is low indicating the large influence of bimanual loading activities on both males and females (Sakaue, 1998; Churchill et al., 1996). This lends further support to the idea that rowing and swimming, as bimanual activities, had a large impact on male Jomon humeral morphology. Activities that may have also had influence on Jomon male robusticity and shape include the use of fishing spears and harpoons, which would cause torsional loading through throwing movements, at least unilaterally. It is also possible that throwing and lifting of nets had an impact on male humeral robusticity and shape. From the presence of stone and bone arrowheads at Yoshigo males may have also been utilizing spears or bows and arrows in hunting.

In comparison to Jomon males, Jomon females have less robust humeral diaphyses, but are similar in possessing relatively circular diaphyseal shape. This suggests that females were loading their upper limbs less intensively, but in a similar manner. Based on the Jomon sexual division of labor, archaeological remains and low bilateral asymmetry (Sakaue, 1998), it is plausible that female humeral morphology was

influenced by dynamic loading during bimanual activities such as swimming, grinding for processing foods, and in digging tubers and shellfish collecting, both of which may have been bilateral or unilateral. Although previous studies have demonstrated that grinding and shellfish collecting produce a more elliptical shape indicative of habitual loading in a single plane (Ruff and Larsen, 1990; Stock and Pfeiffer, 2004), it is possible that Jomon female humeral morphology was affected by a combination of habitual activities that produced the circular morphology. This is plausible based on the relatively circular humeral shape of the females in the Aleut, California and Georgia comparative groups who also actively grinded and dug shellfish, but performed bimanual activities as well.

Although inferring specific activities of the upper limbs is challenging due to the complexity of the mechanical environment of the humeri, a general impression of the manual activities that the Jomon were habitually involved in are gained from the study. Overall, the sexual dimorphism of Jomon robusticity and shape of the femora and humeri is typical of other hunter-gatherers. As interpreted in the framework of the Ainu sexual division of labor, the Jomon at Yoshigo likely demonstrated sex-specific task differentiation whereby males were hunting, females were collecting and processing plants and raw materials, and both sexes cooperated in fishing procurement.

Based on indirect evidence from Ainu ethnographic accounts, the archaeological record of Late to Final Jomon sites in the area around Yoshigo and the tools within Yoshigo, and evidence for the marine heavy diet of Yoshigo inhabitants, it is plausible to infer that male Jomon were intensively loading their upper limbs in rowing ocean watercraft, swimming, fishing with spears, harpoons and nets, and possibly using bows

and arrows in hunting. Jomon females, in contrast, were less intensively loading their humeri but participated in a combination of activities such as bimanual swimming, grinding of foods, digging for tubers and shellfish collecting. In this sense, structural adaptations between the sexes are associated with similar movements, though greater intensity of strains in Jomon males.

IV. GENERAL CONSIDERATIONS

Several general issues must be taken into consideration to understand the results and conclusions of this study. For instance, no bone image comparison was available to obtain the density threshold values in Image J for the Yoshigo femora and humeri cross-sections. The density threshold values affect the area of the bone used for calculating the cross-sectional properties. By recommendation of Dr. Daniel Wescott appropriate density threshold values were obtained based on previous experience with the program and values of percent cortical area around 70%. After the data were collected, it was determined that femora and humeri percent cortical areas were on average between 70-78%. Also raw femoral cross-sectional values were compared with the available data in Kimura (2006) and were determined to fall within the ranges provided. Therefore, it was concluded that the Yoshigo properties were appropriate for use in the present study.

Also at issue is the fact that cross-sectional properties were compared between samples that were derived using different techniques. In particular, while CT scans were used to obtain cross-sectional properties for the Jomon and Aleut samples, and direct sectioning was used for the Georgia coast sample (Ruff and Larsen, 1990), the California

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sample's cross-sectional properties were derived from radiographs (Weiss, 2009). Stock (2002) and O'Neill and Ruff (2004) noted that when compared with true cross-sectional property values, radiographic methods overestimate second moments of area, but reasonably estimate cross-sectional areas. Thus, this suggests that the second moments of area in the California sample may be inflated. Although this may the case, the Jomon have large enough mean humeral cross-sectional values to be significantly different than the California in all comparisons except the shape ratio.

In addition, the Jomon sample size utilized in this study may be problematic. The sample size for Jomon femora ($N_\male = 9$, $N_\female = 11$) and, especially, humeri ($N_\male = 6$, $N_\female = 4$) is small relative to the comparative samples. This may have an effect on the results of the statistical analyses. Specifically, the small Jomon sample size grants less power to the statistical tests (Type II error) and thus increases the probability of incorrectly accepting the null hypothesis if it is false. Thus, the conclusions of the study may be partially limited.

Another limitation of the study is in the use of samples that are derived from different geographical regions, and consequently, different climates. As Pearson (2000) and Weaver (2003) demonstrated, cold-adapted groups have more robust long bone diaphyses and, at least in the femora, a more circular midshaft shape than warm-adapted groups. Thus, the differences in body size and body shape may be at issue in this study. However, in the femora body size and shape were accounted for by size standardizing the cross-sectional properties to the product of body mass and limb length (Ruff, 2000). As a result, the cold-adapted limb proportions and body shape of the Aleut were controlled for, thus minimizing the affect of over estimating robusticity in comparison with the Jomon.

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In terms of the humeri, body size was accounted for through size standardization by powers of bone length (Ruff et al., 1993). Body shape is still an issue when utilizing cross-sectional properties standardized using this method. As a result, the cold-adapted Aleut may have over estimated robusticity values. However, since the results generally correspond with the trends outlined in Weiss' research (2003), which revealed similar trends when additionally accounting for body mass, this does not affect the conclusions on marine mobility or sexual dimorphism in the humeri of the Jomon.

Although there were issues with 1) obtaining the cross-sectional properties of the Jomon sample, 2) the small sample size of Jomon humeri and femora, in addition to the issues with 3) comparing samples from different climates with 4) cross-sectional properties obtained from variable techniques, these may not be problematic for the interpretations of the current study. When applicable, problematic effects were minimized such as in the case of obtaining cross-sectional properties from the Jomon sample in Image J and in appropriately size standardizing the femora with values that take into consideration body shape and limb proportions. From evaluation of the humeral comparison results in general and the California sample specifically, it is likely that these issues had little effect on the overall results of the study. Also, the small size of the Jomon sample from Yoshigo does not necessarily invalidate the conclusions of the present study—it limits the ability to identify significant differences.

CHAPTER 5: CONCLUSIONS

This primary goal of the present study was to document and interpret prehistoric Jomon femoral and humeral diaphyseal structure within the context of the mechanical environment. By applying the principles of bone functional adaptation and archaeological knowledge, cross-sectional geometric analysis was utilized to infer Jomon subsistence behavior and related activities from comparisons with coastal hunter-gatherers of North America.

Specifically, there were three objectives of the present study. The first objective was to analyze the robusticity and shape of Jomon femoral midshafts in comparison with Aleut femora to infer the level and pattern of terrestrial mobility of the Yoshigo Jomon. Second, the robusticity and shape of humeral mid-distal diaphyses were examined between the Jomon and coastal hunter-gatherers from the Aleutian Islands, California coast and Georgia coast to infer the level and pattern of marine mobility in the Jomon inhabitants at the Yoshigo site. Finally, differences in sexual dimorphism in femoral midshaft and humeral mid-distal diaphyseal shape and robusticity were investigated between the Jomon and the coastal hunter-gatherer comparative samples to reconstruct sex specific activities of the Jomon people at Yoshigo.

I. TERRESTRIAL MOBILITY

Results from the comparison of femoral midshaft diaphyses of the Jomon and

Aleut groups demonstrate that robusticity and shape are similar between these groups.

This suggests that the Jomon had a similar level of terrestrial mobility as the Aleut.

Indirect lines of evidence from the archaeological record and ethnographic accounts

provide insight into the habitual activities that influenced Jomon femoral and humeral

robusticity and shape, and furthermore support the conclusions of the current study. The

similarity in Jomon and Aleut femoral midshaft robusticity and shape are indicative of a

similar level and pattern of terrestrial mobility. As a result, both the Jomon and Aleut

were likely traveling across the landscape in the same manner. It is plausible that this

connection is due to similarity in residential mobility between the groups. Ethnographic

accounts document that the Aleut retain a residentially stable society with permanent

winter villages. Ethnographic accounts from the Ainu, which settled in permanent

villages, further reveal that it is likely that the Ainu sent out specialized task groups to

procure seasonal food resources while remaining at their permanent settlements.

Archaeological and ethnoarchaeological evidence suggest that the Jomon were also

residentially sedentary hunter-gatherers and likely sent out specialized task groups to

procure food.

Alternatively, similarity in femoral robusticity and shape in the Jomon and Aleut

may be attributed to the effects of terrain. Terrain relief for the Aleuts is predominantly

rugged, which may be influencing the robusticity in the femora of this group. The terrain

at the Yoshigo site is not particularly rugged, but northeast of the site where the Jomon

inhabitants may have been traversing the terrain, relief is comparably high. If these

rugged areas were traversed by the Yoshigo people, then the similarity between the Jomon and Aleut femoral robusticity can be explained by this environmental factor. Also, it is not possible to rule out the influence of a similarity in workload intensity between these groups. Taken together, it is plausible that the structural adaptation of femora among the Yoshigo Jomon were associated with terrestrial mobility, rugged terrain and workload intensity.

II. MARINE MOBILITY

Comparisons of the humeri reveal that robusticity is generally different between the Jomon and comparative groups, while shape is similar. In particular, the Jomon exhibit the greatest level of robusticity in the humeral mid-distal region compared to the coastal hunter-gatherer groups. This trend indicates that the Jomon were likely marine mobile and utilizing ocean watercraft to exploit food resources. Archaeological evidence provides support for the conclusions on marine mobility in the Jomon at Yoshigo. In particular, based on stable isotope analyses, discoveries of logboat remains throughout the Jomon period, and fishing gear assemblages, it can be concluded that the inhabitants of the Yoshigo site were exploiting and consuming marine foods through the use of ocean watercraft. Furthermore it is also plausible that the Jomon at Yoshigo were swimming and diving. This is based on studies that show a high frequency of auditory exostoses in Jomon from coastal sites.

Taken together, the evidence indicates that marine activities such as rowing and fishing likely contributed to the high humeral robusticity in the Yoshigo Jomon,

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particularly in males. It is also likely that the high humeral robusticity and shape

exhibited in the Yoshigo was obtained through habitual loading from throwing activities.

The fact that Aleut males also have a relatively circular, though slightly more AP

elongated, humeral diaphysis also supports this idea, since throwing of harpoons and

bolas was practiced during food procurement activities. It may be that throwing and

lifting of nets in fishing activities is differentiating the Jomon from the Aleut. However,

humeral asymmetry data is needed to differentiate these activities since throwing causes

bilateral asymmetry in the humerus. Thus, additional factors such as swimming should

be considered as contributing to differences in the Jomon and Aleut. Frigid temperatures

of the arctic waters would have deterred the Aleuts from pursuing this activity.

II. SEXUAL DIVISION OF LABOR, MOBILITY & SEX-SPECIFIC TASKS

In terms of differences in sexual dimorphism, the Jomon are generally similar to

the comparative samples, suggesting a similarity in the sexual division of labor and sex-

specific tasks between the groups. These results propose that, overall, the Jomon at the

Yoshigo site are comparable to other coastal hunter-gatherers in terms of the activities

carried out by males and females. Specifically, the terrestrial and marine mobility and

sex-specific activities of the Jomon are generally most similar to the ocean-rowing Aleut

hunter-gatherers.

In the context of sexual dimorphism of the femora, the Jomon demonstrate a

pattern whereby males have a larger overall robusticity and more AP elongated femoral

midshaft than females. This demonstrates that the Jomon were sexual dimorphic in the

lower limbs. It is plausible that Jomon males pursued hunting activities while females practiced gathering of plants and raw materials, with both sexes cooperating in fishing activities.

Also, based on the disparity in activities fields of Ainu males and females, it is possible to designate the difference between the Jomon sexes as due to differences in terrestrial mobility. Thus, it plausible that Jomon males were traveling across the landscape differently than females. Specifically, Jomon males were likely experiencing higher levels of mechanical loading contributing to their higher overall bending rigidity from traveling on longer forays outside the permanent residential base to procure food resources at seasonal hunting camps that may have been located in areas of more rugged terrain. Females in contrast likely stayed close to the permanent settlement even during resource procurement activities.

In the upper limbs, analysis of sexual dimorphism in humeral robusticity and shape can help clarify the manual activities that each sex engaged in. Based on the interpretation of Jomon sexual division of labor from the Ainu, archaeological remains and low bilateral asymmetry of the Jomon it is plausible that male humeral mid-distal robusticity was influenced by dynamic loading primarily during rowing activities on the open ocean, but also activities during fishing and terrestrial hunting. It is plausible that rowing and swimming, as bimanual activities, had a large impact on male Jomon humeral morphology. Activities that may have also had influence on Jomon male robusticity and shape include the use of fishing spears and harpoons, which cause torsional loading through throwing movements, at least unilaterally. It is also possible that throwing and lifting of nets also had an impact on male humeral robusticity and shape. From the

presence of stone and bone arrowheads at Yoshigo males may have also been utilizing bows and arrows in hunting.

In contrast, Jomon females have less robust humeral diaphyses, but are similar in possessing relatively circular diaphyseal shape. This suggests that females were loading their upper limbs less intensively, but in a similar manner. It is plausible that female humeral morphology was influenced by dynamic loading during bimanual activities such as swimming, grinding for processing foods, and in digging tubers and shellfish collecting, both of which may have been bilateral or unilateral. Although previous studies have demonstrated that grinding and shellfish collecting produce a more elliptical shape indicative of habitual loading in a single plane, it is possible that Jomon female humeral morphology was affected by a combination of habitual activities that produced the circular morphology. This is plausible based on the relatively circular humeral shape of the females in the Aleut, California and Georgia comparative groups who also pursued these activities.

Bringing together these diverse lines of evidence, a general reconstruction of the subsistence behaviors of the Jomon inhabitants of the Yoshigo site is achieved. Specifically, the Jomon at Yoshigo likely demonstrated sex-specific task differentiation whereby males were hunting, females were collecting and processing plants and raw materials, and both sexes were cooperating in fishing activities. In particular, Yoshigo males were more intensively loading their femora and humeri than females, indicating the higher level of terrestrial and marine mobility in the males. Yoshigo females, in contrast, were not as mobile and likely stayed close to the home settlement for procurement activities while Jomon males hunted and fished farther from the home base, traveling to

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seasonal base camps for these activities. The manual activities that Yoshigo males were likely participating in include open ocean rowing, swimming, bow and spear hunting, and fishing with the use of spears, harpoons and nets. Yoshigo females, on the other hand, performed less intensive manual tasks, possibly including swimming, grinding, digging, processing of food and shellfish collecting.

IV. FUTURE DIRECTIONS

The current research raises several possible directions for future study. For example, it is possible to utilize cross-sectional geometry to study Jomon femoral and humeral robusticity and shape across the regions of the Japanese archipelago. Based on previous research it is well established that resource procurement methods differed between eastern and western sites. Although Jomon people in the west and east were both relying on terrestrial and marine resources, variation in diet existed based on resource availability. Specifically, Jomon in the east had more year round access to food, while Jomon in the west had seasonal access to different food resources. It is also noted that tool kits between regions varied. Therefore, the conclusions on terrestrial and marine mobility and the manual activities of the inhabitants of Yoshigo—an eastern Jomon site—could be compared to the inhabitants of a western coastal site. As a result, applying an analysis of cross-sectional geometry of humeri and femora between Jomon from the east and west could further elucidate differences in food exploitation patterns and activities.

Another direction for future research is to examine bilateral asymmetry in the inhabitants of the Yoshigo site. Previous studies demonstrate that differences between robusticity and shape between the upper limbs of the Jomon people are generally symmetric. This is especially apparent when comparing the Jomon to other hunter-gatherers which exhibit bilateral asymmetry of the upper limbs. Studying differences between loading intensity and patterns between limbs in the Jomon at Yoshigo can further help clarify the specific manual activities performed by males and females. Specifically, this type of analysis has the potential to reveal participation in bimanual and unimanual activities within the group.

Finally, the results from the current study can be used in conjunction with past mortuary analyses of Yoshigo. Previous analyses reveal that indicators of identity at Yoshigo reflect the achieved social identities of individuals. Further study determined that the group identities associated with different forms of ritual tooth ablation and may relate to kin-based social units with lifetime achievements acting as the basis for group membership. The possibility that members of each group represented subsistence task members is open to testing. Application of cross-sectional geometric analysis of the inhabitants of Yoshigo can further elucidate the presence of occupational differentiation between members of identity groups.

APPENDIX 1

Table 15. Jomon male standardized femoral midshaft cross-sectional properties[1,2].

Specimen	TA	CA	Ix	Iy	Imax	Imin	Ix/Iy	J	%CA
271	970.520	747.462	14018.724	8700.532	14553.194	8166.061	1.611	22719.256	77.017
380	905.053	681.518	11500.525	7764.595	11561.065	7704.055	1.481	19265.120	75.301
418	936.700	731.452	9851.958	7498.696	10099.705	7250.949	1.314	17350.654	78.088
419	920.033	684.720	10634.178	8021.244	10826.925	7828.497	1.326	18655.422	74.423
421	1022.458	741.993	13583.094	7827.579	13662.284	7748.389	1.735	21410.673	72.570
436	942.780	784.241	11669.211	9548.499	12312.335	8905.375	1.222	21217.710	83.184
492	990.105	730.360	10672.103	7922.415	10739.336	7855.182	1.347	18594.517	73.766
514	881.596	628.612	7151.547	7269.052	7892.648	6527.950	0.984	14420.599	71.304
538	1098.761	788.980	13736.771	9259.898	14231.800	8764.869	1.483	22996.669	71.806

[1]Cross-sectional properties size standardized and with area multiplied by 10^2 and second moments of area multiplied by 10^4.
[2]Areas in mm^2 and second moments of area in mm^4.

Table 16. Jomon female standardized femoral midshaft cross-sectional properties[1,2].

Name	TA	CA	Ix	Iy	Imax	Imin	Ix/Iy	J	%CA
279	811.085	614.855	6407.383	7603.983	7627.842	6383.524	0.843	14011.366	75.806
302	744.718	620.433	5916.749	6008.186	6516.332	5408.604	0.985	11924.935	83.311
305	709.380	593.235	7018.863	4816.852	7025.242	4810.472	1.457	11835.714	83.627
310	879.123	721.653	7392.510	8299.647	8572.873	7119.284	0.891	15692.157	82.088
325	822.055	625.069	7309.157	7728.713	8400.836	6637.035	0.946	15037.870	76.037
352	659.563	497.775	4835.637	4741.573	4887.718	4689.492	1.020	9577.210	75.470
353	796.349	570.854	7370.873	6075.692	7968.666	5477.899	1.213	13446.566	71.684
361	777.398	575.265	5836.697	6277.164	6883.469	5230.391	0.930	12113.860	73.999
463	878.656	652.518	7920.292	8316.832	8442.517	7794.606	0.952	16237.123	74.263
541	811.774	627.976	6127.046	6375.558	6426.043	6076.561	0.961	12502.604	77.358
495	786.524	608.487	7541.959	6539.162	7762.333	6318.788	1.153	14081.121	77.364

[1]Cross-sectional properties size standardized and with area multiplied by 10^2 and second moments of area multiplied by 10^4.
[2]Areas in mm^2 and second moments of area in mm^4.

Table 17. Jomon male standardized humeral mid-distal cross-sectional properties[1,2].

Specimen	TA	CA	Ix	Iy	Imax	Imin	Ix/Iy	J	%CA
271	1683.343	1175.234	8160.998	9957.127	10311.214	7806.911	0.820	18118.125	69.815
273	1111.516	825.665	4279.268	3916.472	4473.811	3721.928	1.093	8195.740	74.283
380	1283.468	911.572	5148.718	5590.777	5664.217	5075.278	0.921	10739.495	71.024
396	1302.882	945.435	5960.076	5356.500	6040.018	5276.558	1.113	11316.576	72.565
418	1301.377	1072.650	5446.853	6132.461	6152.254	5427.060	0.888	11579.313	82.424
436	1130.504	866.120	4041.491	4570.553	4583.636	4028.408	0.884	8612.044	76.614

[1]Cross-sectional properties size standardized and with area multiplied by 10^8 and second moments of area multiplied by 10^{13}.
[2]Areas in mm^2 and second moments of area in mm^4.

Table 18. Jomon female standardized humeral mid-distal cross-sectional properties[1,2].

Specimen	TA	CA	Ix	Iy	Imax	Imin	Ix/Iy	J	%CA
305	1390.010	820.192	5217.427	5601.245	5878.516	4940.156	0.931	10818.672	59.006
310	1086.490	838.566	3484.223	4373.499	4679.601	3178.121	0.797	7857.722	77.181
541	1103.662	825.948	4025.664	3669.480	4480.054	3215.090	1.097	7695.144	74.837
558	1137.076	771.488	4034.339	3899.628	4881.621	3052.346	1.035	7933.967	67.848

[1]Cross-sectional properties size standardized and with area multiplied by 10^8 and second moments of area multiplied by 10^{13}.
[2]Areas in mm^2 and second moments of area in mm^4.

Figure 8. Example of Jomon male femoral midshaft cross-section from specimen 271.
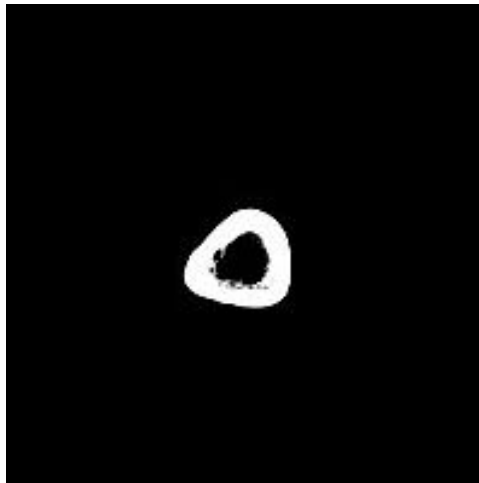

Figure 9. Example of Jomon male humeral mid-distal cross-section from specimen 271.
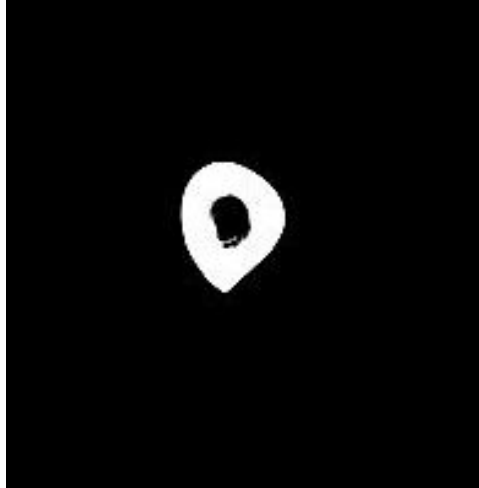
Figure 10. Example of Jomon female femoral midshaft cross-section from specimen 305.
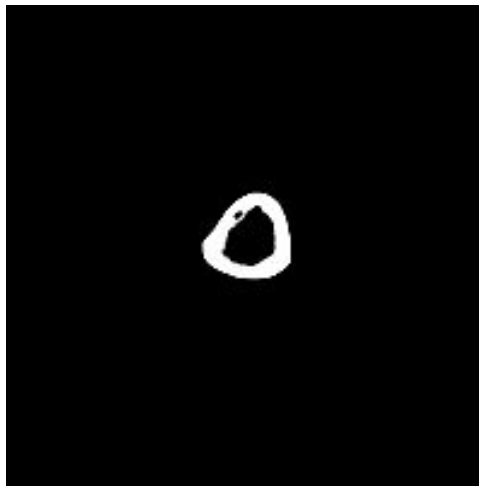

Figure 11. Example of Jomon female humeral mid-distal cross-section from specimen 305.

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