ADAPTING IN THE ARCTIC: COMPARING FUNCTIONAL ADAPTATION IN THE
LONG BONE DIAPHYSES OF ALASKAN HUNTER-GATHERERS

by

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A Thesis
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DEDICATION

This thesis is dedicated to the hundreds of Alaskan individuals whose skeletal remains provided the data for this research. Although the choice was not yours, I am grateful for the invaluable opportunity to learn from you. Thank you.

ACKNOWLEDGEMENTS

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ABSTRACT

ADAPTING IN THE ARCTIC: COMPARING FUNCTIONAL ADAPTATION IN THE LONG BONE DIAPHYSES OF ALASKAN HUNTER-GATHERERS

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This thesis compares cross-sectional geometric measures of femoral, tibial, humeral, and radial diaphyseal robusticity and compares humeral and radial bilateral asymmetry between three samples of native Alaskan hunter-gatherers with different subsistence strategies and resultant levels of terrestrial and aquatic mobility. Results of unilateral comparisons found significant differences in male and female femoral robusticity between samples, with far north coastal Alaskans demonstrating higher robusticity than inland and coastal groups. The same results were not found in tibial samples. Neither male or female humeri show significant differences in robusticity between site types. Contrastingly, coastal male radii demonstrate increased robusticity compared to other samples. Analyses of bilateral asymmetry found significant differences in robusticity among male humeral samples, with far north coastal populations exhibiting increased asymmetry compared to other samples. Results suggest that terrestrial mobility

significantly impacts femoral robusticity, but that structural optimization or ecogeographical constraints may limit the adaptive capacity of the tibia. In contrast, specific muscle activation during riverine and coastal rowing may explain why radial, but not humeral, robusticity increases among populations with aquatic mobility. Finally, hunting style utilizing harpoons and spears likely explains the increased humeral asymmetry of far north coastal males relative to coastal and inland groups.

INTRODUCTION

Biomechanics and Functional Adaptation

Biomechanics refers to the application of mechanical theories and methods to the study of the structure and function of living systems. The discipline encompasses a broad field of inquiry and may be concerned with the properties of anything from individual cells to an entire species. Given the significance of the musculoskeletal system in generating mechanical energy, skeletal biomechanics has emerged as a prominent subdiscipline which is often applied in clinical contexts to study and improve mobility in patients with musculoskeletal pathological conditions.

However, skeletal biomechanics is not limited to clinical settings. Anthropologists have applied skeletal biomechanics in numerous ways, from studying the efficiency of different forms of locomotion to generate hypotheses regarding the evolution of human bipedalism (Wang et al. 2003) to analyzing the effect of diet and muscle strain on primate skull morphology (Ross et al. 2005). In particular, bioarchaeology, a discipline which seeks to interpret the life of prehistoric humans using skeletal material, has utilized biomechanics to make sense of the behavioral patterns of past populations.

An early theory leading to bioarchaeological uses of biomechanics is known as "Wolff's Law." German surgeon Julius Wolff published *Das Gesetz der Transformation der Knochen* (*The Law of Transformation of Bone*) in 1892 (Brand 2010). In the

publication, Wolff made three observations on the nature of trabecular bone: 1) that

trabecular bone architecture is regular within individuals, 2) that trabeculae intersect at

right angles, and 3) that following fracture, trabeculae reorient to remain at right angles.

Wolff's publication was based in part on the work of other anatomists, and the first two

observations were not unique to Wolff. However, the third – that bone reorients itself

after structural failure– was novel and for the first time indicated the adaptive nature of

bone. From this observation Wolff proposed a "mathematical law according to which

observed alterations in the internal architecture and external form of bone occur as a

consequence of the change in shape and/or stressing of bone" (Brand 2010, 1048).

Wolff failed to define the mathematical formula by which bone supposedly

remodels (Brand 2010), and following the publication, there has been contention

regarding the applicability of a specific mathematical formula to bone remodeling.

However, Wolff's "law" is significant in that it established the general principle that bone

remodels in response to external loading. Because "Wolff's Law" in its original intent

referred to a specific mathematical formula which has not been definitively proven, this

principle is now referred to instead as functional adaptation (Ruff et al. 2006).

It is now known that functional adaptation is the result of the relationship between

osteoblasts and osteoclasts (Ruff 2008). At a basic level, functional adaptation assumes

that every skeletal element can accommodate a baseline level of strain without

deformation. If a bone is subjected to increased loading beyond the optimal level,

osteoblasts will deposit additional material to disperse the increased strain over more

bone. Contrastingly, if a bone is subjected to strain below the optimal level, osteoclasts

will resorb bone to avoid unnecessary maintenance of bone that is not utilized. Figure 1

illustrates the relationship between loading, bone deposition, and bone resorption.
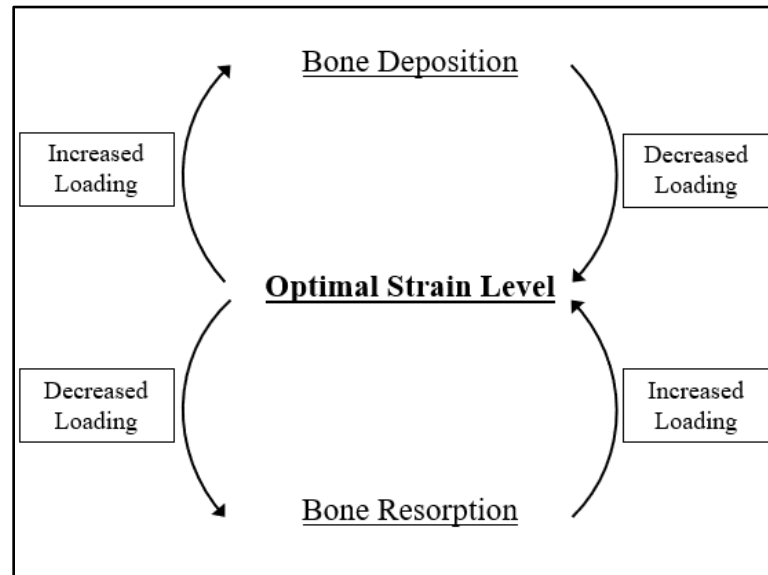
Figure 1. Simple Feedback Loop Illustrating Functional Adaptation (adapted from Lanyon 1982)

Numerous studies have generated support for the validity of functional adaptation

in living human populations. Analyses of athletes playing predominantly unimanual

sports (e.g., tennis, racquetball) are particularly useful because the effects of increased

loading on the playing arm can be compared with the nonplaying arm while controlling

for other factors (e.g., diet, health, age). Jones et al. (1977) compared bilateral humeral

radiographs of 84 professional tennis players with an average of fourteen (females) and

eighteen (males) years playing experience. The authors examined cortical and medullary

size at four sites near the distal epiphysis of the humerus and found that every player

demonstrated humeral hypertrophy – thickened cortical area and reduced medullary canal – in the playing arm compared to the non-playing arm. Average cortical thickness of male and female playing humeri increased by 34.9% and 28.4%, respectively.

Over thirty years later, Shaw and Stock (2009a) found similar evidence of functional adaptation by conducting bilateral comparisons of the humeri of cricket players as well as comparing the humeri of swimmers with sedentary controls. Supporting the theory of functional adaptation, the authors found significantly greater cortical thickness among the playing arm of cricketers compared to non-playing arms. Additionally, the playing arm of cricketers was significantly stronger than the arms of swimmers, which in turn were significantly stronger than sedentary controls. As with Jones et al., Shaw and Stock (2009a) demonstrate that increased mechanical loading leads to skeletal hypertrophy. Numerous other studies have demonstrated hypertrophy of the upper limb in response to loading (Claussen 1982, Kannus et al. 1995, and King et al. 1969); the upper limbs in humans are particularly useful for such studies since the arms are uncoupled from locomotory functions and are utilized in many behaviors.

Additional studies of modern human populations have found support for the contrasting component of functional adaptation – that decreased mechanical loading leads to the loss of bone in affected areas. Peck and Stout (2009) compared bilateral femoral diaphyses of fourteen decedents who had received a total hip arthroplasty (total hip replacement) of one femur. Following implantation of the prosthesis, the authors found a significant reduction in femoral diaphyseal cortical area and an average of 60% increase in the medullary area of the affected femur compared to the intact femur of the same

individual. The results indicate that reduced mobility, likely due to the surgical procedure, diminished mechanical loading on the affected leg and led to bone resorption. Other studies have found similar results following reduced loading due to injury (Jenkins and Cochran 1969) and even due to spaceflight-related weightlessness (Miyamoto et al. 1998).

The previous studies all provide experimental support for skeletal functional adaptation by demonstrating bone deposition in response to increased mechanical loading and bone loss in response to decreased loading. Because the mechanical loading experienced by bones may be indicative of habitual activity patterns, logic infers that functional adaptation is a useful framework through which to interpret activity patterns of prehistoric human populations. However, to ensure accurate analyses, the adoption of universal, objective, and repeatable methods for measuring bone response to mechanical loading is necessary. A common method adopted by bioarchaeologists is one adapted from engineering: beam theory.

Beam Theory and Cross-Sectional Geometry

There are several plausible methods for measuring the reaction of bone to external mechanical loading. To determine the most accurate method, Huiskes (1982) recorded strain levels of a cadaveric left femur subjected to various loadings and then calculated strain using two formulae based on different theories, one assuming anisotropic and one assuming isotropic bone properties. The author then sliced the femur along the transverse plane, recorded cross-sectional properties, and calculated stresses using both beam theory and finite element methods (FEM) theory.

Huiskes (1982) determined that of all methods used to calculate femoral strain, beam theory produced the most accurate results and was relatively simple and cost-effective to utilize. In the wake of Huiskes' results, bioarchaeologists have utilized engineering beam theory to evaluate the response of long bones to loading.

Beam theory essentially posits that certain cross-sectional geometric properties, measured perpendicular to the long axis of a beam (or bone), may be used to measure responses to stresses resulting from externally-applied pressure. Both the engineering concepts of strength (the ability to resist failure or fracture) and rigidity (the resistance to deformation before fracture) are important qualities in beams and bones, and each is calculated in different ways.

Bones may be subjected to a variety of mechanical loading during everyday activity. Both axial tension and compression act on the long axis of a bone; the former pulls apart while the latter presses bone together. Bending simultaneously produces tension and compression on opposing surfaces of a cross section. Torsional forces occur when bone is twisted along the long axis and produce shearing or diagonal stress. The strength and rigidity of bones with respect to these different mechanical loadings may be evaluated with different cross-sectional geometric properties (Table 1).

Table 1. Cross-Sectional Geometric Properties of Long Bones

Property	Abbrev.	Units	Definition
Total Subperiosteal Area	TA	mm^2	Area w/in Subperiosteal Surface
Cortical Area	CA	mm^2	Compressive/Tensile Strength and Rigidity
Medullary Area	MA	mm^2	Area w/in Medullary Cavity
M-L Second Moment of Area	I_x	mm^4	A-P Bending Rigidity
A-P Second Moment of Area	I_y	mm^4	M-L Bending Rigidity
Polar Second Moment of Area	J	mm^4	Torsional Rigidity/Overall Rigidity
Section Modulus (M-L Axis)	Z_x	mm^3	A-P Bending Strength
Section Modulus (A-P Axis)	Z_y	mm^3	M-L Bending Strength
Polar Section Modulus	Z_p	mm^3	Torsional Strength/Overall Strength
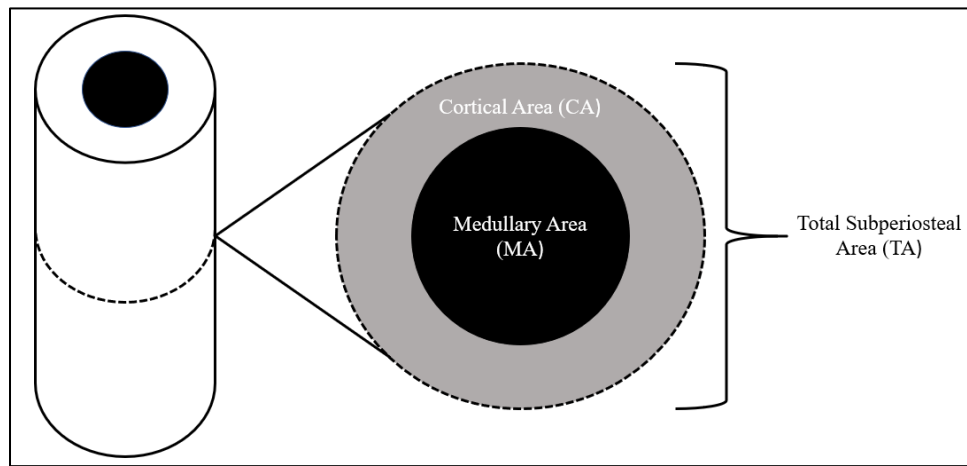
Figure 2. Basic Composition of Long Bone Diaphysis

In pure axial compression and tension, both rigidity and strength are equal to the area of material within a beam. In the case of long bones, this equates to the cortical area (CA). Cortical area is one component of total subperiosteal area (TA), the other being medullary area (MA), the space that, during life, contains adipose tissue and does not contribute to strength and rigidity (Figure 2). However, unlike architectural beams, long bones are rarely subjected to pure compression or tension.

Instead, stress due to bending and torsional loadings normally predominate in long bone diaphyses during life (Rubin and Lanyon, 1982) and are thus more mechanically significant to bioarchaeological studies. Beam theory states that under bending or torsional stress, the magnitude of such stress is proportional to the distance from a neutral axis, where stress is zero (Larsen 2015). In other words, bone material that is furthest from the neutral plane (during bending) or neutral axis (during torsion) will have the greatest resistance to bending and torsional forces. Through inference, this also suggests that "the greater the distance from the neutral axis, the greater the magnitude of stresses to which the bone has been adapted over time" (Larsen 2015, 217).

Bending/torsional rigidity (resistance to deformation before failure) is proportional to second moments of area (SMAs), properties which are the product of small unit areas multiplied by the squared distances of those areas from the neutral axis or centroid point. For analyses of bending rigidity and strength, SMAs are often calculated about the mediolateral (M-L) or anteroposterior (A-P) axes of long bones. An SMA calculated about the M-L axis (I_x) is proportional to anteroposterior bending rigidity while one calculated about the A-P axis (I_y) is proportional to mediolateral bending rigidity. To calculate torsional rigidity, an SMA known as the polar second moment of area (J), is calculated about the central point of a cross section. J is equal to both torsional rigidity and two times the average bending rigidity in any two perpendicular planes. As such, J serves as a good indicator of overall bone rigidity.

Torsional and bending strength (the ability to resist fracture) is measured in properties related to, but slightly differing from, SMAs. Under bending or torsional

stresses, maximum stress occurs on the outermost surface of a cross-section. Therefore, strength-related properties are derived by dividing SMAs by the distance from the outermost surface to the appropriate neutral axis or centroid. The results are known as section moduli, designated Z with various appropriate subscripts. Like I_x and I_y, Z_x and Z_y refer to A-P and M-L bending strengths, respectively. Z_p is equal to torsional strength and twice the average bending strength, and is the strength equivalent of J. Like J, Z_p may be considered a good indication of overall strength within a cross-section.

A final cross-sectional property used to interpret behavioral patterns is the mobility index, or the ratio of A-P to M-L bending rigidities. The index is not measured directly from bone but is calculated by dividing I_x by I_y (I_x/I_y). While CA, I_x, I_y, J, Z_x, Z_y, and Z_p all reflect overall *levels* of mechanical loading experienced by a given cross-section of bone, I_x/I_y reflects *types* of loading because it represents relative bending rigidity between two perpendicular planes. In other words, I_x/I_y indicates whether, over time, a bone has been subjected to predominantly anteroposterior, mediolateral, or proportional loading.

A cross-section demonstrating an I_x/I_y equal to 1.0 would have a perfectly circular shape, suggesting proportional levels of A-P and M-L loading. A cross-section with an I_x/I_y greater than 1.0 would have greater A-P bending rigidity and therefore an ovoid shape oriented in the A-P plane. Finally, an I_x/I_y ratio below 1.0 is indicative of greater M-L than A-P bending rigidity and appears as an oval oriented in the M-L plane. Figure 3 demonstrates the differences between mobility index ratios.

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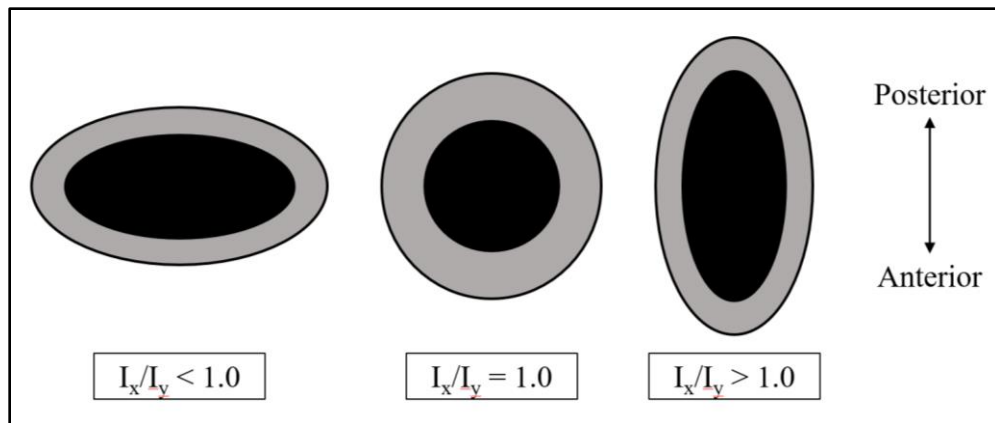
Figure 3. Differences in the Mobility Index

While beam theory can provide reliable calculations of the stresses generated in bone, it is important to note that cross-sectional geometry is not the only factor contributing to bone strength and rigidity. Other properties, such as age, health, and bone mineral density may also influence how bone reacts to loading. However, cross-sectional analysis remains one of the best methods through which to evaluate strength and rigidity within bioarchaeology because factors like general health and bone density are not always accessible in skeletal samples.

Additionally, there is evidence that cross-sectional morphology is a better indicator of mechanical loading than bone material properties like density. Erickson et al. (2002) attempted to reconstruct the biomechanical evolution of the femur spanning over 475 million years. The authors analyzed the material properties of the femora and analogous elements of extinct and extant members of the Kingdom *Animalia* and found minimal changes in material properties over time despite dramatic changes in size and morphology. The authors attribute the diversity of femoral shape and size to changes in

mechanical loading rather than material properties like bone density. Additionally, Robling et al. (2002) found that rats subjected to repeated ulnar loading achieved significantly greater resistance to fracture compared to controls, despite only modest gains in bone mineral content and bone mineral density. Both studies suggest that while the material properties of bone may play some role in strength and rigidity, bone geometry serves as a better indicator of functional adaptation to mechanical strain.

Use of Diaphyseal Cross-Sectional Measurements

In addition to addressing the possible influence of bone material properties, it is important to determine what region of bone is most useful for analyzing functional adaptation. Lieberman et al. (2001) compared subchondral articular surface area (ASA) size and diaphyseal cross-sectional properties between a group of exercised and control male sheep at juvenile, subadult, and adult phases of growth. Exercised sheep were subjected to running at approximately 4 km/hour for one hour per day for ninety days. Control animals were restricted to limited locomotion and sedentary weight support to reduce confounding variables. The authors euthanized the animals and measured ASA size at the distal scapula, distal humerus, proximal femur, proximal tibia, anterior and posterior astragalus, proximal and distal metacarpal, and proximal and distal metatarsal. Researchers also obtained midshaft diaphyseal cross-sectional properties of the humerus, femur, and tibia.

The ASAs of exercised sheep were larger than those of the control sheep at all ages; however, these differences were not statistically significant in any age group (Lieberman et al. 2001). Additionally, no trend was observed in ASA size between distal

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and proximal joints. Midshaft diaphyseal loading response (measured in second moments of area and polar moments of area), however, was significantly greater in the hindlimbs of exercised juvenile animals while subadult and adult sheep showed no such significant differences. The findings suggest that ASA morphology may be more buffered from mechanical influences throughout ontogeny than diaphyseal cross-sectional properties, despite increases in mechanical loading. The results support the use of long bone diaphyses, rather than joint surface areas, as indicators of habitual mechanical loading.

Cross-Sectional Geometry of Prehistoric Populations

The relationship between mechanical loading and diaphyseal cross-sectional geometry is well supported. Although there are additional factors (e.g., genetics, age, health) that can alter this relationship, in general it can be said that increased mechanical loading on a bone will result in increased measures of strength and rigidity as defined above. Given this relationship, it becomes possible to interpret the general activity patterns of past human populations. Populations showing increased diaphyseal robusticity may be inferred to have been subjected to greater mechanical loading than those with decreased diaphyseal robusticity. However, it is important to note that prehistoric populations have resided in a broad range of environments, practiced numerous subsistence methods, and engaged in various habitual activities. Previous research has identified some of the factors which have significant effects on measures of long bone robusticity, which will help to contextualize the current study.

Effects of Subsistence Strategy. Prehistoric human populations have developed numerous subsistence strategies, or methods of satisfying basic survival needs, depending

on geographic location, resource availability, technological advances, and more. Different subsistence patterns can require varying levels of physical engagement; for example, contemporary industrialized populations devote less energy to obtaining food than did preindustrial farming populations or hunter-gatherers. Inference suggests that, with all other factors controlled for, a population engaging in a less strenuous subsistence pattern would demonstrate lower cross-sectional indicators of robusticity than would a population practicing highly strenuous subsistence patterns.

Many studies have documented the effects of subsistence pattern on cross-sectional diaphyseal properties, and several have focused on determining the effects of the transition from hunting and gathering to agriculture. Ruff et al. (1984) compared the femoral cross-sectional characteristics of 20 preagricultural (2200 BCE – 1150 CE) with 20 agricultural (1150-1550 AD) Amerindian adults along the Georgia coast. The authors found that the agricultural group showed significant declines in most indicators of robusticity as well as relatively reduced medullary cavities, reduced subperiosteal diameter, and more circular cross-sectional shape (mobility index closer to 1.0) compared to the preagricultural group. Given the reduced robusticity indicators in agricultural femora, Ruff et al. contend that agricultural Amerindians experienced reduced mechanical loading in the lower limbs, possibly because an agricultural subsistence was less physically demanding than hunting and gathering.

Bridges (1989) found conflicting results regarding the effect of the agricultural transition on long bone morphology. Utilizing 1,937 burials in northwestern Alabama ranging in chronology from the Middle Archaic to the Mississippian period, Bridges

sought to identify changes in habitual physical activities (indicated by cross-sectional parameters) with the shift from hunting and gathering to maize agriculture. Additionally, the author sought to determine if the introduction of maize agriculture brought about noticeable changes in the sexual division of labor.

Unlike Ruff et al. (1984), Bridges (1989) found significantly greater indicators of robusticity in the long bones of Mississippian agriculturalists than in prehistoric hunter-gatherer populations. Although significant in both sexes, the difference was more pronounced among females than males. Bridges concludes that maize agriculture in northwestern Alabama was more physically strenuous than was hunting and gathering. In particular, the exaggerated increase in robusticity among females suggests that growing maize placed an increased burden on women relative to men.

To clarify conflicting results regarding the impact of agriculture on long bone robusticity, Bridges et al. (2000) analyzed differences in femoral and humeral diaphyseal morphology among west Illinois cultural groups during an agricultural transition era from the Middle Woodland, Late Woodland, and Mississippian periods. Native populations from all three eras are known to have utilized domesticated plants, but with varying degrees of dependency. The study allowed the authors to examine habitual activity associated with native seed horticulture (Middle Woodland group), early maize agriculture (Late Woodland group), and maize intensification agriculture (Mississippian group).

Bridges et al. (2000) found an overall increase in femoral robusticity through the chronological sequence, which was more pronounced among females than males. For the

lower limb, increasing dependence on food crops appears to correlate to increased

mechanical loading, especially for women. Humeral robusticity, however, does not

follow this trend. The greatest and most significant changes in humeral morphology

occurred in the Late Woodland period, prior to the intensification of maize agriculture.

During this period male humeral robusticity declined while female humeral robusticity

increased. Bridges et al. conclude that increases in femoral robusticity predate intense

maize agriculture and that the shift to agriculture placed a greater physical toll on the

upper limbs of females than males.

Ruff and Larsen (2001) found yet another pattern of long bone robusticity when

analyzing skeletal remains of pre- and post-contact Native Americans. The authors

examined 168 femora and 189 humeri from the La Florida region in present-day Florida

and Georgia comprising six distinct temporal and subsistence groups: Early Prehistoric

Guale (400 BCE – 1000 CE), Late Prehistoric Guale (1000-1450 CE), Early Mission

Guale (1600-1680 CE), Late Mission Guale (1680-1700 CE), Early Mission Yamasee

(1600-1680 CE), and Early Mission Timucua (1600-1680 CE).

Ruff and Larsen (2001) found that, among Guale males, overall loading of the

upper and lower limb was at a maximum among hunter-gatherers, decreased among early

horticulturalists, and increased again among postcontact populations. Female Guale

femora showed a similar pattern, while female Guale humeral loading reduced between

hunter-gatherers and horticulturalists but did not increase among post-contact groups.

The authors conclude that while hunting and gathering place greater mechanical loads on

the upper and lower limbs than does early agriculture, forced labor by Spanish missions may be responsible for the increase in robusticity seen in most postcontact samples.

Given the above research, there does not appear to be a universal correlation between long bone robusticity and subsistence pattern; some studies suggest that pre-agricultural populations are more robust while others support greater robusticity in agricultural groups. Wescott (2006) attempted to clarify the conflicting results by comparing femoral midshaft cross-sectional parameters of almost 2,500 individuals belonging to one of nine subsistence strategy groups: broad spectrum hunter-gatherers, woodland hunter-gatherers, marine hunter-gatherers, equestrian hunter-gatherers, incipient horticulturalists, village horticulturalist-hunters, maize-dependent horticulturalists, early modern industrialists, and late modern industrialists. The author predicted that more mobile groups would demonstrate greater overall robusticity and greater levels of sexual dimorphism.

Instead, Wescott (2006) found that femoral midshaft shape and robusticity did not consistently correspond to the above expectation. More mobile populations did demonstrate greater levels of sexual dimorphism, which may reflect changes in sex-specific activities among more sedentary groups. However, within the sexes, the author found no significant correlation between mobility pattern and femoral diaphyseal robusticity. This study, coupled with conflicting results of the previous research, suggests that subsistence strategy and associated mobility patterns cannot fully explain the variation in long bone robusticity. Other factors likely play a role in determining the robusticity of prehistoric populations.

Effects of Terrain. One such additional variable shown to influence long bone cross-sectional parameters is terrain. All other factors being constant, living and working on mountainous or other rugged terrain is more strenuous than is living on flat terrain, particularly for the lower limbs. Therefore, rugged terrains should place the body, primarily the legs, under more mechanical loading and theoretically result in more robust cross-sectional parameters than would smooth land. Relatedly, the interaction of a population with aquatic terrain may influence robusticity of the arms, since habitual swimming and rowing should theoretically result in more robust upper limb bones.

Stock and Pfeiffer (2001) found support for these hypotheses through the comparison of skeletal samples belonging to Later Stone Age foragers of South Africa with Andaman Islanders from Bengal Bay. The populations have similar physiques, age distributions, and technological capabilities but differ in inhabited terrain. South African foragers are characterized by high terrestrial mobility while the Andaman Islanders are known to have high marine mobility. Based on biomechanical theory, the authors predict that the South African foragers will demonstrate more robust lower limbs while the Andaman Islanders will have more robust upper limbs.

Through comparisons of 65 adult South African foragers with 39 adult Andaman Islanders, Stock and Pfeiffer (2001) found support for that prediction. Among both sexes, Andaman Islanders displayed significantly stronger humeri while male and female Later Stone Age African foragers had significantly more robust femora. Differences were most significant and consistent in maximum bending and torsional strengths of the long bones. The study establishes that populations traversing rugged terrestrial terrain are likely to

demonstrate increased lower limb robusticity while populations engaging in aquatic mobility are likely to exhibit increased upper limb strength.

Stock and Pfeiffer (2001) established that populations with habitually high marine mobility should demonstrate greater humeral robusticity than groups with low marine mobility. However, the study did not consider differing forms of aquatic lifestyles. To determine if various aquatic-based lifestyles result in different levels of humeral robusticity, Weiss (2003) compared humeral diaphyseal cross-sectional parameters of ocean-rowing (Alaskan Aleuts and British Columbian Amerindians), non-ocean-rowing (Georgian nonagricultural and agricultural Amerindians), and non-rowing (New Mexican agriculturalists and EuroAmerican industrialists) populations to determine if variation in rowing behavior affects the upper limbs to the same degree as variation in terrain affects the lower limbs.

Weiss (2003) found that ocean-rowing populations averaged more robust humeri than either non-ocean rowing and non-rowing groups, even when controlling for subsistence strategy. Additionally, despite evidence of rowing being a male-dominated activity, greater humeral robusticity was evident among both sexes in the ocean-rowing samples. This suggests that the act of rowing is not solely responsible for increased humeral properties; instead, activities related to an ocean-rowing lifestyle appear to produce greater strength and rigidity in all individuals, even those who are not habitually rowing. This research confirms that marine mobility results in greater humeral robusticity than terrestrial mobility with the added evidence that particular patterns of aquatic mobility lead to different degrees of humeral robusticity.

Bilateral Asymmetry. Another factor which may impact the ability to interpret prehistoric activity patterns is bilateral asymmetry, or differences in morphology of analogous structures on opposite sides of the body. In humans, asymmetry is often compared along the sagittal plane, detailing differences between structures on the left and right sides. Most studies of skeletal asymmetry concentrate on the bones of the arms and hands. The evolution of human bipedality has uncoupled the upper limbs from locomotor functions, and as a result the upper limbs are now utilized in a variety of habitual activities which may induce different levels of loading on the left and right sides. In contrast, the lower limbs are restricted to a primarily locomotory role, which is not expected to produce significantly different mechanical loads on each side.

Population-level asymmetry is often described as either directional, fluctuating, or antisymmetry. Directional asymmetry refers to "consistent greater development of one side of the body among individuals in a population. The distribution of differences between sides is normally distributed with a mean that differs significantly from zero" (Reeves et al. 2016). One example of directional asymmetry among humans is handedness. Approximately 90% of humans preferentially use the right upper limb (Cashmore et al. 2008), which, according to the biomechanical model, should induce different mechanical loads on the left and right sides. As such, directional asymmetry may be used to evaluate the effects of different levels of loading within and between populations, since external factors which may affect functional adaptation (e.g., genetics, health, age, bone density) are controlled for.

There is evidence among contemporary populations that handedness influences manual long bone robusticity. Roy et al. (1994) calculated cortical area, total area, medullary area, and second moments of area of the second metacarpal from radiographs of 992 healthy adults. The authors found that in both right and left-handed individuals, second moments of area and total and cortical area of the dominant hand (as reported by participants) were significantly greater than those of the nondominant hand. Because hormonal, dietary, and health factors are held constant within individuals, the authors cite the results as evidence for functional adaptation within the dominant hand in response to greater mechanical loading relative to the nondominant hand.

To assess the degree of humeral asymmetry in populations with and without clear levels of unilateral loading, Trinkaus et al. (1994) compared bilateral humeral cross-sectional properties of five human populations: Pleistocene Neandertals, Jōmon from Japan, Georgian and Californian Amerindians, modern EuroAmericans, and modern tennis players. The authors tested the assumption that gracile modern humans should have low levels of humeral asymmetry compared to tennis players and Neandertals, who each have unique patterns of upper limb loading.

The authors found little evidence of asymmetry in humeral length or distal articular dimensions (Trinkaus et al. 1994). In contrast, almost all diaphyses demonstrated asymmetry in CA, MA, J, and measures of relative loading within a cross-section. For example, median I_{max}/I_{min} asymmetry was modest (5-14%) in the four non-athletic human samples, greater among modern human tennis players (28-57%), and variable but high (2-101%) among Neandertals.

While these results suggest that humeral diaphyseal bilateral asymmetry may be present in varying degrees in populations with and without specialized behavioral patterns, caution must be taken in comparing these results to those of the current study. Results obtained by Trinkaus et al. (1994) were generated with measurements of median humeral I_{max}/I_{min}, while the current study utilizes mean I_x/I_y (See Chapter 3). Analyses of I_{max} and I_{min} generate higher asymmetry percentages than those of I_x/I_y due to averaging effects of left-handed individuals in right/left analyses. Therefore, while the work of Trinkaus et al. may be indicative of general patterns of humeral asymmetry, the exact asymmetry percentages generated in that study should not be taken as baseline results against which to compare the results of the current study.

Auerbach and Ruff (2006) undertook a comparison of upper and lower limb bilateral asymmetry in a large population of adult Holocene humans belonging to a broad range of temporal and geographic groups and exhibiting different assumed levels of activity (pre- and post-industrial populations). The authors studied maximum upper and lower limb lengths, periarticular breadths, and midshaft diaphyseal properties of 780 Holocene adult humeri, radii, femora, and tibiae and found that despite broad differences in time and space, samples showed a consistent, significant right-biased asymmetry of all upper limb dimensions. The authors did find a weaker, yet still significant left bias for some lower limb dimensions, such as midshaft diaphyses and femoral length. However, the upper limbs displayed greater directional and overall symmetry than did the lower limbs. This research suggests that, across a broad temporal and geographic range, human

upper limb diaphyses are likely to show some degree of bilateral asymmetry due to limb preference, even among humans without special adaptations or behavioral patterns.

Although most analyses of bilateral asymmetry utilize populations engaging in unimanual activities, experimental evidence suggests that bimanual activities may also result in exaggerated humeral asymmetry. During analyses of Neanderthal upper limbs, Churchill et al. (1996) and Churchill and Formicola (1997) used upper Paleolithic and more recent human samples, including Alaskan Aleuts, for comparative purposes. Compared to recent industrialized and early agricultural samples, Aleutian males demonstrate hyper-robusticity, with significantly greater CA, I_x, I_y, and J and elevated levels of humeral bilateral asymmetry. Aleutian populations are known to have engaged in habitual open-ocean rowing, and these results indicate that such rowing, although bimanual, may generate greater mechanical strain on one upper limb to the point of engendering humeral bilateral asymmetry.

In another analysis, Schmitt et al. (2003) sought to investigate whether bilateral humeral strength asymmetry found among Neandertals and early modern humans was due solely to unimanual activities such as spear-throwing. However, the authors contend that there is no evidence for projectile spears among these populations. The authors thus investigate whether a bimanual activity, such as spear-thrusting, could produce similar levels of humeral strength asymmetry. Throwing a spear, the authors contend, would produce torsional loads in the active humerus while thrusting would produce bending forces in the dominant (trailing) humerus.

Schmitt et al. (2003) asked eight adult participants to engage in three varieties of bimanual spear-thrusting exercises. All participants used the dominant arm in the trailing position while the non-dominant hand was used in front to guide the instrument. Strain gauges analyzed the force levels on both the participants' arms and the spear. Results suggest that bimanual spear-thrusting is theoretically capable of producing bilateral humeral asymmetry. During striking motions, average force applied to the dominant (trailing) arm was 1.7 times greater than the lead arm. In particular, at the moment of impact, the trailing arm could experience as much as 6.6 times the force of the leading limb. The study suggests that "spear thrusting is likely to engender loads of sufficient magnitude to stimulate modelling responses in the bone of the upper limbs" (Schmitt et al. 2003, 111) and that the differences in relative force applied to the trailing and leading limbs during a bimanual activity like spear thrusting may be capable of producing bilateral humeral asymmetry.

Mobility Index and Diaphyseal Shape. As previously stated, the mobility index (I_x/I_y) represents the ratio of anteroposterior (A-P) to mediolateral (M-L) bending rigidities and indicates the general shape of a diaphyseal cross-section. Experimental evidence among contemporary populations suggests that bending rigidities and ratios respond to directional loading during life. Macdonald et al. (2009) analyzed differences in tibial midshaft shape between preadolescent boys subjected to different levels of physical activity for sixteen months. Control boys participated in pre-established physical education classes while the experimental group engaged in two additional sessions of activity four and five days per week.

Macdonald et al. (2009) found that the tibiae of boys engaged in additional physical activity showed a significant increase in A-P bending rigidity and a nonsignificant increase in M-L bending rigidity compared to the control group. The exercise group also showed nonsignificant gains in cortical area and cortical thickness in the anterior, medial, and posterior planes compared to the control boys. However, there was no significant increase in the I_x/I_y ratio between groups possibly, the authors contend, because subadult long bones are bent in both the A-P and M-L directions, resulting in proportional bending loads between planes. Other research suggests that in adults, such loading is not proportional and can result in significant changes in bending rigidity ratios (Vainionpää et al. 2007). However, the significant increase in A-P bending suggests that functional adaptation occurs in the direction in which long diaphyses are loaded (Macdonald et al 2009).

Research on adult populations also finds evidence for changes in the mobility index in response to directional loading. Shaw and Stock (2009b) compared tibial midshaft rigidity and cross-sectional shape of 15 male field hockey players, 15 distance runners, and 20 age and size-matched sedentary controls. Hockey players and runners both had significantly greater tibial robusticity than did the control group, although there was no significant difference in robusticity between the two athletic groups.

However, the ratio of bending rigidities did significantly differ between all three groups, with each group demonstrating a distinct tibial midshaft morphology (Shaw and Stock 2009b). Distance runners had the highest I_x/I_y ratio, resulting in anteriorly-elongated "isosceles triangle" tibiae. I_x/I_y ratios among hockey players, contrastingly,

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were more proportional, giving this group "equilateral triangle" tibiae. Tibial diaphyseal shape among the sedentary control group was intermediate between the two extremes. The results are consistent with mechanical loads applied during athletes' activities; running primarily generates A-P bending forces while field hockey is likely to generate both A-P and M-L forces. Both this study and that by Macdonald et al. (2009) suggest that the ratio of A-P to M-L bending rigidities (I_x/I_y) provides a reliable indication of type of loading applied during habitual activity. By inference, this variable may be used to interpret types of habitual activity of prehistoric human populations.

Ruff (1987) conducted a large-scale analysis of multiple femoral and tibial cross-sectional geometric properties, including femoral I_x/I_y, of males and females across geographic and temporal populations. Femoral midshaft I_x/I_y represents the amount of relative A-P bending around the knee, a variable which can be indicative of long-distance travel over rugged terrain. Ruff found that the degree of sexual dimorphism of femoral midshaft I_x/I_y is significantly correlated with subsistence pattern. I_x/I_y sexual dimorphism is greatest among hunter-gatherers, reduced in early agriculturalists, and almost nonexistent among industrial populations. Ruff concludes that the results support ethnographic and historic evidence of highly differentiated activities of male and female hunter-gatherers that gradually became less differentiated following the onset of agriculture and industrialization.

Relatedly, Ruff et al. (2015) compared relative A-P and M-L bending strengths of the femoral and tibial midshaft of over 1,800 European individuals spanning a broad temporal and geographic range. In both male and female femora and tibiae, a consistent

and gradual decline in relative A-P bending strength occurred from the Neolithic (7.3-4.0 KYA) to the Iron/Roman (2.3-1.7 KYA) period, while reductions in M-L bending strength in both bones and both sexes were less consistent during the same period. The authors attribute the decrease in relative A-P bending strength of the lower limb to reduced mobility brought about by the initiation of food production. The lack of a significant continuing reduction of lower limb bending strength from the Iron/Roman period to the 20th century supports the primary effect that reduced mobility, rather than technological innovations, has on lower limb diaphyseal shape.

Additional studies have utilized the mobility index to interpret the lifeways of past populations. Ruff (1999) analyzed then newly-discovered skeletal samples of hunter-gatherers from the North American Great Basin region to identify the effect of numerous variables (geographical terrain, subsistence pattern, and sex) on femoral diaphyseal cross-sectional morphology and indicators of robusticity. Compared with agricultural prehistoric Amerindians, the Great Basin populations demonstrate significantly greater sexual dimorphism in I_x/I_y ratios. This result corresponds with previous research suggesting greater division of labor and greater male mobility among hunter-gatherers. However, even in comparison to other hunter-gatherers, the Great Basin samples showed significantly greater percentages of sexual dimorphism of I_x/I_y ratios; while most hunter-gathers samples demonstrated around 15%, the Great Lakes samples ranged between 20-26%. Ruff hypothesizes that sexual dimorphism in the mobility index is exaggerated in Great Basin hunter-gatherers because of the region's rugged terrain, which would place greater mechanical strain along the A-P plane of the femur.

Additional research supports the effect of terrain on lower limb diaphyseal shape. Holt et al. (2018) compared over 1,800 adult skeletons from seven European regions spanning the past forty thousand years to demonstrate how femoral, tibial, and humeral robusticity and diaphyseal shape have changed in response to socioeconomic transitions during that period. Among other factors analyzed within the study, the authors used digital elevation models to calculate the "hilliness" of regions to quantitatively compare any impacts of terrain on diaphyseal geometry.

The authors found significant differences in femoral and tibial shape between terrain categories, with populations inhabiting mountainous or hilly terrain demonstrating increased A-P/M-L bending strength compared to groups residing in flat regions (Holt et al. 2018). Femoral shape differences remained, yet became nonsignificant, when highly-mobile pre-Neolithic hunter-gatherers were removed from the comparison; contrastingly, tibial differences were only significant in the absence of this group. This study provides evidence that, regardless of time period or geographic location, terrain has a correlation with lower limb diaphyseal shape and should be considered when comparing diaphyseal cross-sectional geometry of different populations.

Predictions for Current Study

The current study will use femoral, tibial, humeral, and radial cross-sectional properties to compare activity patterns of prehistoric Alaskan populations, and the research cited above allows for predictions of the outcome of this study. First, populations practicing different subsistence strategies may not have discernable differences in patterns of robusticity. The research of Ruff et al. (1984), Bridges (1989),

Bridges et al. (2000), and Ruff and Larsen (2001) found conflicting results regarding the effect of the agricultural transition on long bone diaphyseal robusticity, and Wescott's (2006) large-scale study found no consistent pattern between subsistence strategy and related mobility and femoral robusticity. Therefore, if differences in long bone robusticity are identified between populations practicing different subsistence strategies within this study, subsistence should not necessarily be attributed as the primary variable affecting cross-sectional measurements.

Instead, previous research on the effect of terrain provides a more definitive hypothesis for this study. Stock and Pfeiffer (2001) found that populations with high levels of marine mobility will demonstrate greater humeral robusticity and that populations with high levels of terrestrial mobility will demonstrate greater femoral robusticity. Additionally, as revealed by Weiss (2003), populations engaging in open ocean rowing should demonstrate greater humeral robusticity than groups practicing non-ocean rowing or those engaging in no rowing. Lastly, Holt et al. (2018) found that more rugged terrestrial environments engender increased lower limb robusticity and increased anteroposterior bending strength relative to flat terrain. Therefore, within this study, Alaskan populations believed to have engaged in marine or riverine rowing should display greater levels of humeral robusticity than those engaging in primarily terrestrial mobility, and those traversing rugged terrain should exhibit more robust lower limbs than those traversing flat terrain.

Studies of bilateral asymmetry suggest that limb preference may result in bilateral upper limb asymmetry, likely favoring the right side, in human populations, even those

without specialized behavior patterns (Roy et al. 1994, Trinkaus et al. 1994). Furthermore, populations confirmed to engage in habitual and strenuous unimanual activities demonstrate exaggerated asymmetry in the engaged limb. Therefore, it is likely that the results of this study will find at least some degree of upper limb asymmetry. If exaggerated asymmetry is identified, it is possible that the given population engaged in habitual strenuous unimanual activities that placed greater relative mechanical loading on one limb. However, as demonstrated by Schmitt et al. (2003), Churchill et al. (1996), and Churchill and Formicola (1997), a variety of activities may generate relatively greater mechanical loading on one limb, so any asymmetry identified in the current study should not necessarily be attributed just to unimanual activities.

Research on contemporary and prehistoric populations indicates that the shape of tibial and femoral diaphyseal cross sections, or the I_x/I_y ratio, reflects habitual mobility, with more mobile populations showing greater ratios (Macdonald et al. 2009, Shaw and Stock 2009b, Ruff 1987, Ruff et al. 2015, and Ruff 1999). Related to mobility, terrain is an additional factor influencing diaphyseal shape, with populations traversing more rugged terrain demonstrating greater A-P bending strength (Ruff 1999 and Holt et al. 2018). Therefore, within this study, groups evidenced to be more habitually mobile or have resided on mountainous or hilly terrain should have greater I_x/I_y ratios than relatively more sedentary populations.

One aspect of this study for which there are limited predictions are the outcomes of radial analyses. Most of the previous research has focused upon diaphyseal cross-sectional properties of the femur, tibia, and humerus, possibly because these elements are

more well-represented within archaeological samples or because the elements are believed more mechanically significant. While it is possible that results of radial analyses will reflect those of the humerus, that may not be the case. It is also possible that, depending on the habitual motions and activities of a given population, mechanical loading may vary between the proximal and distal portions of the upper limb, resulting in different patterns in diaphyseal robusticity and/or shape between the humerus and radius.

PREHISTORY OF ALASKA

Alaskan Environment

By land mass, Alaska is the largest state in the United States at over 570,000 miles^2. Given the state's expansive latitudinal and longitudinal range, it is unsurprising that the Alaskan environment is not uniform. The Köppen climate classification system identifies between seven and ten distinct climatic zones in the state (ISC 2019). Despite this variation, there exist generalizations about the Alaskan environment which may contextualize the experiences of prehistoric populations.

Perhaps the most notable feature of the Alaskan environment is low average temperatures resulting from minimal exposure to solar radiation. A substantial portion of the state lies north of the Arctic Circle, and thus experiences long periods of minimal to no sunlight in the winter months. Even regions south of the Arctic Circle remain cold for much of the year. Reduced insolation results in mean annual air temperatures below freezing statewide (Stager and McSkimming 1984). In addition to low temperatures, permafrost is a common feature of the Alaskan environment. The water content of permafrost soils can vary, but those with high moisture content are susceptible to the formation of ice wedges (vertical masses of pure ice) and horizontal ice sheets. Permafrost is not universal across Alaska but becomes more widespread in higher latitudes.

Consistent low temperatures and permafrost result in additional unique features of the Alaskan environment (Stager and McSkimming 1984). The active layer of soil above permafrost undergoes cyclical freezing and thawing, which act as geomorphic processes. For example, frost heave, or the vertical displacement of material from soil, occurs in the active layer as a result of volumetric changes from ice to water during thawing and freezing. Mass wasting, or the movement of heaved soil and bedrock due to gravity, results in boulder fields and rock glaciers that evidence the geographic effects of the freeze-thaw cycle. Additionally, much of the Alaskan environment was once covered by continental glaciers, the movement of which resulted in erosion and deposition across the landscape. Ground surfaces show evidence of glacial movement in the form of exposed bedrock from which soil was eroded. Glacial deposition is evident in till-covered plains, sand plains, and gravel ridges that cover the landscape.

Alaskan Ecosystems

As described above, the Alaskan environment is characterized by cold temperatures, low sunlight, permafrost, and constantly shifting soils. Such an environment presents unique challenges to the adaptation strategies of floral and faunal populations. Nonetheless, Alaska's marine, freshwater, and terrestrial ecosystems now consist of numerous communities of plants and animals, all of which played critical roles in the lives of prehistoric humans within the harsh Alaskan environment.

Marine ecosystems of Alaska are characterized by populations of animals well-adapted to cold temperatures, including whales, walruses, seals, and polar bears (Freeman 1984). However, five factors restrict the productivity of polar marine environments. First,

cold temperatures prevent the growth of permanent ocean floral populations, leading to the second factor, shortened food chains. Third, many polar marine mammals have low reproductive and growth rates, and population growth is resultingly slow. Fourth, the low diversity of large fauna leads to high population levels of a small number of species, rather than lower populations of more species. Finally, low numbers of arctic fish do not support increased population numbers further up the food chain. These factors contribute to artic oceans being from one-half to one-ninth as productive as more temperate marine environments, when measured in the population of zooplankton.

Like oceans, Alaskan freshwater ecosystems demonstrate low productivity, due in part to thermal stratification and low nutrient quality drainage areas (Freeman 1984). However, freshwater productivity is not as critical as is that of maritime or terrestrial ecosystems, as few human populations depend solely on freshwater resources for survival. Nonetheless, Arctic freshwater environments are home to approximately sixty species of fish, including char and salmon, which are widely exploited by human populations.

In contrast, terrestrial ecosystems are significant to a greater number of Alaska populations (Freeman 1984). As noted, Alaskan soil is subject to freezing and erosion, which result in overall low nutrient content. There is thus a limit on the type and productivity of any flora and fauna that inhabit terrestrial regions. Flora that do adapt to the Alaskan environment must develop extensive root systems to overcome erosion and absorb as many nutrients as possible. As a result of deep roots, the majority of floral surface area is not available to grazing animals, restricting nutrient intake. But fauna that

dominate the terrain, including caribou and musk-ox, have broad food preferences to

combat this limitation. Additionally, long periods of ground snow cover provide needed

moisture to polar flora, which satiates herbivores and supports carnivorous animals.

However, the harsh environment supports only a narrow species of plants, and this

uniformity leads to a general lack of mammalian diversity which human populations may

utilize.

Native Alaskan Cultural Traditions

When considering the prehistory of Alaska, it is helpful to divide the state into

regions based on similar climatic conditions. The succession of cultural traditions within

one region may then be examined. Common organizational systems often divide the state

into the Northern Slope, Bering Sea, Aleutian, and Pacific Coast/Gulf of Alaska regions,

while some (Figure 4) include additional areas such as the Interior and the Southeast.
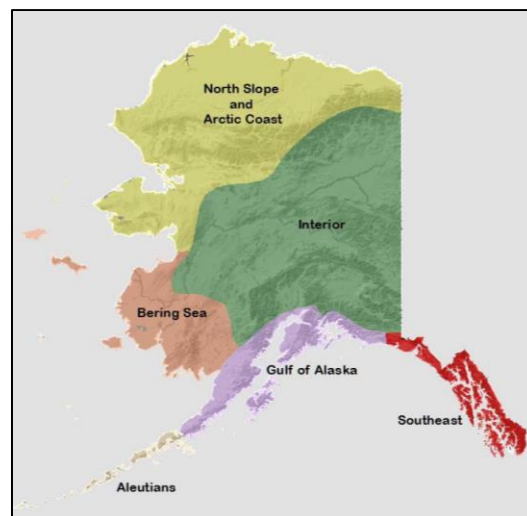
Figure 4. Geographic Regions of Alaska (Gillispie 2018)
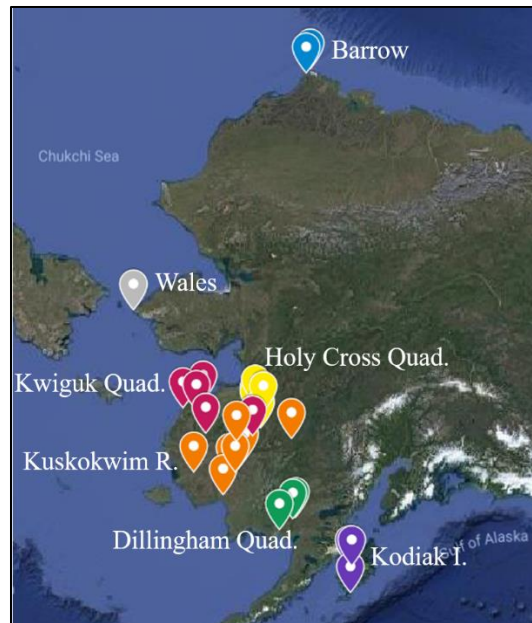
Figure 5. Geographic Origin of Skeletal Materials in the Current Study

Figure 5 demonstrates from where in Alaska the skeletal materials used in this study originated (more detailed information will be provided in Chapter 3). The majority of skeletal remains originate from the Bering Sea or Inland regions. Additionally, a small number of skeletal remains from the North Slope and Gulf of Alaska regions are used. For the sake of clarity, only the cultural traditions of the four included regions will be discussed. This chapter will not explore cultural development of the Aleutian or Southeast regions.

It is important to note that cold weather, diverse terrain, and limited infrastructure make archaeological expeditions into Alaska difficult and time-consuming. Given this limitation and the state's size, a complete archaeological record is difficult to establish. However, enough archaeological work has been conducted across the state to provide a

general timeline of the development of different cultural traditions. This chapter is not

intended as a definitive detailing of such traditions. Rather, it is meant to provide general

information to contextualize the experiences of prehistoric populations for the purposes

of comparing long bone diaphyseal cross-sectional properties (Figure 6).

KYA	North Slope/ Arctic Coast	Kodiak Island/ Gulf of Alaska	Bering Sea	Interior
0		Koniag	Yupik	Athabaskan
1	Neoeskimo			
2		Kachemak	Norton	
3	Paleoeskimo		Arctic Small Tool	Northern Archaic
4				
5		Ocean Bay		
6	Northern Archaic		Northern Archaic	
7				
8	American Paleoarctic			
9		Unknown	American Paleoarctic	American Paleoarctic
10				
11	Northern Paleoindian			
12				
13	Unknown		Eastern Beringian	Eastern Beringian
14				

Figure 6. Timeline of Cultural/Temporal Traditions of Select Regions of Alaska

Barrow, Wales, and the Birnirk Culture. The sites at Barrow and Wales (Figure 5) both fall within the North Slope/Arctic Coast region and share a similar succession of cultural traditions. The oldest cultural tradition identified in far north Alaska is the Northern Paleoindian Tradition, which spans from approximately 12.6-11.9 KYA and possibly earlier from 13.7-13.0 KYA (Bever 2006). Evidence of the Paleoindian Tradition is found near the Brooks Mountain Range and is characterized by site placement on hills or knolls and tools suggestive of terrestrial hunting. Paleoindian sites are not found on any modern coastline. It is likely that coastal sites (if any) would have been submerged by rising sea levels following glacial recession (Jensen 2014).

Following the Northern Paleoindian, far north Alaska experienced a succession of cultural traditions, including the American Paleoarctic, Northern Archaic, Arctic Small Tool, Paleoeskimo, and Neoeskimo Traditions (Jensen 2014). However, as will be described in detail in Chapter 3, the Barrow and Wales skeletal samples have been reliably attributed to the Birnirk cultural phase within the larger Neoeskimo Tradition. Since these skeletal samples have been narrowed down to a specific cultural phase, only the Birnirk and preceding Ipiutak cultures will be described in detail.

Ipiutak culture (1.6-1.0 KYA) is considered the culmination of the broader Paleoeskimo Tradition and was originally defined by the excavations of Larsen and Rainey at Point Hope on the Lisburne Peninsula (1948). However, subsequent analyses have found Ipiutak sites as far south as Norton Sound, suggesting the cultural phase covers a wider geographic region than originally believed (Mason 2014).

Ipiutak sites are predominantly coastal, although a small number of inland sites have been identified (Mason 2014). While there is evidence for high seasonal mobility among inland Ipiutak hunters, coastal groups were more sedentary and likely engaged in trade with inland populations. Villages are large and organized into separate precincts. Dwellings are constructed aboveground and consist of single rooms, although variability in home size is possibly indicative of differences in social status. Additionally, settlements demonstrate caches, differing forms of summer and winter houses, and shared community structures. There is also evidence of interpersonal conflict between Ipiutak groups. Sites have yielded skeletons displaying traumatic injuries, and some dwellings were found containing hoards of arrow points, suggesting a perceived need for protection from intruders.

Subsistence among the Ipiutak depends on site location (Mason 2014). Coastal populations relied primarily on ringed and bearded seal, although there is evidence for possible whaling, walrus hunting, and reliance on caribou at individual locations. Inland populations typically consumed caribou and possibly fish at interior lakes. In addition to these staple resources, recent quantitative archaeological analysis suggests that small mammals and birds likely played a larger role in the Ipiutak diet than previously assumed (Moss and Bowers 2007).

Chronologically, the Birnirk culture succeeds the Ipiutak. However, the relationship between populations with these cultural traditions is not clear (Jensen 2014). Geographically the cultures are separated; Birnirk sites are exclusively coastal while Ipiutak sites are both inland and coastally-oriented. Radiocarbon dating of both traditions

suggests overlap between late Ipiutak and early Birnirk populations (Gerlach and Mason 1992). It may be that the phases represent two entirely separate political groups or related persons who utilized different tool kits (Mason 1998). Whatever the relationship, archaeological excavation has identified sufficiently different material remains to distinguish Birnirk as a separate cultural entity from the Ipiutak phase.

Neoeskimo is the final broad cultural tradition to develop in northern Alaska and spans from 1.5 KYA – Present (Jensen 2014). The primary cultural phases within the Neoeskimo Tradition include Birnirk (1.5-1.0 KYA) and Thule (1.1-0.5 KYA). Birnirk culture appears to be a geographically broad tradition, with evidence of the phase spanning from Siberia to Canada and as far south in Alaska as the northern portion of the Seward Peninsula.

A defining characteristic of Birnirk culture is that all sites are coastal (Jensen 2014). To date, no inland Birnirk sites have been identified. Technologically, Birnirk culture is marked by utilitarian implements such as ground slate weapon points, discoidal scrapers, chipped chert knives, and bifurcated and trifurcated spur harpoon heads. Although flaked weapon points show continuity with previous traditions, the presence of harpoon heads with decorative spurs, single barbs, and decorated medial grooves is unique to Birnirk culture. Organic artifacts include a variety of bone, ivory, wooden, and baleen-based objects. Plain ceramic pottery and oil lamps appear in the Birnirk and subsequent Neoeskimo phases, as do ivory effigies and baleen containers. There is in general a lack of figurative art, with any abstract designs limited to linear motifs.

Birnirk settlements demonstrate small groups of dwellings constructed on midden mounds, each dwelling containing a long entrance tunnel to conserve heat (Gillispie 2018). Dwellings are often single rooms, but there is evidence for designated kitchen areas. Given the exclusively coastal location of Birnirk sites, it is unsurprising that a large portion of Birnirk subsistence is based on the hunting of sea mammals. Stanford (1976) found that ringed seals, bearded seals, and walruses were important food sources. While baleen-based material culture indicates a degree of whaling, large whales were likely not hunted on a regular basis. Individual Birnirk settlements indicate low numbers of residents in one location at a given time, which would have placed a logistical restriction on the ability to perform large-scale whale hunts. In addition to marine subsistence, there is evidence that Birnirk communities relied on terrestrial food sources including caribou, polar bears, wolves, and birds.

Gulf of Alaska and the Koniag Culture. A small number of skeletal samples used in this study originate from Kodiak Island, the largest island in the Kodiak Archipelago located in the Gulf of Alaska (Figure 5). Overall, the Gulf of Alaska experiences a cool, temperate climate marked by high precipitation and the absence of sea ice throughout the year (Clark 1984). Islands within the archipelago demonstrate complex coastlines and resultant lengthened shorelines. Mild temperatures, abundant rainfall, the presence of estuaries, and a wide continental shelf lead to a productive marine ecosystem in terms of fish spawn, especially compared to more northerly locations in Alaska.

Unsurprisingly, fish, particularly salmon, constitute the most commonly utilized resource in the region (Clark 1984). Other marine resources include shellfish, ocean fin-fish, migratory and residential birds, porpoises, sea lions, and whales. Given the abundance of freshwater and marine resources, most archaeological settlements in the Kodiak Archipelago are unsurprisingly oriented towards harvesting aquatic resources and are located along shorelines, although some salmon fishing camps were located along major streams on Kodiak Island (Clark 1998). In comparison, terrestrial resources in the Gulf of Alaska are relatively limited. Inland environments demonstrate temperate rainforests dominated by poplar, cottonwood, birch, and spruce trees, and commonly hunted animals include brown bear, red fox, and river otter.

The progression of cultural traditions in the Kodiak Archipelago region does not demonstrate drastic changes over time (Clark 1998). Rather, because geographical constraints necessitate dependence on maritime and freshwater resources, cultural changes are gradual and represent changes in social structure, cultural preferences, and stylistic choices rather than dramatic changes in subsistence and adaptation. However, archaeological research has identified a progression of three major cultural traditions unique to the Gulf of Alaska region: Ocean Bay, Kachemak, and Koniag.

The Gulf of Alaska likely deglaciated between 14-13 KYA. However, there is no evidence for the development of the earliest cultural tradition, Ocean Bay, until 8.6-4.0 KYA (Clark 1998). As is expected of an island cultural tradition, archaeological evidence suggests that Ocean Bay populations relied heavily on maritime resources for subsistence. Sites suggest that small mobile groups lived adjacent to tidewaters, either in

coves or at the mouth of rivers. The Ocean Bay toolkit includes bifacially worked stone tools and microblades. Additionally, a cobblestone industry was present, and there is evidence of stone lamps, which suggest access to either mammal or fish oil for fuel. Reliance on maritime resources is indicated by harpoon heads, spear prongs, fishhooks, and needles. However, the absence of net weights in the archaeological record suggests that salmon and other fish were likely caught via traps or weirs rather than with nets.

Approximately 4.0 KYA, there is evidence for a shift from the Ocean Bay to the subsequent Kachemak Tradition (Clark 1998). Kachemak sites demonstrate evidence for mass fish harvests as well as sites and objects related to the preparation, processing, and storage of fish. This is suggestive of increasing reliance on fish, including salmon and cod, for subsistence and a reduced reliance on the hunting of large sea mammals. Similarly, there is evidence for a shift away from seasonal procurement of resources to the production and long-term storage of surplus fish. Some Kachemak sites also demonstrate dwellings with rooms dedicated to fish processing and storage. Additionally, fishing method appears to change during the Kachemak period; sinkers indicate the use of nets, rather than traps or weirs, to catch fish.

Technological markers of the Kachemak phase include greater use of grooved cobble and notched pebble weights, a shift away from slate tools with saw-scrape grind sequences, and toggle harpoon heads (Clark 1998). Additionally, stone lamps become larger and are often carved with symbols of whales, seals, and humans. There is evidence for population growth during the Kachemak phase, indicated by an increase in the number of sites, large middens, and intensification of food storage. Houses of the

Kachemak Tradition become larger, demonstrating dedicated rooms for fish processing and storage. Both factors suggest a decrease in seasonal movement and more permanent settlement. Despite assumed population growth, there is no evidence of major differentiations in status, wealth, or access to resources within Kachemak populations.

Between 950-650 years ago, a visible shift occurred in the Kachemak phase during the transition to the Koniag Tradition (Clark 1998). There is yet another increase in the size, number, and variety of sites in the Kodiak region. Houses transition from single pits to larger structures with multiple rooms, each with specific functions. The movement of food storage inside of homes hints at a shift from communal to individual ownership of food. Additionally, large village sizes are possible evidence of social competition and conflict. Middens indicate continued reliance on salmon, and new technologies including weirs, fish traps, and salmon harpoons contribute to greater salmon harvests.

By 450 years ago, the transition to Koniag culture was complete (Clark 1998). Houses in semi-permanent villages are large and have satellite rooms dedicated to food processing and storage. Furthermore, there is evidence for differences in wealth and status, as villages tend to be laid out in organized rows and larger houses are built near each other, resembling wealthy neighborhoods. By this point, apparent population growth may have prompted the westward migration of Koniag peoples to relieve population pressure.

Bering Sea and Interior Cultures. The remaining skeletal materials in this study originated from the Dillingham, Holy Cross, and Kuskokwim Quadrangles and the

Kuskokwim River region. These areas are almost all located within the Bering Sea region, although some of the Holy Cross samples fall within the Interior region (Figure 5). The Bering Sea and Interior regions of Alaska share many cultural traditions throughout much of prehistory, which will be discussed as one. However, it will be noted when cultural traditions diverge between regions.

Both the Interior and Bering Sea regions contain evidence for the earliest confirmed prehistoric cultural tradition in Alaska, the Eastern Beringian Tradition, spanning from approximately 14-12 KYA (Gillispie 2018). During this time, Beringia experienced a period of climatic warming known as the Allerød interval. This warming melted some continental glacial sheets covering North America, but Beringia remained isolated from the rest of the continent. Global warming resulted in the growth of more shrub tundra and forests in Alaska; the appearance of flora with wood may have been utilized as a resource by early populations.

Beringian sites, many of which are located in the Tanana River basin of the Alaskan interior, provide evidence of hunting technology resembling that from Upper Paleolithic sites in Asia (Gillispie 2018). A distinctive feature noted at Beringian sites is hunting technology centered around lightly constructed spears propelled using an atlatl, which served as an extension of a hunter's arm. Spear tips were made of a combination of ivory, horn, or bone and flaked stone; these were inset into osseous rods to form spears.

Beringian populations likely consumed a narrow range of prey including bison, horses, canids, and waterfowl (Gillispie 2018). Campsites were small yet organized into specialized work areas around fires. Younger Beringian sites indicate an expansion of

prey animals to include elk, caribou, sheep, moose, hare, marmots, squirrels, canids, and

otter. Populations typically relied on local sources for tool stones and used simple tool

kits that could be easily assembled and quickly discarded. This indicates that populations

were likely highly mobile. The presence of non-local volcanic glass at some Beringian

sites suggests that groups were either willing to travel long distances for high quality

materials or that elaborate trade networks were in place.

Approximately 12.9-11.7 KYA, the Allerød interval was succeeded by a period of

cooler and drier climatic conditions known as the Younger Dryas (Gillispie 2018). By

this period, shrub tundra had spread across most of Alaska, and the Beringian Tradition

was gradually succeeded by the American Paleoarctic Tradition in both the Bering Sea

and Inland regions (Gillispie 2018). Archaeological evidence suggests that Paleoarctic

populations used similar stone tool technology as the previous tradition, with only minor

variations in manufacturing method and style. For example, the atlatl throwing system

was still utilized, and evidence suggests that similar prey animals were eaten. However,

populations appear to have placed a greater emphasis on transporting higher quality

materials from site to site rather than relying on low quality local materials for tools.

Another major development during this tradition is the first evidence of salmon

consumption emerging approximately 11.5 KYA in the Tanana River Basin.

By about 7.0 KYA, The Northern Archaic Tradition developed in both the Bering

Sea and Inland regions of Alaska (Gillispie 2018). Although present in both regions, the

tradition persisted until about 1.8 KYA in the Interior and until 5.0 KYA in the Bering

Sea region. The technology of the Northern Archaic Tradition is marked by the rise of

spear points made of fine-grained stones over the use microblades. These stone spear points are not standardized in outline, demonstrate thin cross sections, and have faces shaped by the removal of small flakes. Despite the use of stone weapons, bone and antler remain important in the Northern Archaic toolkit. During this period caribou became an increasingly important resource, as caribou bone begins to appear in greater percentages than bison bones in Northern Archaic sites.

Following the Northern Archaic Tradition, the Bering Sea and Interior regions experience different successions of cultural phases (Gillispie 2018). Within the Bering Sea area, the Northern Archaic tradition was succeeded by the Arctic Small Tool Tradition, which persisted from approximately 5.0-2.5 KYA. Overall, the tradition is marked by the use of microblades, specific forms of burins and spalls, small bifaces, and the scarcity of ground or polished artifacts. Excavations at two locations – Cape Denbigh and the Naknek Drainage – have yielded most of the information about this tradition.

At Cape Denbigh, along the Norton Sound, there are numerous forms of microblades, small burins, small bifacially chipped sideblades and endblades, and some triangular bifacial implements interpreted as harpoon endblades (Dumond 1984). The site yielded no signs of excavations for the purposes of dwelling construction, although fires are indicated by burnt beach pebbles and charcoal flecks. The only osteological material found was charred seal bones. The abundance of sideblades and endblades suggest the site was a camp established for the hunting of migrating caribou herds, although the bones strongly suggest that some sealing took place as well.

The Naknek Drainage on the northern portion of the Alaskan Peninsula yielded

implements similar to those found at Cape Denbigh, although the supposed harpoon

blade was not found (Dumond 1984). There is also a lower frequency of burins and

microblades and a higher frequency of double-pointed endblades and hide scrapers.

Naknek Drainage also yielded adz blades with polished bits. Organic materials consist

mainly of salmon bones and teeth and some crushed mammalian bone. Four square meter

single-occupation habitations with sloping entranceways and central fireplaces are

common at the site, although there is also evidence of informal campsites along the river,

typically at salmon-rich locations.

Following Arctic Small Tool, the subsequent tradition in the Bering Sea region is

the Norton cultural phase, the culmination of the broader Paleoeskimo Tradition

(Gillispie 2018). The Norton Tradition continues from approximately 2.4-1.0 KYA and is

widespread across Alaska, ranging from the Alaskan Peninsula north along the Bering

Sea coast and east along the Chukchi and Beaufort Sea coasts in far north Alaska.

Because the Norton Tradition spans a large geographic area, there is no uniform

subsistence pattern. However, in general Norton subsistence and settlement patterns are

based on three major resources depending on geographic location (Gillispie 2018). Along

the coasts, populations depended primarily on sea mammal hunting, especially of small

seals. At estuaries and along rivers, there is evidence that salmon were collected using

weighted nets. Finally, nonriverine inland Norton populations likely pursued migrating

caribou herds.

Semi-permanent Norton villages are found at resource-rich coastal and riverine

locations, and these range in size from a few structures to several hundred pit structures

(Gillispie 2018). Dwellings are characterized by short entrance tunnels and internal

hearths. Inland hunting sites tend to represent small seasonal camps, although at resource-

rich areas, larger camps are seen, which may be indicative of larger social groups and

more complex levels of social development.

Meanwhile, the Interior region of Alaska followed a different succession of major

cultural traditions. In this region, the Northern Archaic Tradition was succeeded by the

Athabaskan Tradition, which persisted from 1.7 KYA – Present (Gillispie 2018). This

period saw cooler climatic conditions than the Holocene average, and boreal forests

covered lowland areas while shrub and alpine tundra dominated highlands. Permafrost

was – and continues to be – widespread across the region.

The Athabaskan Tradition demonstrates a technological break from the Northern

Archaic phase (Gillispie 2018). For example, the atlatl system gave way to the bow and

arrow. Additionally, projection point style changed. Stone points became on average

smaller with stemmed, rather than notched, hafts. Bone projectile points also appeared

during this time and gradually become more abundant than flaked stone points. The use

of copper, derived from deposits in the Wrangle Mountains, is documented in knives,

projectile points, bracelets, and other personal adornments. Finally, pestles, adzes, and

picks made of igneous and metamorphic rocks appear in the archaeological record.

Athabaskans constructed large winter villages at salmon-rich locations (Gillispie

2018). These villages consisted of many large house pits and subsurface food storage

caches. The houses were built of poles and bark and arranged along elevated river caches. Similar short-term villages are found at some locations on interior lakes where freshwater fish are available. Drive fences suggest that inland populations intercepted and hunted migrating caribou, and such mass hunts might have temporarily resulted in the organization of larger social groups. Besides caribou, moose became increasingly important to Athabaskans, as moose bones are recovered from three quarters of Athabaskan sites. These populations also consumed Dall sheep, bear, beavers, canids, and many species of fish.

Predictions for Current Study

The information presented in this chapter, coupled with the research presented in Chapter 1, allow for more refined predictions regarding the results of the current study. As described above, all Alaskan populations whose skeletal remains are utilized in this study are hunter-gatherers. There should therefore be no significant differences in any cross-sectional properties based on overall subsistence strategy. However, the populations do differ in respective forms of hunting and gathering, which could impact long bone cross-sectional properties.

For example, the North Slope populations (Barrow and Wales) resided in and traversed rugged, arctic terrain to pursue sea mammals and caribou. Such terrain likely placed exaggerated mechanical strain on the lower limbs of these populations and should result in greater indicators of robusticity in the Barrow and Wales femora. These populations should also demonstrate increased femoral I_x/I_y values as a result of increased mobility. In contrast, Koniag populations on Kodiak Island were relatively sedentary,

establishing semi-permanent village near fish procurement sites. Therefore, Koniag and other coastal femora should demonstrate lower indicators of both robusticity and mobility than North Slope samples. Bering Sea and Inland femoral robusticity and mobility may be intermediate, as these populations appear to have divided subsistence between pursuing large game and harvesting fish.

Regarding the upper limb, North Slope populations, despite being coastally-oriented, likely did not have high marine mobility. Low temperatures and sea ice likely prevented habitual rowing. But these groups likely generated high degrees of mechanical strain in the arm when driving projectile points into large prey, which may produce hyper-robust humeri. Kodiak populations, in contrast, were largely not actively pursuing prey, instead utilizing nets, traps, or weirs to catch fish. But the absence of sea ice could allow for at least occasional rowing, and there is some evidence for rowing in the archaeological record. Similarly, inland riverine populations likely engaged in habitual rowing, which should result in increased upper limb robusticity. Although all three populations engaged in activities likely to place mechanical strain on the arm, previous research suggests that those with higher aquatic mobility should exhibit higher humeral robusticity than populations from the north slope.

Regarding upper limb asymmetry, results may not be as clear-cut. Limb preference may produce some degree of asymmetry, likely right-biased, within all populations. North Slope populations participated in the hunting of large mammals, which likely required bimanual thrusting of projectiles to kill. Beam theory infers that habitual bimanual activity should not result in exaggerated asymmetry. However, as

demonstrated by Schmitt et al. (2003) in Chapter 1, bimanual spear thrusting can, in theory, generate enough force to bring about asymmetry in humeral robusticity. Therefore, it is possible that North Slope samples could demonstrate high levels of humeral bilateral asymmetry.

It is possible that Bering Sea and Inland populations may show exaggerated levels of asymmetry from documented use of the atlatl, which is a predominantly unimanual activity. Furthermore, these populations and those from Kodiak Island also likely engaged in bimanual rowing. As documented by Churchill et al. (1996) and Churchill and Formicola (1997), bimanual rowing, at least in the open ocean, results in elevated asymmetry levels among Alaskan Aleuts. Therefore, since all the populations used in this study engaged in activities theoretically capable of producing upper limb bilateral asymmetry, there may be no significant differences in asymmetry between populations.

MATERIALS AND METHODS

Materials

The skeletal materials used in this study are curated by the Department of Anthropology within the Smithsonian Institution's National Museum of Natural History (NMNH). Dr. Chris Dudar of the Smithsonian Institution provided lists of the skeletal remains of 273 individuals from seven Alaskan geographic locations and/or cultural traditions for potential analysis in this study. Groups include the Dillingham, Holy Cross, and Kwiguk Quadrangles, regions near the cities of Barrow and Wales, the Koniag cultural tradition from Kodiak Island, and the Kuskokwim River region. Inventory lists were then analyzed for applicability in the study. Six individuals indicated as lacking any postcranial remains were immediately removed from the analysis. The remaining 267 individuals were individually examined to determine eligibility for analysis. A total of 71 additional individuals were eliminated from the study for one of the following reasons:

- The individual was not located in the provided location;

- The individual was comingled with other individuals;

- A recent repatriation request prevented any further study on the individual;

- The individual was estimated to be a subadult or over 55 years of age at death (see below);

- No long bones were present;

- The individual lacked at least one complete femur, tibia, humerus, or radius;

- Any femora, tibiae, humeri, or radii were damaged or fragmented; or

- The individual showed evidence of antemortem trauma or pathological condition likely to have impeded mobility;

In total, at least one complete femur, tibia, humerus, and/or radius from 196 adult individuals with no obvious pathological conditions or trauma were included in this study. Unilateral analyses utilized 170 femora, 154 tibiae, 167 humeri, and 147 radii. Analyses of bilateral asymmetry utilized 196 humeri (98 left-right pairs) and 188 radii (94 left-right pairs).

Origin of Skeletal Materials

Skeletal material used in the current study was excavated and accessioned into the Smithsonian Institution in the first half of the 20th century, and most skeletal specimens were excavated by Dr. Aleš Hrdlička, curator of the Division of Physical Anthropology of the NMNH from 1910-1942 (Table 2). During his tenure, Hrdlička conducted fieldwork across the globe, directing studies of indigenous populations and collecting ethnological, skeletal, biological, and archaeological samples to accession into the Smithsonian collections. Hrdlička spent most summers between 1926 and 1938 conducting such fieldwork across Alaska for the Smithsonian Institution and, at least once, for the Bureau of American Ethnology. A small portion of the skeletal remains in this study were excavated and accessioned by other individuals.

Table 2. Excavation and Accession Information for Skeletal Remains

Accession Number	Excavator	Accession Year	General Region of Excavation
093522	Hrdlička	1926	Wales and Holy Cross Quad.
097209	Krieger	1927	Holy Cross Quad.
107380	Hrdlička	1929	Holy Cross and Kwiguk Quads.
112273	Hrdlička	1930	Holy Cross Quad. and Kuskokwim R.
115748	Hrdlička	1931	Dillingham Quad.
117220	Hrdlička	1931	Kodiak Island
119325	Hrdlička	1932	Kodiak Island
122649	Ford	1933	Barrow
141349	Collins	1936	Wales
209131	Van Valin	1956 (exc. 1917-19)	Barrow

Due to a repatriation request, an inventory and assessment of human remains providing a summary and detailed excavation history of skeletal material from the Barrow region was compiled by Smithsonian personnel (Hollinger et al. 2004). Skeletal material from the Barrow area was collected from four sites during two excavations (Figure 7). The Kugok and Birnirk sites were excavated by James A. Ford, an archaeologist and Smithsonian Institution associate, in 1931-1932 and accessioned into museum collections the following year. Based on observed mortuary practices and associated funerary artifacts, Ford believed the remains were associated with the Birnirk cultural tradition, and later radiocarbon dating of artifacts from the sites supported Ford's assumption (Hollinger et al. 2004).
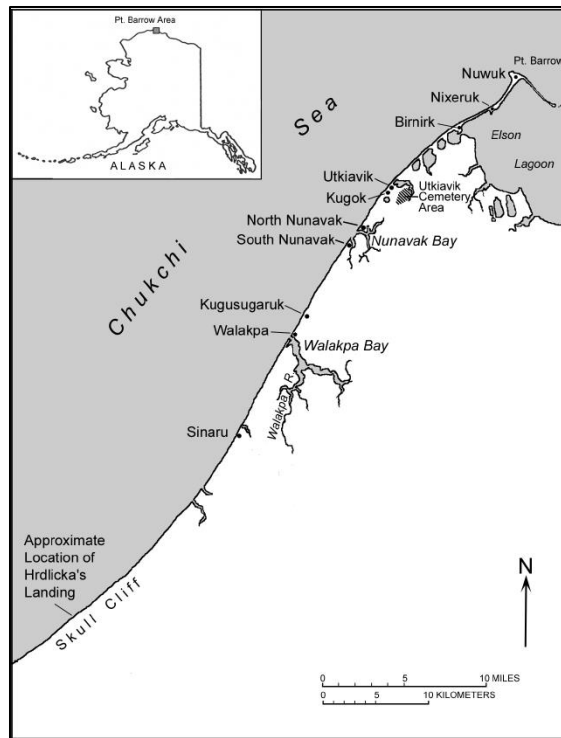
Figure 7. Map of Barrow Region Excavation Sites (Hollinger et al. 2004)

The Kugusugaruk and Nunavak sites (Figure 7) were excavated by William B.

Van Valin in 1917-1919 under the sponsorship of the University of Pennsylvania

Museum of Anthropology and Archaeology (Hollinger et al. 2004). The Nunavak

remains were first sent to the Wistar Institute in 1928 until both site collections were

accessioned into the Smithsonian Institution in 1956. Radiocarbon dates acquired from

wooden handles and trays from the Kugusugaruk site date the burials to approximately

900 CE and support the classification of the skeletal remains to the Birnirk cultural

tradition.

Skeletal remains from the Dillingham Quadrangle were excavated by Aleš

Hrdlička during the spring and summer of 1931 (Hrdlička 1932). The Dillingham

55

Quadrangle is located in southwestern Alaska, just west of the Alaskan Peninsula. The quadrangle contains the city of Dillingham and a defining geographic feature is the drainage of the Wood River into the Nushagak River. Hrdlička reported traveling by boat over 600 miles of the Nushagak River and its tributaries collecting skeletal material but limited material artifacts. Sites yielding skeletal material used in the current study include Ekwok, Kokwok, and Nushagak. Hrdlička attributed burials to the "Kuskokwim type" (1932, 92), or Athabaskan. On the same expedition, Hrdlička traveled to Kodiak Island and collected a portion of the Koniag skeletal sample from the Larsen Bay region.

Skeletal remains from the Holy Cross Quadrangle were collected during four separate excavations between 1926 and 1930, three of which were undertaken by Hrdlička. Holy Cross is located in western Alaska and lies on the bank of the Yukon River. Hrdlička's first expedition into Alaska took place in 1926 under the auspices of the Bureau of American Ethnology, which was later incorporated into the Department of Anthropology. During this time, Hrdlička traveled over 900 miles from Tanana to the mouth of the Yukon River, collecting artifacts and remains from sites including Anvik, Ghost Creek, Grayling River, Holy Cross, and Shageluk (Hrdlička 1927). On the same journey, Hrdlička collected a portion of the skeletal remains from the Wales area, specifically from the village of Shishmaref. During this expedition, Hrdlička collected over 1,300 specimens including 211 human skulls and 50 skeletons.

The following year, Herbert Krieger, then-curator of the Division of Ethnology, conducted an archaeological and ethnological expedition of the lower Yukon Valley (Krieger 1928). During the journey, Krieger excavated at the Shageluk, Anvik, and

Hologochakat sites along the Yukon River, although the majority of the 105 specimens collected during this journey originated from the Bonasila region. The remaining Holy Cross samples were collected during two excavations conducted by Hrdlička in 1929 and 1930. In 1929, Hrdlička returned to Alaska and collected artifacts along a 1500-mile expanse of the Yukon River from Fort Yukon to the river's mouth (Hrdlička 1930). During the same expedition, Hrdlička collected all of the skeletal samples from the Kwiguk Quadrangle region, from sites including Kotlik, Kwiguk Pass, Hamilton, Old Andreafsky, and Paimiut. Finally, the remaining Holy Cross samples and all samples from the Kuskokwim River region were collected by Hrdlička in 1930, during which he surveyed the Kuskokwim River from Bethel south to Apogak and north to Stony River (Hrdlička 1931). This trip produced 128 skeletons and 22 skulls from the Kuskokwim sites plus six skeletons and one skull from the Yukon region.

Remaining Kodiak Island skeletal remains were excavated by Hrdlička in 1932 (Hrdlička 1933). During this expedition, Hrdlička excavated at sites across the island, including Jones Point, Chief's Point, and a general archaeological survey of the entire island. Finally, the remaining Wales samples were excavated by Henry B. Collins, then-Assistant Curator of the Division of Ethnology, in 1936 under a joint venture between the Smithsonian Institution and the National Geographic Society (Collins 1937). Collins excavated just south of the village of Wales itself and at another isolated midden site known as Kurigitavik (Figure 8) and attributed skeletal and material artifacts to the Birnirk cultural tradition.
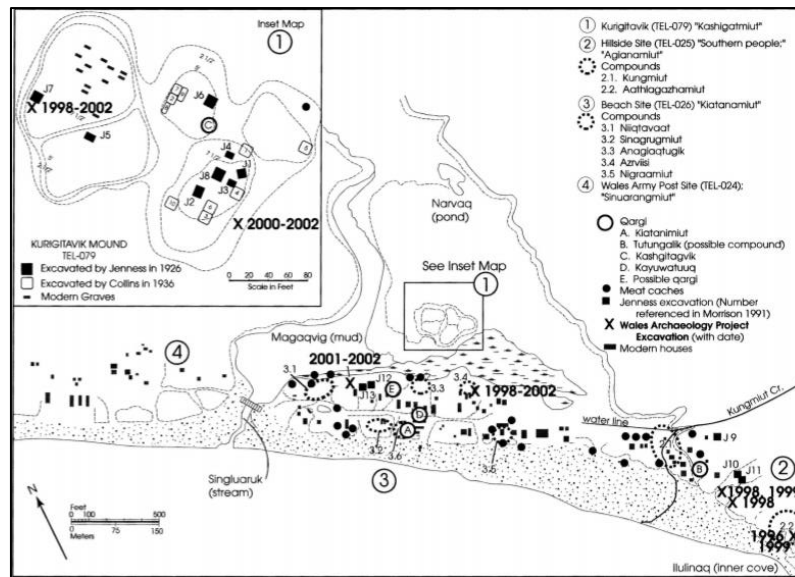
Figure 8. Excavation Sites at Kurigitavik (Harritt 2004)

Methods

Mapping. As stated previously, all individuals used in this analysis originated

from one of seven broad geographic areas: the Dillingham, Holy Cross, and Kwiguk

Quadrangles, the cities of Barrow and Wales, Kodiak Island, and the Kuskokwim River

region. In addition to these broad locations, every individual was indicated as originating

from a secondary, more geographically-specific location. Specific locations were mapped

using Google Maps (Figure 9) software, and mapped locations were analyzed and used to

categorize all individuals into one of three site types based on different geographic

conditions.
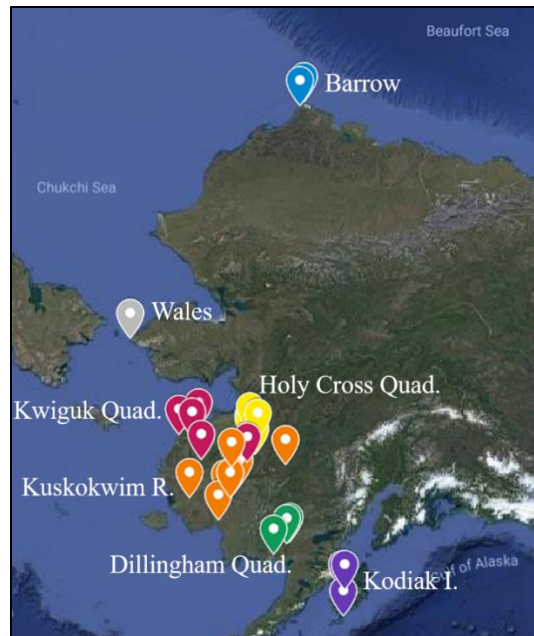
Figure 9. Locations of Alaskan Samples

The cities of Wales and Barrow are located just below and hundreds of miles above the Arctic Circle, respectively, and as such experience polar climate conditions. Such conditions include extended periods of subfreezing temperatures, snowfall, extended periods of darkness in the winter, and the existence of permafrost. Additionally, both cities are coastal and surrounded by stretches of tundra terrain, and skeletal remains within both regions are attributed to the same cultural traditions. Given the shared climatic and cultural traditions of these sites, all individuals excavated from the Wales and Barrow regions are classified in this study into the Far North Coastal (FNC) site type.

Mapping reveals that individuals from the remaining five areas (the Dillingham, Holy Cross, and Kwiguk Quadrangles, Kodiak Island, and the Kuskokwim River) all originate from a subarctic climate zone according to the Köppen climate scale (ISC

2019). Such individuals would have experienced relatively similar climatic conditions.

Despite similar climatic conditions, a major distinction can be made between these

locations in terms of accessible bodies of water. While all individuals were excavated

adjacent to a body of water, some were located inland on the banks of rivers while others

were located at the mouth of rivers, or on coastlines. Since type of aquatic mobility is

known to have implications for limb robusticity (see Chapter 1), the remaining

individuals were distinguished by these differences. Any individuals from the

Dillingham, Holy Cross, and Kwiguk Quadrangles, Kodiak Island, and the Kuskokwim

River region located at the mouth of a river or on an island were classified as belonging

to the Coastal/Bay (CB) site type. In contrast, individuals located further inland on

continental Alaska and along a riverbank were classified into the Inland River (IR) site

type. Table 3 presents a breakdown of bones used in this study by site type for unilateral

analyses while Table 4 presents the same breakdown for bilateral analyses.

Table 3. Bones Used in Unilateral Analyses by Site Type

Bone	Site Type	Number
Femur	Coastal/Bay	33
	Far North Coastal	32
	Inland River	105
	Total	**170**
Tibia	Coastal/Bay	29
	Far North Coastal	29
	Inland River	96
	Total	**154**
Humerus	Coastal/Bay	28
	Far North Coastal	40
	Inland River	99
	Total	**167**
Radius	Coastal/Bay	23
	Far North Coastal	36
	Inland River	88
	Total	**147**

Table 4. Bones Used in Bilateral Analyses by Site Type

Bone	Site Type	Number (Left-Right Pairs)
Humerus	Coastal/Bay	14
	Far North Coastal	23
	Inland River	61
	Total	**98**
Radius	Coastal/Bay	12
	Far North Coastal	20
	Inland River	62
	Total	**94**

Age Estimation. The deposition and resorption of bone in response to mechanical stimuli demonstrates different patterns in adults and subadults (Ruff et al. 1994). Any analysis of cross-sectional geometric properties should therefore not compare the results obtained from an adult population to those obtained from subadults. Standard age estimation techniques were utilized to remove any subadults from this analysis.

Without genetic material or microscopic analysis of tooth development, determining the exact age of an individual at time of death is not possible. However, other skeletal elements may be utilized to estimate a general age range that can distinguish between subadults and adults. Age estimation in this analysis was undertaken in accordance with established osteological standards, including the assessment of tooth development and long bone epiphyseal fusion (Buikstra and Ubelaker 1994).

Analysis of general tooth development was used whenever possible, as teeth have been shown to relate more closely to chronological age than other skeletal elements and because there is evidence that tooth development and eruption are under a high degree of genetic control (White et al. 2012). In contrast, although long bone epiphyseal fusion follows a general pattern during ontogeny, there is greater individual variation in epiphyseal fusion compared to tooth development. Using analyses of tooth development and epiphyseal fusion, all individuals estimated to be under fifteen years of age at death were categorized as subadults and immediately excluded from this study.

A small number of individuals were estimated to be between fifteen to twenty years of age at time of death. Individuals within this age range may approximate adult size and, depending on cultural affiliation, may participate in adult-oriented activities. However, in some individuals this remains a period of bone formation and epiphyseal fusion, which can affect the analysis of cross-sectional geometric measurements. Therefore, long bone epiphyseal fusion was used to distinguish between individuals within this age range; those with fused epiphyses were considered adults and included in

this study while those with unfused epiphyses were categorized as subadults and excluded.

When tooth development and epiphyseal fusion are complete, the estimation of age in the human skeleton becomes more complicated and error prone. Age estimation of adults is based on relatively predictable patterns of degeneration and wear of skeletal elements including the pubic symphysis, auricular surfaces, enamel surfaces, cranial sutures, and sternal rib ends. However, these elements are not as closely correlated to chronological age as are those used to estimate subadult age. Additionally, degeneration can be exaggerated by strenuous activity or pathological conditions, making an individual appear older than reality. This analysis did not require exact attributions of age to adult individuals, so more precise adult age estimation was not undertaken. However, to counteract the effect of age-related bone loss on cross-sectional measurements, individuals believed to be over approximately 55 years of age at death were excluded from this study.

Sex Estimation. Male and female humans show some degree of sexual dimorphism, with males tending to be taller, heavier, and more muscularly robust than females. Greater muscle mass in males may result in more robust corresponding skeletal elements relative to females. Additionally, cultural practices may lead to males and females performing different habitual activities. Such differences could result in different degrees of skeletal strength and rigidity between the sexes; therefore, the estimation of sex is necessary to control for differences in cross-sectional properties.

The estimation of biological sex from skeletal remains is possible due to the morphological effects of sex hormones beginning at puberty. Because morphological changes between the sexes are dependent upon the onset of puberty, sex estimation of subadult skeletal remains without DNA evidence is not reliable. Adult males tend to display larger and more robust skeletal elements than do adult females, although there is overlap between the sexes. Due to adaptations for childbirth, the *ossa coxae* are the most reliable indicators of sex. When *ossa coxae* are not available or are highly fragmented, the skull may also be used for sex estimation.

Sex estimation of all adult individuals in this study was completed using the *ossa coxae* and skull. Following standards established by Buikstra and Ubelaker (1994), pelvic traits scored for sex estimation include the greater sciatic notch, ventral arc, subpubic concavity, and medial aspect of the ischiopubic ramus. In addition to the pelvic girdle, or in cases where the *ossa coxae* were poorly preserved or absent, certain cranial elements, including the nuchal crest, mastoid process, supraorbital margin, glabella, and mental eminence were scored. All traits were scored 1-5, representing a continuum of morphological variation between male and female expression, and scores were averaged to reach a final sex estimation. In some cases, sex estimations previously performed by Smithsonian Institution personnel accompanied remains and were compared to current sex estimations. Tables 5-8 present the breakdown of skeletal elements utilized in this study by sex and site type for unilateral analyses, while Tables 9 and 10 present the same information for bilateral analyses.

Table 5. Unilateral Analyses Femora by Site Type and Sex

	Male	Female	Total
Coastal/Bay	13	20	33
Far North Coastal	20	12	32
Inland River	46	59	105
Total	79	91	170

Table 8. Unilateral Analyses Radii by Site Type and Sex

	Male	Female	Total
Coastal/Bay	10	13	23
Far North Coastal	22	14	36
Inland River	41	47	88
Total	73	74	147

Table 6. Unilateral Analyses Tibiae by Site Type and Sex

	Male	Female	Total
Coastal/Bay	11	18	29
Far North Coastal	18	11	29
Inland River	43	53	96
Total	72	82	154

Table 9. Bilateral Analyses Humeri by Site Type and Sex

	Male (Pairs)	Female (Pairs)	Total (Pairs)
Coastal/Bay	4	10	14
Far North Coastal	15	8	23
Inland River	30	31	61
Total	49	49	98

Table 10. Bilateral Analyses Radii by Site Type and Sex

	Male (Pairs)	Female (Pairs)	Total (Pairs)
Coastal/Bay	4	8	12
Far North Coastal	14	6	20
Inland River	32	30	62
Total	50	44	94

Table 7. Unilateral Analyses Humeri by Site Type and Sex

	Male	Female	Total
Coastal/Bay	10	18	28
Far North Coastal	23	17	40
Inland River	44	55	99
Total	77	90	167

Long Bone Measurements. Although not of direct statistical interest in this study, the measurement of long bones is necessary for purposes of standardization (Ruff 2000). Individuals with longer bones may be taller or larger than those with shorter bones, and larger individuals may demonstrate greater cross-sectional measurements by nature of being larger rather than due to increased robusticity. Size standardization prevents the skewing of data towards abnormally large or small individuals. All useable long bones were measured in accordance with standards established by Buikstra and Ubelaker (1994) using a digital osteometric board and digital calipers manufactured by Mitutoyo Corporation.

Maximum femoral length was obtained by placing the femoral diaphysis parallel to the osteometric board and measuring the distance from the femoral head to the most distal portion of the medial condyle. Bicondylar femoral length was measured by placing both the medial and lateral condyles against the stationary end of the osteometric board and measuring the length to the femoral head on the sliding end of the board. Tibial length was measured from the superior surface of the lateral condyle to the talar surface. Humeral length was obtained by placing the diaphysis parallel to the osteometric board and measuring from the most superior aspect of the humeral head to the most distal portion of the trochlea. Finally, radial length was measured from the most superior portion of the radial head to the most distal portion of the styloid process, regardless of diaphyseal orientation relative to the osteometric board.

Femoral head breadth was also measured in accordance with osteological standards (Buikstra and Ubelaker 1994). Again, this variable is not of direct interest, but is necessary for the estimation of body mass (see below). Femoral head breadth was obtained with digital calipers by recording the distance from the most superior to the most inferior aspects of the femoral head.

Body Mass Estimation. Body mass is not directly analyzed in this study but is estimated for the purposes of standardization to prevent skewing results in favor of unusually small or large individuals. Several formulae for estimating the body mass of bioarchaeological samples from femoral head breadth have been developed, including that of Grine et al. (1995), McHenry (1992), and Ruff et al. (1991). However, an inherent issue in the estimation of body mass using such formulae is the bias of the referent

population. Each formula was developed using individuals of known weight at death belonging to different geographic and/or cultural populations, and each respective formula is most accurate when used on skeletal samples of the same geographic or cultural group. For example, a formula derived from white Euroamericans may not generate accurate estimates of body mass for a Native American archaeological population.

However, Auerbach and Ruff (2004) found no significant differences in the body mass estimations generated by the formulae of Grine et al. (1995), McHenry (1992) and Ruff et al. (1991). In the absence of a body mass estimation formula from a corresponding population, Auerbach and Ruff recommend utilizing Ruff et al.'s (1991) formula in most analyses. Therefore, all femoral head breadths obtained in this study were applied to the following formulae to generate estimations of adult body mass:

Males: Body Mass(kg) = (2.741 * Femoral Head Breadth[mm] – 54.9) * 0.90

Females: Body Mass(kg) = (2.462 * Femoral Head Breadth[mm] – 35.1) *0.90

Imaging. Following sex and age estimation, long bone measurement, and body mass estimation, cross-sectional images of long bone diaphyses were obtained from all useable skeletal elements. Numerous methods for obtaining such images are available, including radiography, external molding, and computed tomography (CT) scanning. While the former method has been found to be accurate within five percent of the latter (O'Neill and Ruff 2004), CT imaging is the preferable method of obtaining images because "it is very rapid and produces accurate two-dimensional images of inner and

outer bone contours" (Ruff 2008, 187). Because remains are held at the Smithsonian Institution, use of Smithsonian-owned CT equipment was feasible.

Remains were transported from the Smithsonian Institution's Museum Support Center in Suitland, Maryland to the National Museum of Natural History in Washington, D.C. for computed tomography (CT) imaging. All viable humeri, radii, femora, and tibiae were transported and scanned. In cases where individuals had bilaterally-preserved long bones, bilateral scans were taken to allow for the analysis of bilateral asymmetry in addition to unilateral comparisons. Radial, femoral, and tibial scanning was completed at 50% of total bone length (bicondylar length in femora). These scan locations differ slightly from those used in previous research (e.g., Ruff and Hayes 1983, Ruff 2002), which utilize scans taken at 50% of biomechanical length; this difference should be noted if the results of this study are compared to other research. Humeral imaging was completed at 66% craniocaudal length (33% of length from the distal portion) to avoid scanning the deltoid tuberosity.

Images were generated on the Smithsonian Institution's Siemens SOMATOM Emotion 6 CT Scanner, manufactured in 2007. Bones were placed in standard anatomical position on the scanning bed. Foam wedges were used under the proximal and distal portions of all bones for purposes of stabilization and to ensure proper alignment of diaphyses for scanning (Ruff 2002). The SOMATOM CT Scanner generates guiding crosshair lights along the sagittal, coronal, and transverse planes (when the subject is in standard anatomical position), and the machine was calibrated to capture scans at the intersection of these crosshairs. Therefore, the diaphysis of each bone at the

predetermined length (see above) was centered as closely as possible around the intersection of the guiding crosshairs while in standard anatomical position.

Each long bone was scanned individually at its predefined location in 2mm slices. Following comparisons of multiple settings and consultation with both the Smithsonian Institution's CT Specialist and other colleagues, machine settings of 80 kilovolts (kV) and 110 milliampere-seconds (mAs) with a reconstruction kernel at u90s ultra sharp were found to produce adequate thresholds distinguishing between bone and air. Software settings restricted the CT machine from producing fewer than three two-dimensional images of each bone; only the first of these three images was utilized for obtaining cross-sectional measurements. Images obtained from CT scanning were saved as DICOM files on the Smithsonian Institution server and transferred via external hard drive to a personal computer. *MicroDicom Viewer*, a free software (MicroDicom 2019), was used to convert each DICOM image into a TIF file (Figures 10-13) for purposes of obtaining geometric measurements (see below).

Figure 10. Sample CT Image of Left Femur

Figure 12. Sample CT Image of Left Radius

Figure 11. Sample CT Image of Left Humerus

Figure 13. Sample CT Image of Left Tibia

Geometric Measurements and Standardization. TIF files of scans were uploaded into the free software *ImageJ* (NIH 2018), and diaphyseal cross-sectional properties were calculated using the macro plugin *MomentMacro* (Ruff 2016). *MomentMacro* generates TA, CA, I_x, I_y, I_{max}, I_{min}, Theta, Z_x, Z_y, J, and Z_p, directly from each scan image (Table 11). MA was calculated by subtracting CA from TA.

Table 11. Cross-Sectional Geometric Properties Generated by MomentMacro

Property	Abbrev.	Units	Definition
Total Subperiosteal Area	TA	mm^2	Area w/in Subperiosteal Surface
Cortical Area	CA	mm^2	Compressive/Tensile Strength
Medullary Area	MA	mm^2	Area w/in Medullary Cavity
Second Moment of Area (M-L Axis)	I_x	mm^4	A-P Bending Rigidity
Second Moment of Area (A-P Axis)	I_y	mm^4	M-L Bending Rigidity
Max. Second Moment of Area	I_{max}	mm^4	Maximum Bending Rigidity
Min. Second Moment of Area	I_{min}	mm^4	Minimum Bending Rigidity
Theta	Theta	degrees	Orientation
Section Modulus (M-L Axis)	Z_x	mm^3	A-P Bending Strength
Section Modulus (A-P Axis)	Z_y	mm^3	M-L Bending Strength
Polar Second Moment of Area	J	mm^4	Torsional Rigidity
Polar Section Modulus	Z_p	mm^3	Torsional Strength

Relevant areas (TA, CA, and MA) and second moments of area (I_x, I_y, and J) to be used in the analysis were then statistically standardized. Preferred standardization is by body mass for section areas or by (body mass*bone length^2) for second moments of area (SMAs), as these formulae account for the mechanical load placed on bone by body weight (Ruff 2000). Femoral and tibial standardization in particular should take into account body mass to account for the role these skeletal elements play in supporting the body. In accordance with standards, all femoral and tibial section areas were standardized by body mass, and all femoral and tibial SMAs were standardized by (body mass* length^2).

Humeral and radial properties may also be standardized by the above formulae. However, a significant number of individuals with viable humeri and radii did not contain well-preserved femora from which to estimate body mass. Eliminating these variables from the analysis would have resulted in reduced humeral and radial sample sizes. Instead, humeral and radial properties were standardized by alternative criteria utilizing

powers of bone length: bone length^3 for section areas and bone length$^{5.33}$ for SMAs (Ruff et al. 1993). Finally, all standardized I_x were divided by corresponding standardized I_y to generate a ratio of A-P to M-L bending rigidity of all sampled bones.

Calculation of Bilateral Asymmetry. The analysis of bilateral directional asymmetry was completed following Auerbach and Ruff (2006). Left-right asymmetries in TA, CA, MA, I_x, I_y, J, and I_x/I_y were first converted into directional asymmetry percentages (%DA) using the following formula:

$$\%DA = (right - left)/((right - left)/2) *100$$

This formula is used because it "standardizes all raw asymmetric differences to percentages of directional asymmetry within elements, allowing for direct comparison of asymmetries in dimensions of different size" (Auerbach and Ruff 2006: 205). In other words, analyses of bilateral asymmetry do not require the size standardization detailed in the previous section.

Statistical Analyses. Standardized TA, CA, MA, I_x, I_y, J, and I_x/I_y were then statistically analyzed to identify any significant differences in these properties between the Coastal/Bay, Far North Coastal, and Inland River site categories. Different statistical methods were utilized for different geometric properties within the unilateral analysis and for the bilateral analyses. Within all analyses, site type is the independent variable while geometric properties are the dependent variables.

Unilateral analyses of TA, CA, MA, I_x, I_y, and J involve two or more dependent, continuous variables (geometric properties), an independent variable divided into two or more groups (site types), independence of observations between and within groups, and a

large sample size. Since these assumptions are met, comparisons of unilateral TA, CA, MA, I_x, I_y, and J were undertaken using a multivariate analysis of variance (MANOVA) test. Additionally, because equal sample sizes and variances are not assumed, the Games-Howell post-hoc test was implemented in these comparisons.

Unilateral analyses of I_x/I_y and bilateral directional asymmetry analyses of all variables involve the comparison of ratios (of either I_x to I_y or left to right measurements). The analysis of ratio-level data, as well as an independent variable divided into three independent groups and independence of observations between and within groups, prompts use of the nonparametric Kruskal-Wallis test in the analysis of unilateral I_x/I_y and bilateral TA, CA, MA, I_x, I_y, J, and I_x/I_y.

Descriptive Statistics: Unilateral Analyses

Male Femora. Summary statistics for male femoral analyses are presented in Table 12. Figures 14-20 present box plots of male femoral TA, CA, MA, I_x, I_y, J, and I_x/I_y by location, respectively (all calculations standardized). Median femoral TA (Figure 14) appears greatest among Far North Coastal and lowest among Coastal/Bay males. The interquartile range (IQR) of the Far North Coastal sample overlaps with a portion of the Inland River IQR, which in turn overlaps with a portion of the Coastal/Bay IQR. The IQRs of the Far North Coastal and Coastal/Bay samples do not appear to overlap. While the IQRs of the Coastal/Bay and Far North Coastal groups are skewed towards the 10th percentile, that of the Inland River sample appears more centrally placed between whiskers.

Median male femoral CA (Figure 15) appears greatest among the Inland River sample and lowest among the Coastal/Bay group. The upper portion of the Coastal/Bay IQR overlaps with the lower portion of the Far North Coastal IQR, the upper portion of which overlaps with the lower portion of the Inland River IQR. The IQRs of all samples appear relatively centrally distributed between the upper and lower whiskers. While the Inland River and Coastal/Bay samples contain one outlier each below the 10th percentile, the Far North Coastal sample shows two such outliers.

Male femoral MA (Figure 16) appears greatest among the Far North Coastal sample in terms of both median value and IQR range, neither of which overlap with the respective values in either the Coastal/Bay or Inland River samples. In contrast, the median values of the Inland River and Coastal/Bay groups are relatively similar and the IQRs of these samples show significant overlap. Unlike the centrally-positioned Inland River sample, the IQR of both the Coastal/Bay and Far North Coastal groups are distributed closer to the 10th percentile.

Median femoral I_x is greatest among the Far North Coastal and lowest among the Coastal/Bay sample (Figure 17). The IQRs of the Far North Coastal and Inland River samples overlap to some extent, while the Coastal/Bay IQR does not appear to overlap with the IQR of the other samples. All IQRs are relatively centrally positioned between whiskers, and only one outlier is present well above the 90th percentile within the Far North Coastal group.

The Far North Coastal sample shows the highest median value of femoral I_y (Figure 18), while median value is lowest within the Coastal/Bay group. The Inland River and Far North Coastal IQRs show substantial overlap, while the Coastal/Bay IQR only overlaps with a portion of the Inland River IQR. The Coastal/Bay IQR is skewed towards the upper whisker, and the Coastal/Bay sample shows four outliers – two below and two above the whiskers.

Median male femoral J (Figure 19) is greatest among the Far North Coastal sample. Both the median and IQR values of this group appear significantly greater than either the Coastal/Bay or Inland River samples. While the lower portion of the Far North

Coastal IQR just overlaps with that of the Inland River group, the Coastal/Bay IQR does not interact with the other two samples. All IQRs appear relatively centrally skewed between upper and lower whiskers, and all groups show at least one outlier: two (one above and one below the whiskers) within the Coastal/Bay sample, one (well above the 90th percentile) within the Far North Coastal sample, and one (just above the upper whisker) within the Inland River sample.

Figure 20 shows male femoral I_x/I_y by location. All median values are greater than 1.0, suggesting that anteroposterior (A-P) bending rigidity is greater than mediolateral (M-L) bending rigidity in all samples. The Far North Coastal group shows a median value slightly greater than that of the Inland River sample, which in turn is greater than that of the Coastal/Bay group. All IQRs overlap to some extent, with the Far North Coastal IQR showing the greatest values. The Coastal/Bay and Far North Coastal IQRs are both significantly distributed towards the 10th percentile, while that of the Inland River group is more centrally positioned between whiskers.

Female Femora. Summary statistics of female femoral analyses are shown in Table 13, and Figures 14-20 show box plots of female femoral TA, CA, MA, I_x, I_y, J, and I_x/I_y by location, respectively (all measurements standardized). The greatest median value of female femoral TA (Figure 14) is found among the Far North Coastal sample and the lowest among the Coastal/Bay sample. Additionally, the Far North Coastal IQR is greater than that of the other two groups, showing no overlap with either. IQRs of Coastal/Bay and Inland River samples overlap to some extent. The Inland River IQR appears slightly skewed towards the 90th percentile while the Coastal/Bay IQR appears skewed towards

the 10th percentile. Three outliers are present: one just above the upper whisker among the Coastal/Bay sample and two below the lower whisker among the Inland River sample.

Median values of female femoral CA (Figure 15) appear relatively similar between sites, with the Far North Coastal and Inland River groups appearing slightly above that of the Coastal/Bay site. The IQRs of the Far North Coastal and Inland River groups appear almost identical and overlap with the Coastal/Bay IQR, which is less widely distributed. The Far North Coastal IQR is skewed closer to the lower whisker than are the other two. The Coastal/Bay sample shows two outliers – one above and one below the whiskers – while the Inland River sample contains three outliers, all of which are well below the 10th percentile.

The Far North Coastal group shows the largest median value of female femoral MA (Figure 16) and the Inland River group the smallest. Additionally, the Far North Coastal IQR is greater than, and does not appear to overlap with, the Coastal/Bay or Inland River IQRs. The Coastal/Bay IQR completely overlaps that of the Inland River site. While the Far North Coastal sample shows no outliers, the Coastal/Bay group contains one outlier well above the 90th percentile, and the Inland River site shows one outlier below and five outliers above the whiskers.

Median female femoral I_x is greatest among the Far North Coastal sample and approximately equal between the Coastal/Bay and Inland River groups (Figure 17). While the Inland River and Coastal/Bay IQRs show substantial overlap, the Far North Coastal IQR only just overlaps with that of the Inland River group. The IQRs of the Far

North Coastal and Inland River samples appear relatively centrally distributed between whiskers, while that of the Coastal/Bay sample is skewed closer to the 10th percentile. The Coastal/Bay and Inland River groups both show one outlier above and one outlier below the whiskers.

Median female femoral I_y is highest within the Far North Coastal group, while median I_y appears equal between the Coastal/Bay and Inland River samples (Figure 18). The IQRs of all three groups overlap, although that of the Far North Coastal group has greater numerical value than the other two samples. While the Far North Coastal and Inland River IQRs are centrally positioned between the 10th and 90th percentiles, that of the Coastal/Bay group is skewed towards the 10th percentile. Additionally, the Coastal/Bay group shows one outlier below the lower whisker, and the Inland River sample shows two outliers below and one outlier above the whiskers.

The Coastal/Bay and Inland River groups show almost identical median values and IQR distributions of female femoral J (Figure 19). In contrast, the Far North Coastal median value and IQR are much greater, and the latter does not overlap with IQRs of the other groups. Additionally, the Far North Coastal IQR is situated more closely to the upper whisker than are the other IQRs. All location samples show at least one outlier: two among the Coastal/Bay site (one above and one below the whiskers), one above the 90th percentile within the Far North Coastal sample, and five among the Inland River group (three below the 10th percentile and two above the 90th percentile).

Median values of female femoral I_x/I_y (Figure 20) are all greater than 1.0, suggesting that average A-P bending rigidity is greater than M-L bending rigidity in all

sites. The Coastal/Bay and Far North Coastal samples have similar median values slightly above that of the Inland River group. The IQRs of all three samples overlap and are similar, although the Coastal/Bay IQR is more widely distributed than are the other two. Only the Inland River sample contains outliers – two above the 90th percentile.

Table 12. Summary Statistics, Male Femora

Site Type		TA	CA	MA	I_x	I_y	J	I_x/I_y
Coastal/Bay	N	13	13	13	13	13	13	13
	Mean	771.51	560.45	211.06	16.56	15.55	32.12	1.08
	Std. Deviation	73.63	58.12	61.81	2.85	3.67	6.13	0.16
	Std. Error of Mean	20.42	16.12	17.14	0.79	1.01	1.70	0.04
	Variance	5422.67	3378.48	3821.03	8.14	13.51	37.61	0.02
Far North Coastal	N	20	20	20	20	20	20	20
	Mean	924.18	604.32	319.85	24.15	19.40	43.56	1.26
	Std. Deviation	125.46	70.51	101.27	5.95	4.36	9.63	0.21
	Std. Error of Mean	28.05	15.76	22.64	1.33	0.97	2.15	0.04
	Variance	15741.44	4972.63	10256.22	35.46	19.08	92.77	0.04
Inland River	N	46	46	46	46	46	46	46
	Mean	841.73	657.28	184.45	20.81	17.41	38.23	1.20
	Std. Deviation	67.29	81.77	50.92	4.09	3.04	6.52	0.17
	Std. Error of Mean	9.92	12.05	7.50	0.60	0.44	0.96	0.02
	Variance	4527.97	6687.39	2593.40	16.77	9.29	42.55	0.03
Total	N	79	79	79	79	79	79	79
	Mean	851.05	627.94	223.10	20.96	17.61	38.57	1.19
	Std. Deviation	98.78	83.65	88.81	5.04	3.69	8.14	0.19
	Std. Error of Mean	11.11	9.41	9.99	0.56	0.41	0.91	0.02
	Variance	9757.78	6998.87	7887.63	25.42	13.64	66.32	0.03

Table 13. Summary Statistics, Female Femora

Site Type		TA	CA	MA	I_x	I_y	J	I_x/I_y
Coastal/Bay	N	20	20	20	20	20	20	20
	Mean	704.68	508.68	195.99	14.95	13.40	28.35	1.12
	Std. Deviation	54.03	86.47	76.19	3.40	2.80	5.72	0.17
	Std. Error of Mean	12.08	19.33	17.03	0.76	0.62	1.28	0.03
	Variance	2919.53	7477.99	5805.21	11.57	7.87	32.79	0.03
Far North Coastal	N	12	12	12	12	12	12	12
	Mean	809.45	556.14	253.31	18.90	16.84	35.74	1.13
	Std. Deviation	57.78	63.96	65.52	3.38	3.15	5.85	0.16
	Std. Error of Mean	16.68	18.46	18.91	0.97	0.91	1.69	0.04
	Variance	3339.56	4091.35	4293.48	11.47	9.94	34.33	0.02
Inland River	N	59	59	59	59	59	59	59
	Mean	708.42	525.22	183.19	14.66	13.83	28.50	1.07
	Std. Deviation	91.75	90.79	72.60	3.41	3.14	6.13	0.17
	Std. Error of Mean	11.94	11.82	9.45	0.44	0.40	0.79	0.02
	Variance	8418.49	8244.51	5270.91	11.64	9.86	37.66	0.03
Total	N	91	91	91	91	91	91	91
	Mean	720.92	525.67	195.25	15.28	14.13	29.42	1.09
	Std. Deviation	87.49	87.06	75.44	3.65	3.22	6.44	0.17
	Std. Error of Mean	9.17	9.12	7.90	0.38	0.33	0.67	0.01
	Variance	7655.92	7579.94	5691.97	13.36	10.38	41.53	0.03
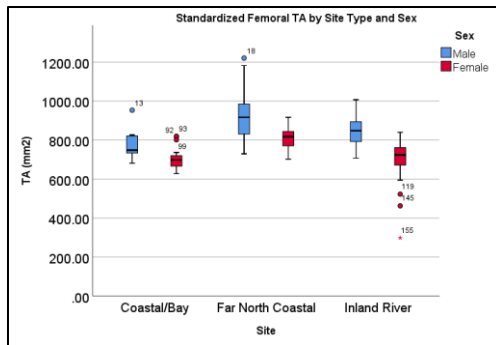
Figure 14. Femoral TA
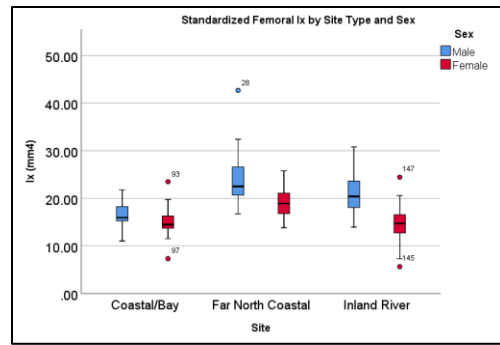
Figure 17. Femoral I$_x$
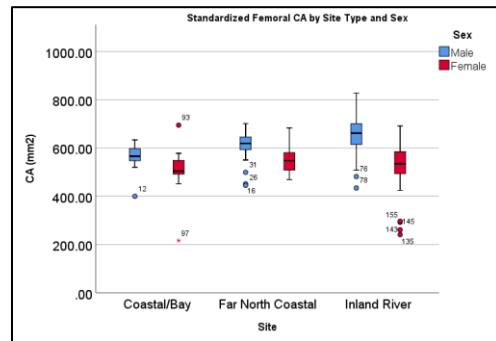
Figure 15. Femoral CA
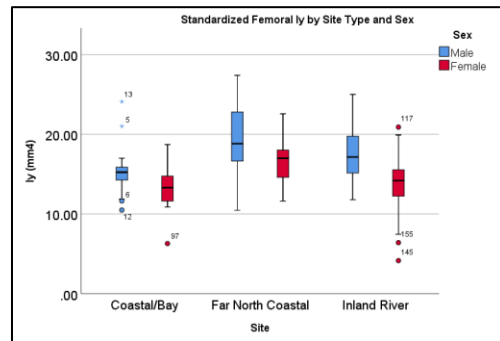
Figure 18. Femoral I$_y$
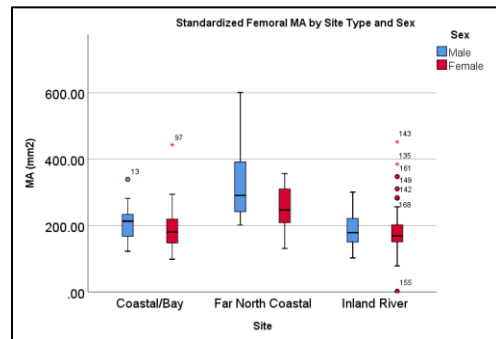
Figure 16. Femoral MA
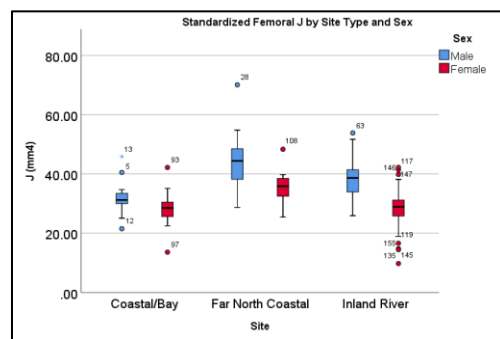
Figure 19. Femoral J
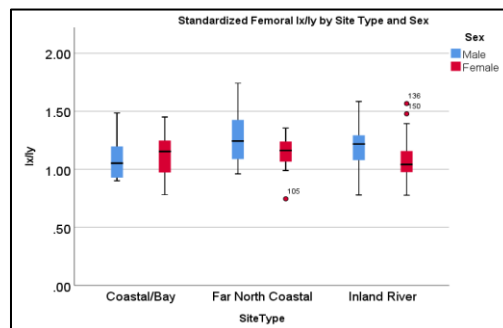
Figure 20. Femoral I$_x$/I$_y$

Figures 14-20. Standardized Femoral Cross-Sectional Properties by Site Type and Sex

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Male Tibiae. Table 14 presents summary statistics for male tibial analyses, and Figures 21-27 show boxplots of male tibial TA, CA, MA, I_x, I_y, J, and I_x/I_y by location, respectively (all measurements standardized). Median male tibial TA (Figure 21) is highest among the Far North Coastal sample and followed closely by the Inland River group, with the Coastal/Bay sample showing the lowest median value. The IQRs of all groups show significant overlap, with those of the Coastal/Bay and Inland River samples appearing almost identical. The IQR of the Coastal/Bay group shows a skewed distribution towards the lower whisker.

Median male tibial CA (Figure 22) appears greatest among the Inland River and lowest among the Far North Coastal sample. The IQR of the Coastal/Bay site shows a narrower range than do those of the other samples. The Far North Coastal IQR shows the lowest numerical values, although the upper portion does overlap with the lower portions of both the Inland River and Coastal/Bay IQRs. All interquartile ranges appear to be centrally distributed between the respective 10th and 90th percentiles.

The Far North Coastal sample shows the greatest median value of male tibial MA (Figure 23), followed by the Coastal/Bay site, and lastly the Inland River sample. The IQRs of both the Coastal/Bay and Inland River groups show significant overlap; in contrast, the Far North Coastal IQR has greater numerical value and overlaps only with the upper portion of the Coastal/Bay IQR. A single outlier above the 90th percentile is present within the Coastal/Bay sample.

The median value of male tibial I_x is approximately equal between sites, with the Inland River sample appearing slightly greater than either the Far North Coastal or

Coastal/Bay groups (Figure 24). All three IQRs show substantial overlap, although the

Far North Coastal IQR demonstrates skewing towards the 10th percentile while the Inland

River and Coastal/Bay IQRs are more centrally positioned between whiskers. No outliers

are present among the samples.

The Coastal/Bay group shows the highest median value of male tibial I_y, with the

median values of the Inland River and Far North Coastal groups appearing equal (Figure

25). While the three IQRs display significant overlap and are all centrally positioned

between the upper and lower whiskers, the median value within the Coastal/Bay sample

is skewed towards the upper end of the IQR more so than those of the other two samples.

The Far North Coastal and Inland River groups show numerous outliers each; the former

has two outliers above and two below the whiskers, and the latter shows three outliers

above the 90th percentile.

The median values of male tibial J (Figure 26) appear relatively similar between

all three samples, with that of the Inland River group appearing slightly greater than that

of the Coastal/Bay and Far North Coastal samples. Sample IQRs are also similar, with

those of the Coastal/Bay and Far North Coastal sites appearing almost identical and that

of the Inland River group appearing only slightly greater. Additionally, all IQRs are

centrally-distributed between whiskers.

The median value of male tibial I_x/I_y within all three groups is above 2.0,

suggesting that average A-P bending rigidity is double the M-L bending rigidity across

locations (Figure 27). Median value is greatest among the Inland River sample, followed

by the Far North Coastal group, and lowest among the Coastal/Bay group. All IQRs show

prominent overlap, although the Inland River IQR has greater numerical value than those of the other samples. The Coastal/Bay IQR additionally shows significant skewing towards the upper whisker.

Female Tibiae. Summary statistics for female tibial analyses are presented in Table 15. Figures 21-27 show box plots of female tibial TA, CA, MA, I_x, I_y, J, and I_x/I_y by location, respectively (all measurements standardized). The greatest median value of female tibial TA (Figure 21) is found among the Far North Coastal group and the lowest among the Inland River group. The IQR of the Coastal/Bay group appears to overlap with the lower portion of the Far North Coastal IQR and most of the Inland River IQR. All three IQRs appear centrally positioned between whiskers. The Far North Coastal group shows one outlier below the 10th percentile while the Inland River group shows three outliers: one below and two above the whiskers.

Median values of female tibial CA (Figure 22) appear similar between the Inland River and Far North Coastal samples while that of the Coastal/Bay group is slightly lower. The IQR of the Coastal/Bay sample is less widely distributed than are the other two, while the IQR of the Far North Coastal site is skewed closer to the 90th percentile than are the other two. However, all IQRs overlap to some degree. Both the Coastal/Bay and Inland River samples contain outliers; the former has two below and one above the whiskers, while the latter shows one below the 10th percentile.

The Far North Coastal and Coastal/Bay samples have similar median values of female tibial MA (Figure 23) while that of the Inland River group appears significantly lower. The IQRs of all three samples overlap to some extent, although the Coastal/Bay

IQR appears significantly more widely distributed than the IQRs of the other two samples. Three outliers above the upper whisker are present within the Inland River sample.

The greatest median value of female tibial I_x is found among the Far North Coastal sample while the lowest is within the Inland River group (Figure 24). Although the IQRs of all three groups overlap, that of the Far North Coastal sample has a greater range than the other two groups. Additionally, the Coastal/Bay and Far North Coastal IQRs are skewed towards the lower and upper whiskers, respectively. The Inland River sample contains two outliers (one above and one below the whiskers) while the Coastal/Bay sample demonstrates three outliers above and two outliers below the whiskers.

Median female tibial I_y is greatest among the Coastal/Bay site, intermediate among the Far North Coastal group, and lowest among the Inland River sample (Figure 25). All IQRs overlap, and the IQRs of the Inland River and Far North Coastal groups appear to have similar ranges below that of the Coastal/Bay sample. The Coastal/Bay IQR is skewed towards the 90th percentile, and both the Inland River and Far North Coastal IQRs are centrally distributed between whiskers. A single outlier above the upper whisker is present in the Inland River group.

The greatest median value of female tibial J (Figure 26) is found in the Far North Coastal group while lowest is among the Inland River sample. The IQRs of the Coastal/Bay and Inland River samples are similar in value and range, while that of the Far North Coastal group is higher in value and is more closely skewed towards the 90th

percentile. Both the Coastal/Bay and Inland River samples each show one outlier below and one outlier above the whiskers.

All median values of female tibial I_x/I_y (Figure 27) are above 2.0, indicating greater A-P than M-L bending rigidity in all three samples. Median values are similar between samples and IQRs show significant overlap, although the Inland River IQR has more widely distributed whiskers than do the other samples. Additionally, the Inland River IQR shows one outlier above and one outlier below the whiskers.

Table 14. Summary Statistics, Male Tibiae

Site Type		TA	CA	MA	I_x	I_y	J	I_x/I_y
Coastal/Bay	N	10	10	10	10	10	10	10
	Mean	1066.47	740.28	326.18	3802.63	3806.59	7609.23	1.00
	Std. Deviation	133.63	115.04	96.25	924.62	891.72	1734.01	0.14
	Std. Error of Mean	42.26	36.38	30.43	292.39	281.98	548.34	0.04
	Variance	17859.23	13236.19	9265.44	854923.29	795170.61	3006813.22	0.02
Far North Coastal	N	23	23	23	23	23	23	023
	Mean	1047.59	654.41	393.17	3563.31	3469.86	7033.17	1.03
	Std. Deviation	110.90	91.92	114.81	682.76	630.44	1261.64	0.11
	Std. Error of Mean	23.12	19.16	23.94	142.36	131.45	263.07	0.02
	Variance	12299.59	8451.00	13182.42	466163.88	397455.59	1591741.50	0.01
Inland River	N	44	44	44	44	44	44	44
	Mean	963.43	700.84	262.58	3385.82	3210.14	6595.96	1.05
	Std. Deviation	205.17	143.64	122.26	1385.59	1223.71	2583.35	0.10
	Std. Error of Mean	30.93	21.65	18.43	208.88	184.48	389.45	0.01
	Variance	42097.31	20633.50	14948.45	1919887.12	1497474.67	6673735.94	0.01
Total	N	77	77	77	77	77	77	77
	Mean	1001.95	692.10	309.85	3492.97	3365.18	6858.15	1.03
	Std. Deviation	177.56	128.32	129.61	1158.96	1048.49	2171.64	0.11
	Std. Error of Mean	20.23	14.62	14.77	132.07	119.48	247.48	0.01
	Variance	31530.96	16467.53	16800.72	1343196.30	1099343.86	4716061.65	0.01

Table 15. Summary Statistics, Female Tibiae

Site Type		TA	CA	MA	I_x	I_y	J	I_x/I_y
Coastal/Bay	N	18	18	18	18	18	18	18
	Mean	904.92	591.33	313.58	2809.34	2289.92	5099.27	1.23
	Std. Deviation	128.61	114.95	119.65	793.46	579.33	1314.70	0.19
	Std. Error of Mean	30.31	27.09	28.20	187.02	136.54	309.87	0.04
	Variance	16540.80	13214.42	14316.71	629584.07	335626.07	1728449.27	0.03
Far North Coastal	N	17	17	17	17	17	17	17
	Mean	976.60	591.69	384.91	3053.06	2620.45	5673.52	1.17
	Std. Deviation	134.14	71.53	112.88	749.23	584.26	1267.23	0.16
	Std. Error of Mean	32.53	17.34	27.37	181.71	141.70	307.34	0.04
	Variance	17994.44	5116.81	12742.27	561350.14	341368.55	1605881.45	0.02
Inland River	N	55	55	55	55	55	55	55
	Mean	875.25	614.54	260.71	2682.05	2339.60	5021.66	1.16
	Std. Deviation	129.46	115.21	100.58	718.24	692.25	1377.10	0.14
	Std. Error of Mean	17.45	15.53	13.56	96.84	93.34	185.68	0.01
	Variance	16761.57	13275.54	10118.00	515881.77	479218.40	1896416.96	0.02
Total	N	90	90	90	90	90	90	90
	Mean	900.33	605.58	294.74	2777.59	2382.72	5160.31	1.17
	Std. Deviation	134.41	107.82	116.21	744.66	655.68	1353.67	0.16
	Std. Error of Mean	14.16	11.36	12.24	78.49	69.11	142.68	0.01
	Variance	18068.55	11626.32	13505.08	554520.71	429925.82	1832429.23	0.02
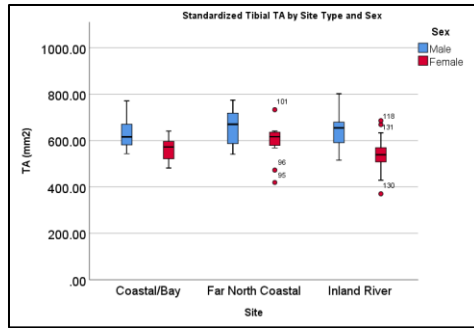
Figure 21. Tibial TA
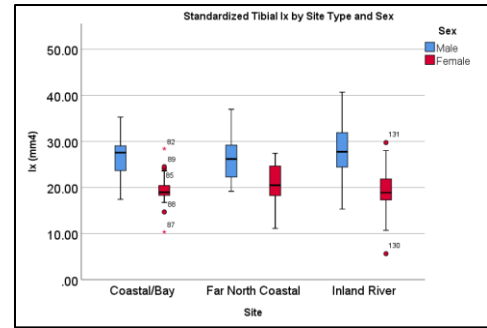
Figure 24. Tibial I_x
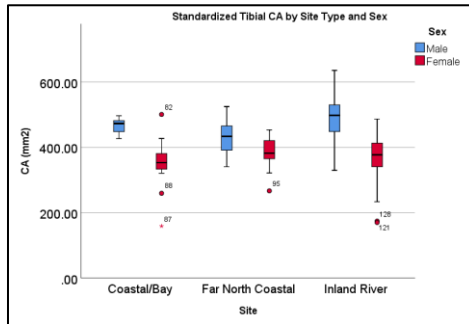
Figure 22. Tibial CA
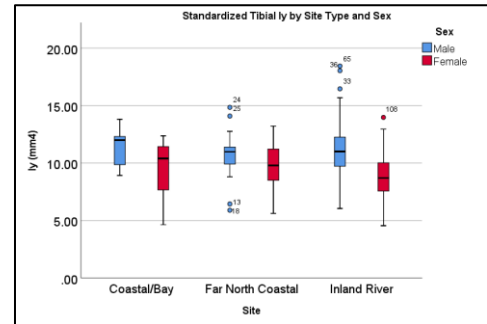
Figure 25. Tibial I_y
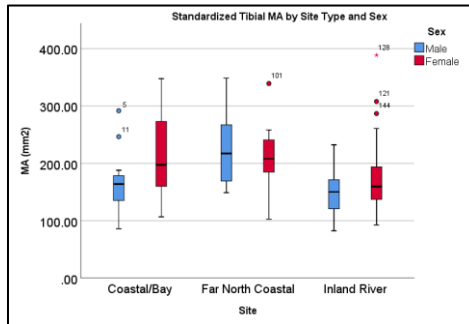
Figure 23. Tibial MA
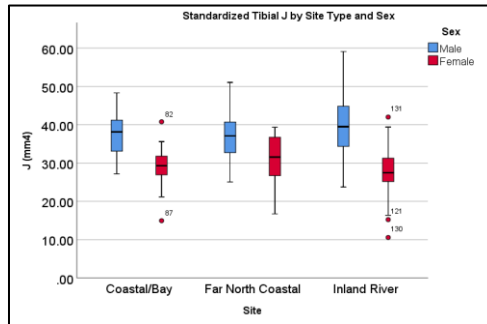
Figure 26. Tibial J
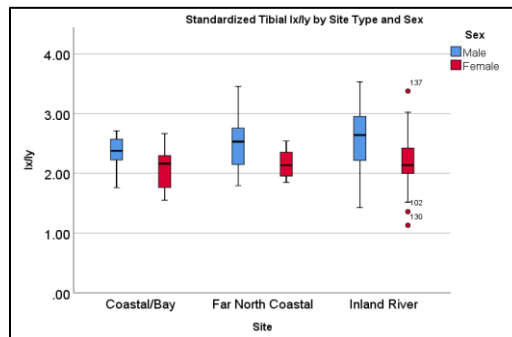
Figure 27. Tibial I_x/I_y

Figures 21-27. Standardized Tibial Cross-Sectional Properties by Site Type and Sex

Male Humeri. Summary statistics for male humeral analyses are presented in Table 16 while Figures 28-34 present box plots of male humeral TA, CA, MA, I_x, I_y, J, and I_x/I_y by site, respectively (all measurements standardized). Median values for male humeral TA (Figure 28) are similar between sites, with that of the Far North Coastal group appearing slightly greater than that of the other two samples. In contrast, sample IQRs differ; the Inland River IQR shows the lowest numerical value, overlapping only with the lower portions of the Far North Coastal and Coastal/Bay IQRs. Additionally, the Far North Coastal IQR has a narrower distribution than do the other two. Finally, the Inland River sample shows two outliers above the 90th percentile.

The median value for male humeral CA (Figure 29) is lowest among the Far North Coastal sample and approximately equal between the Coastal/Bay and Inland River sites. Although the IQRs of all three groups overlap to some extent, the Far North Coastal IQR is skewed towards the 10th percentile while those of the other sites are more centrally positioned between whiskers. Additionally, an outlier is present well above the 90th percentile within the Inland River sample.

Median male humeral MA (Figure 30) is greatest among the Far North Coastal group, followed by the Coastal/Bay, and lowest among the Inland River sample. IQR values also differ; the Far North Coastal sample shows the highest values and the Inland River sample the lowest; the Inland River IQR does not overlap with the Far North Coastal IQR at all. All IQRs are centrally positioned between whiskers, while the Inland River group contains two outliers, both well above the 90th percentile.

Median male humeral I_x is greatest among the Coastal/Bay and lowest among the Inland River sample (Figure 31). The IQRs of all samples overlap to some extent, and the Inland River IQR shows the greatest range of all groups. Both the Inland River and Coastal/Bay IQRs are skewed towards the 10th percentile, and the Far North Coastal IQR is centrally distributed between the 10th and 90th percentile. The only two outliers are within the Inland River sample above the 90th percentile.

Median male humeral I_y is also greatest among the Coastal/Bay and lowest among the Inland River samples (Figure 32). While the IQRs of all samples do overlap, only the lowermost portion of the Coastal/Bay IQR overlaps with the uppermost portion of the Inland River group. Those groups also have IQRs with higher ranges than the Far North Coastal IQR. Several outliers are present: two in the Far North Coastal group (one above and one below the whiskers) and three above the 90th percentile in the Inland River group.

Median values of male humeral J (Figure 33) are similar between the Inland River and Coastal/Bay samples, with the Far North Coastal site showing a slightly greater value. The IQRs of all samples overlap, although the Inland River sample shows the lowest and the Coastal/Bay sample shows the greatest numerical value. The Coastal/Bay IQR is skewed towards the lower whisker while the other IQRs are more centrally distributed. Lastly, the Inland River site contains two outliers above the upper whisker.

The median value of male humeral I_x/I_y (Figure 34) appears similar between samples; however, that value is less than 1.0 among the Coastal/Bay group. This suggests that M-L bending rigidity is greater than A-P bending rigidity at this site. Interquartile

ranges of all samples overlap, although that of the Coastal/Bay group is more widely distributed than those of the Far North Coastal and Inland River samples. Finally, a single outlier above the 90th percentile is present among the Far North Coastal sample.

Female Humeri. Table 17 presents summary statistics for female humeral analyses, and Figures 28-34 show box plots of female humeral TA, CA, MA, I_x, I_y, J, and I_x/I_y, respectively, by location (all measurements standardized). The highest median value of female humeral TA (Figure 28) is among the Far North Coastal group while the lowest is among the Inland River sample. IQRs of all samples have similar distributions, but that of the Far North Coastal site has greater value than the other two groups, which are similar and overlap almost completely. The Inland River IQR shows a slight skew towards the 10th percentile. One outlier above the 90th percentile is present among the Inland River group.

Median values of female humeral CA (Figure 29) are roughly equal between samples. Additionally, all IQRs overlap with one another. However, the IQRs vary in range, with the Coastal/Bay sample being the most widely distributed and the Far North Coastal sample the most narrowly distributed. Additionally, the Coastal/Bay IQR is skewed more closely to the upper whisker than the other two groups, which are centrally positioned.

The greatest median value of female humeral MA (Figure 30) is found in the Far North Coastal sample, and the lowest is among the Inland River group. The Far North Coastal group also shows the greatest IQR. However, the Coastal/Bay group has the most widely distributed IQR, which overlaps with both the Far North Coastal and Inland River

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IQRs. The Coastal/Bay IQR is more skewed towards the 10th percentile than are the IQRs of the other two groups.

The highest median value of female humeral I_x appears in the Far North Coastal group, although the median value of all three samples appear similar (Figure 31). There is substantial overlap between the three IQRs, although the range of the Far North Coastal and Coastal/Bay IQRs appear greater than that of the Inland River group. The Coastal/Bay and Inland River IQRs appear more skewed towards the lower whisker than does that of the Far North Coastal sample. A single outlier above the 90th percentile is present in the Inland River sample.

Median female humeral I_y is greatest in the Far North Coastal sample and approximately equal between the Coastal/Bay and Inland River samples (Figure 32). All three IQRs overlap substantially and appear to have similar ranges. While the Coastal/Bay and Far North Coastal IQRs are centrally distributed between whiskers, that of the Inland River group is skewed towards the lower whisker. The Inland River sample contains an outlier above the 90th percentile.

The Coastal/Bay and Inland River samples show approximately similar median values of female humeral J (Figure 33), which are below that of the Far North Coastal sample. While all three IQRs overlap, the Far North Coastal group shows the highest values, followed by the Coastal/Bay sample, and lastly the Inland River sample. The whiskers of the Inland River sample are much more widely distributed than are those of the other two groups, and both the Coastal/Bay and Inland River IQRs are skewed closer to the 10th percentiles than is the Far North Coastal IQR.

All median values of female humeral I_x/I_y (Figure 34) are above 1.0, suggesting greater A-P than M-L bending rigidity in all three locations. Median values of the Far North Coastal and Inland River samples are almost identical and just below that of the Coastal/Bay group. While all IQRs overlap, the IQR of the Inland River group is more narrowly distributed than that of the Far North Coastal or Coastal/Bay samples. Finally, the Far North Coastal IQR is skewed towards the lower whisker more so than the other two groups.

Table 16. Summary Statistics, Male Humeri

Site Type		TA	CA	MA	I_x	I_y	J	I_x/I_y
Coastal/Bay	N	10	10	10	10	10	10	10
	Mean	1066.47	740.28	326.18	3802.63	3806.59	7609.23	1.00
	Std. Deviation	133.63	115.04	96.25	924.62	891.72	1734.01	0.14
	Std. Error of Mean	42.26	36.38	30.43	292.39	281.98	548.34	0.04
	Variance	17859.23	13236.19	9265.44	854923.29	795170.61	3006813.22	0.02
Far North Coastal	N	23	23	23	23	23	23	23
	Mean	1047.59	654.41	393.17	3563.31	3469.86	7033.17	1.03
	Std. Deviation	110.90	91.92	114.81	682.76	630.44	1261.64	0.11
	Std. Error of Mean	23.12	19.16	23.94	142.36	131.45	263.07	0.02
	Variance	12299.59	8451.00	13182.42	466163.88	397455.59	1591741.50	0.01
Inland River	N	44	44	44	44	44	44	44
	Mean	963.43	700.84	262.58	3385.82	3210.14	6595.96	1.05
	Std. Deviation	205.17	143.64	122.26	1385.59	1223.71	2583.35	0.10
	Std. Error of Mean	30.93	21.65	18.43	208.88	184.48	389.45	0.01
	Variance	42097.31	20633.50	14948.45	1919887.12	1497474.67	6673735.94	0.01
Total	N	77	77	77	77	77	77	77
	Mean	1001.95	692.10	309.85	3492.97	3365.18	6858.15	1.03
	Std. Deviation	177.56	128.32	129.61	1158.96	1048.49	2171.64	0.11
	Std. Error of Mean	20.23	14.62	14.77	132.07	119.48	247.48	0.01
	Variance	31530.96	16467.53	16800.72	1343196.30	1099343.86	4716061.65	0.01

Table 17. Summary Statistics, Female Humeri

Site Type		TA	CA	MA	I_x	I_y	J	I_x/I_y
Coastal/Bay	N	18	18	18	18	18	18	18
	Mean	904.92	591.33	313.58	2809.34	2289.92	5099.27	1.23
	Std. Deviation	128.61	114.95	119.65	793.46	579.33	1314.70	0.19
	Std. Error of Mean	30.31	27.09	28.20	187.02	136.54	309.87	0.04
	Variance	16540.80	13214.42	14316.71	629584.07	335626.07	1728449.27	0.03
Far North Coastal	N	17	17	17	17	17	17	17
	Mean	976.60	591.69	384.91	3053.06	2620.45	5673.52	1.17
	Std. Deviation	134.14	71.53	112.88	749.23	584.26	1267.23	0.16
	Std. Error of Mean	32.53	17.34	27.37	181.71	141.70	307.34	0.04
	Variance	17994.44	5116.81	12742.27	561350.14	341368.55	1605881.45	0.02
Inland River	N	55	55	55	55	55	55	55
	Mean	875.25	614.54	260.71	2682.05	2339.60	5021.66	1.16
	Std. Deviation	129.46	115.21	100.58	718.24	692.25	1377.10	0.14
	Std. Error of Mean	17.45	15.53	13.56	96.84	93.34	185.68	0.01
	Variance	16761.57	13275.54	10118.00	515881.77	479218.40	1896416.96	0.02
Total	N	90	90	90	90	90	90	90
	Mean	900.33	605.58	294.74	2777.59	2382.72	5160.31	1.17
	Std. Deviation	134.41	107.82	116.21	744.66	655.68	1353.67	0.16
	Std. Error of Mean	14.16	11.36	12.24	78.49	69.11	142.68	.01
	Variance	18068.55	11626.32	13505.08	554520.71	429925.82	1832429.23	0.02
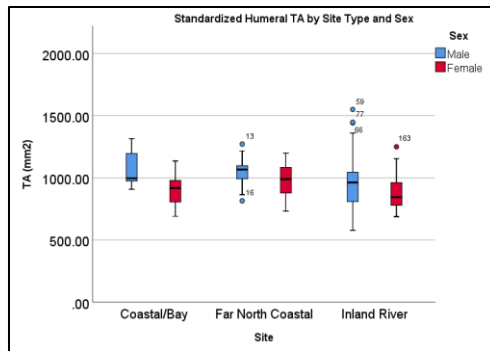
Figure 28. Humeral TA
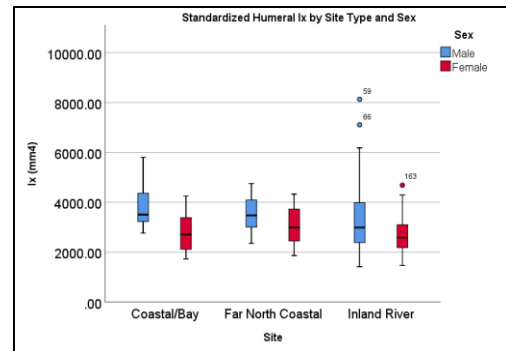
Figure 31. Humeral I$_x$
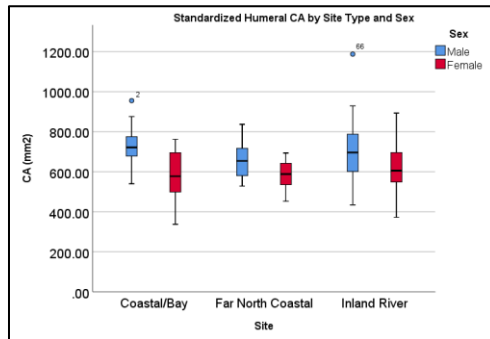
Figure 29. Humeral CA
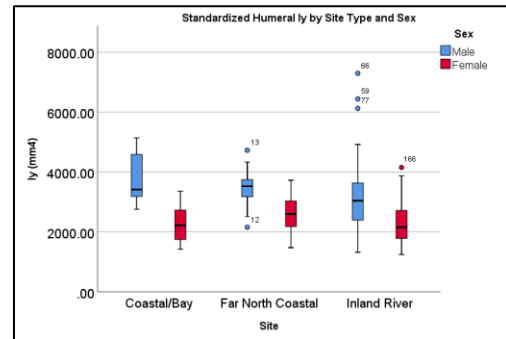
Figure 32. Humeral I$_y$
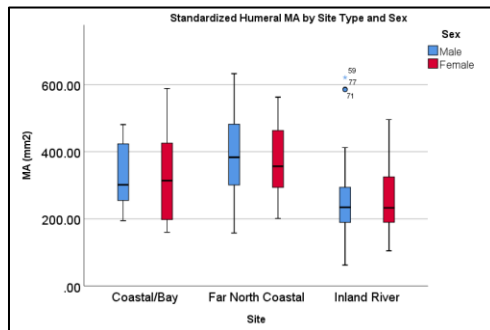
Figure 30. Humeral MA
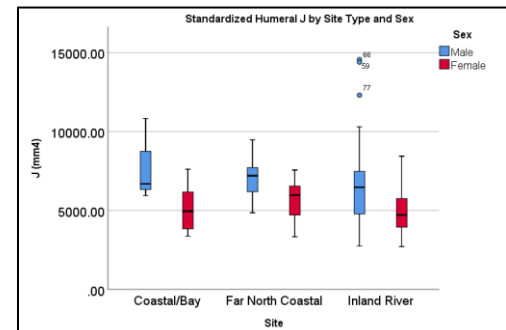
Figure 33. Humeral J
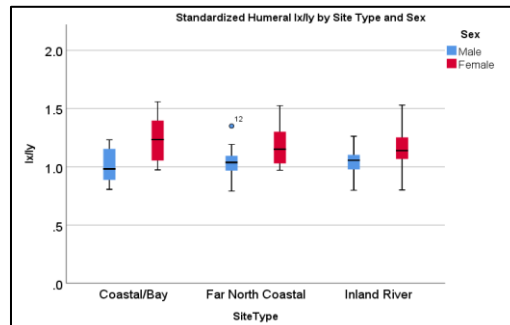
Figure 34. Humeral I$_x$/I$_y$

Figures 28-34. Standardized Humeral Cross-Sectional Properties by Site Type and Sex

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Male Radii. Summary statistics for male radial analyses are presented in Table 18. Figures 35-41 present male radial TA, CA, MA, I_x, I_y, J, and I_x/I_y by location, respectively (all measurements standardized). Median male radial TA (Figure 35) is greatest among the Coastal/Bay site and lowest among the Far North Coastal sample. While the Inland River and Far North Coastal IQRs are similar, that of the Coastal/Bay group has greater numerical value and does not overlap with either the Far North Coastal or Inland River IQRs. Additionally, the Coastal/Bay IQR is skewed towards the 90th percentile. Three outliers are present: one above the 90th percentile among the Inland River site and one outside of both the 10th and 90th percentiles within the Far North Coastal sample.

The Coastal/Bay group also shows the highest median value of male radial CA (Figure 36), while the median is again lowest among the Far North Coastal site. While the upper half of the Far North Coastal IQR overlaps with the lower half of the Inland River IQR, that of the Coastal/Bay site only just overlaps with the uppermost portion of the Inland River IQR. The Coastal/Bay IQR is additionally more narrowly distributed than are the other two and is skewed towards the 10th percentile. An outlier well below the lower whisker is present among the Coastal/Bay sample, and another outlier just above the upper whisker is present among the Far North Coastal site.

Median values of male radial MA (Figure 37) are similar between the Coastal/Bay and Far North Coastal samples while that of the Inland River sample shows the lowest value. The Coastal/Bay IQR completely overlaps that of the Far North Coastal site, which in turn only overlaps with the upper portion of the Inland River IQR. Both the Far North

Coastal and Coastal/Bay IQRs are more skewed towards the lower whisker than is the centrally distributed Inland River IQR. A single outlier is present above the 90th percentile within the Inland River site.

Median male radial I_x is greatest in the Coastal/Bay group and appears approximately equal between the Far North Coastal and Inland River samples (Figure 38). While the Far North Coastal and Inland River IQRs overlap and have similar ranges, that of the Coastal/Bay group has greater value and does not overlap with the other two IQRs. Additionally, the Coastal/Bay IQR is more sharply skewed towards the 90th percentile than are the other two IQRs. The Coastal/Bay sample demonstrates a single outlier below the 10th percentile while the Inland River group shows two outliers above the 90th percentile.

The Coastal/Bay sample shows the greatest median value of male radial I_y while the Far North Coastal group shows the lowest value (Figure 39). The Inland River and Far North Coastal IQRs show substantial overlap, but only the lowermost portion of the Coastal/Bay IQR overlaps with the uppermost portion of the Inland River IQR. The Inland River IQR is skewed towards the lower whisker, while the other IQRs are more centrally-distributed between whiskers. The Far North Coastal sample contains one outlier above the 90th percentile while the Inland River group shows two outliers above the upper whisker.

The median value of Coastal/Bay male radial J (Figure 40) appears well above that of the other two samples. Additionally, the Coastal/Bay IQR shows higher numerical value and only just overlaps with a portion of the Inland River IQR and does not overlap

with the Far North Coastal IQR. The Coastal/Bay IQR is also more heavily skewed towards the 90th percentile, while both the Inland River and Far North Coastal IQRs are more centrally positioned. Three outliers are present: one above the upper whisker among the Far North Coastal sample and two above the upper whisker among the Inland River sample.

Male radial I_x/I_y (Figure 41) is less than 1.0 in all samples, suggesting greater M-L than A-P bending rigidity across locations. Median value is greatest among the Far North Coastal and lowest among the Coastal/Bay samples. All three IQRs overlap to some degree, although that of the Inland River group shows a narrower range than those of the Coastal/Bay or Far North Coastal sites. Additionally, the Coastal/Bay and Far North Coastal groups show IQRs more closely skewed to the 90th percentile than does the Inland River sample. A single outlier above the upper whisker is present among the Inland River site.

Female Radii. Table 19 shows summary statistic for female radial analyses, while Figures 35-41 present box plots of female radial TA, CA, MA, I_x, I_y, J, and I_x/I_y, respectively, by location (all measurements standardized). Median values of female radial TA (Figure 35) are similar between samples. Additionally, all three IQRs overlap, although the Far North Coastal is the most narrowly distributed while the Coastal/Bay IQR is the most widely distributed of the three. While the Far North Coastal IQR is centrally skewed between whiskers, that of the Coastal/Bay site is skewed towards the 90th percentile, and that of the Inland River group is skewed towards the 10th percentile. The Inland River group shows one outlier well above the 90th percentile.

Median values of female radial CA (Figure 36) are again roughly similar between all three samples, with the Inland River median slightly greater than the other two. All IQRs overlap, and the Far North Coastal IQR is less widely distributed than are the other two. The Coastal/Bay IQR is skewed towards the lower whisker while the other two are more centrally distributed between whiskers.

Median value of female radial MA is highest in the Coastal/Bay group and lowest in the Inland River sample (Figure 37). Although all IQRs overlap with one another, the Coastal/Bay IQR is the most widely distributed of the three. While the Far North Coastal IQR is slightly skewed towards the 90th percentile, the Inland River IQR is heavily skewed towards the lower whisker. The Far North Coastal group contains one outlier well above the 90th percentile.

Median female radial I_x appears equivalent between all samples (Figure 38). Furthermore, the three IQRs all show substantial overlap, although the Far North Coastal IQR has a lower range than the Coastal/Bay and Inland River IQRs. All IQRs show different distributions between the 10th and 90th percentiles; the Coastal/Bay IQR is centrally positioned, the Far North Coastal IQR is skewed towards the upper whisker, and the Inland River IQR is skewed towards the lower whisker. The Far North Coastal sample contains one outlier above the 90th percentile while the Inland River group has two outliers above the 90th percentile.

Median female radial I_y is also approximately equal between samples (Figure 39). All sample IQRs overlap substantially and have similar ranges. While the Coastal/Bay and Far North Coastal IQRs appear centrally positioned between whiskers, that of the

Inland River sample is skewed towards the lower whisker. One outlier is present above the 90th percentile within the Inland River group.

The Far North Coastal and Inland River groups show equal median values of female radial J (Figure 40), while that of the Coastal/Bay sample appears slightly lower. All IQRs overlap, with that of the Far North Coastal site being the most narrowly distributed and the Coastal/Bay the most widely distributed. The Inland River IQR appears slightly skewed towards the 10th percentile. That sample also contains one outlier above the upper whisker.

All median values of female radial I_x/I_y (Figure 41) are below 1.0, suggesting greater M-L than A-P bending rigidity in all locations. The Coastal/Bay and Far North Coastal groups show similar median values, with the Inland River median slightly greater than the other two. The Coastal/Bay and Far North Coastal IQRs are similar and do overlap with the Inland River IQR, although the latter is less widely distributed than are the former. Both the Inland River and Coastal/Bay IQRs are skewed towards the lower whisker while the Far North Coastal IQR is more centrally located between the 10th and 90th percentiles.

Table 18. Summary Statistics, Male Radii

Site Type		TA	CA	MA	I_x	I_y	J	I_x/I_y
Coastal/Bay	N	10	10	10	10	10	10	10
	Mean	1023.65	787.98	235.66	2322.54	4211.95	6534.50	0.56
	Std. Deviation	143.06	105.39	86.03	508.81	1161.38	1588.52	0.08
	Std. Error of Mean	45.23	33.33	27.20	160.90	367.26	502.33	0.02
	Variance	20466.50	11109.02	7401.98	258891.21	1348824.04	2523404.11	0.007
Far North Coastal	N	22	22	22	22	22	22	22
	Mean	863.19	625.68	237.50	1840.32	2722.07	4562.39	0.67
	Std. Deviation	137.13	127.04	63.19	620.95	856.92	1437.54	0.10
	Std. Error of Mean	29.23	27.08	13.47	132.38	182.69	306.48	0.02
	Variance	18807.29	16141.36	3993.75	385590.53	734326.94	2066543.30	0.01
Inland River	N	41	41	41	41	41	41	41
	Mean	901.03	712.63	188.39	1964.70	3294.02	5258.72	0.61
	Std. Deviation	154.70	121.25	70.09	637.61	1236.29	1825.57	0.09
	Std. Error of Mean	24.16	18.93	10.94	99.57	193.07	285.10	0.01
	Variance	23933.76	14703.30	4912.80	406553.84	1528425.62	3332733.60	0.009
Total	N	73	73	73	73	73	73	73
	Mean	906.42	696.75	209.67	1976.23	3247.39	5223.63	0.62
	Std. Deviation	154.39	130.79	73.53	626.94	1202.78	1772.75	0.10
	Std. Error of Mean	18.07	15.30	8.60	73.37	140.77	207.48	0.01
	Variance	23836.47	17107.88	5407.84	393065.66	1446686.14	3142650.56	0.01

Table 19. Summary Statistics, Female Radii

Site Type		TA	CA	MA	I_x	I_y	J	I_x/I_y
Coastal/Bay	N	13	13	13	13	13	13	13
	Mean	941.19	673.21	267.98	1869.45	3318.44	5187.90	0.57
	Std. Deviation	223.22	180.64	128.31	812.90	1487.89	2231.76	0.11
	Std. Error of Mean	61.91	50.10	35.58	225.46	412.66	618.98	0.03
	Variance	49828.84	32633.58	16465.42	660821.24	2213823.98	4980778.32	0.01
Far North Coastal	N	14	14	14	14	14	14	14
	Mean	948.01	694.19	253.81	1845.21	3427.28	5272.50	0.55
	Std. Deviation	149.24	118.08	109.71	510.30	1145.85	1608.94	0.09
	Std. Error of Mean	39.88	31.56	29.32	136.38	306.24	430.00	0.02
	Variance	22273.01	13944.97	12037.24	260407.55	1312989.92	2588702.06	0.009
Inland River	N	47	47	47	47	47	47	47
	Mean	930.77	713.53	217.23	1905.53	3211.52	5117.05	0.60
	Std. Deviation	179.80	163.39	112.80	672.65	1195.70	1834.79	0.08
	Std. Error of Mean	26.22	23.83	16.45	98.11	174.41	267.63	0.01
	Variance	32329.00	26699.14	12723.98	452464.37	1429712.84	3366479.81	0.008
Total	N	74	74	74	74	74	74	74
	Mean	935.86	702.79	233.07	1887.78	3271.12	5158.91	0.59
	Std. Deviation	180.49	157.84	115.45	663.87	1227.19	1845.22	0.09
	Std. Error of Mean	20.98	18.34	13.42	77.17	142.65	214.50	0.01
	Variance	32579.25	24916.15	13329.11	440726.72	1506014.01	3404855.48	0.009
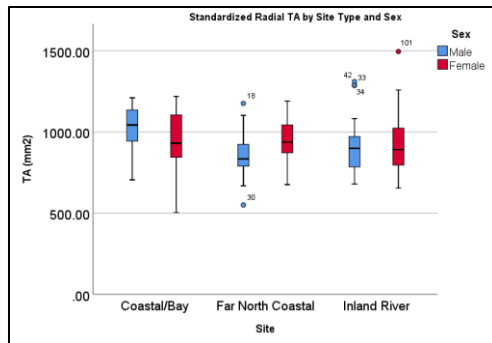
Figure 35. Radial TA
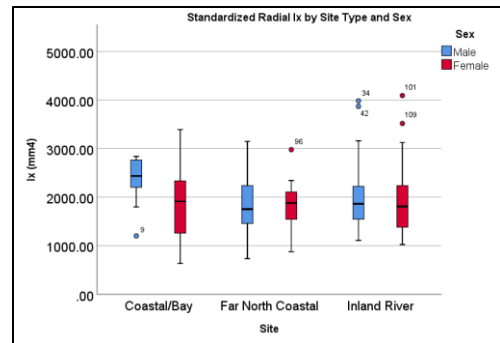
Figure 38. Radial I_x
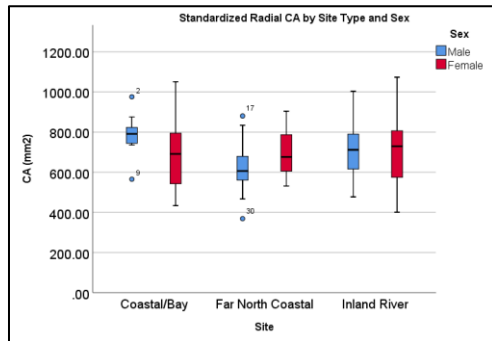
Figure 36. Radial CA
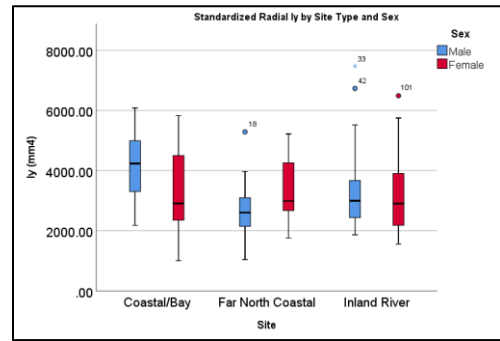
Figure 39. Radial I_y
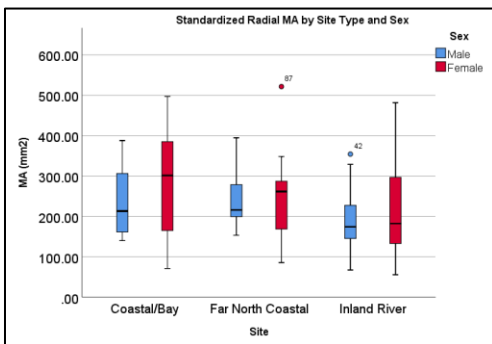
Figure 37. Radial MA
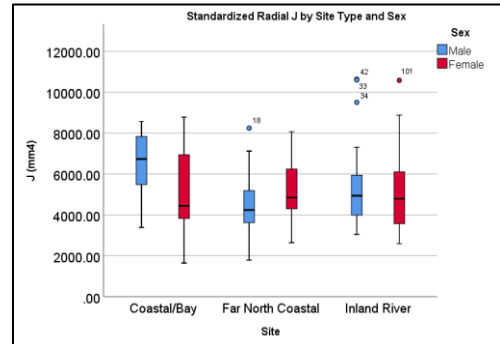
Figure 40. Radial J
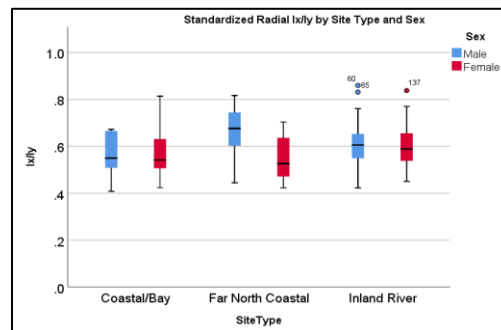
Figure 41. Radial I_x/I_y

Figures 35-41. Standardized Radial Cross-Sectional Properties by Site Type and Sex

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Unilateral Statistical Analyses – MANOVA

Table 20 presents the results of MANOVA tests of male femoral TA, CA, MA, I_x, I_y, and J. The null hypothesis of all comparisons is that there is no significant difference in the given variable between site types.

TA. Results of the Coastal/Bay – Far North Coastal ($p \leq 0.001$), Coastal/Bay – Inland River ($p = 0.016$), and Far North Coastal – Inland River ($p = 0.028$) comparisons are all significant. The null hypothesis is rejected in all instances. Far North Coastal TA is significantly greater than Inland River TA, which is in turn significantly greater than Coastal/Bay TA.

CA. Results of the Coastal/Bay – Inland River ($p \leq 0.001$) and the Far North Coastal – Inland River ($p = 0.029$) comparisons are significant. The null hypothesis is rejected in these cases; Inland River male femoral CA is significantly greater than that of either the Coastal/Bay and Far North Coastal samples. Results of the Coastal/Bay – Far North Coastal comparison are not significant ($p = 0.144$), indicating no significant difference in male femoral CA between these groups and supporting the null hypothesis.

MA. Results of the Coastal/Bay – Far North Coastal ($p = 0.002$) and the Far North Coastal – Inland River ($p \leq 0.001$) analyses are significant. The null hypothesis is rejected in these cases; the Far North Coastal sample shows significantly greater male femoral MA than the Coastal/Bay and Inland River groups. However, the Coastal/Bay – Inland River comparison did not produce significant results ($p = 0.353$).

I_x. The Coastal/Bay – Far North Coastal ($p \leq 0.001$) and the Coastal/Bay – Inland River ($p = 0.001$) analyses produced significant results. In these instances, the null

hypothesis is rejected. Coastal/Bay I_x is significantly less than Far North Coastal or Inland River I_x. However, no significant differences in I_x were identified between the Far North Coastal and Inland River samples ($p = 0.075$).

I_y. Only the Coastal/Bay – Far North Coastal analysis generated significant results ($p = 0.028$). The null hypothesis in this case is rejected, and Coastal/Bay I_y is significantly less than Far North Coastal I_y. Neither the Coastal/Bay – Inland River ($p = 0.245$) or the Far North Coastal – Inland River ($p = 0.173$) comparisons indicate any significant differences in male femoral I_y between those samples.

J. MANOVA tests indicate significant results of the Coastal/Bay – Far North Coastal ($p = 0.001$) and Coastal/Bay – Inland River ($p = 0.014$) analyses. The null hypothesis is rejected; Coastal/Bay J is significantly less than that of the Far North Coastal and Inland River samples. However, there is not a significant difference in male femoral J between the Far North Coastal and Inland River groups ($p = 0.079$).

Table 20. MANOVA Results, Male Femora

Variable	Site Type Comparison	Mean Difference	Sig. (p)
TA	Coastal/Bay – Far North Coastal	-152.66	**0.000**
	Coastal/Bay – Inland River	-70.21	**0.016**
	Far North Coastal – Inland River	82.44	**0.028**
CA	Coastal/Bay – Far North Coastal	-43.87	0.144
	Coastal/Bay – Inland River	-96.82	**0.000**
	Far North Coastal – Inland River	-52.95	**0.029**
MA	Coastal/Bay – Far North Coastal	-108.79	**0.002**
	Coastal/Bay – Inland River	26.60	0.353
	Far North Coastal – Inland River	135.39	**0.000**
I_x	Coastal/Bay – Far North Coastal	-7.59	**0.000**
	Coastal/Bay – Inland River	-4.24	**0.001**
	Far North Coastal – Inland River	-3.34	0.075
I_y	Coastal/Bay – Far North Coastal	-3.84	**0.028**
	Coastal/Bay – Inland River	-1.86	0.245
	Far North Coastal – Inland River	1.98	0.173
J	Coastal/Bay – Far North Coastal	-11.43	**0.001**
	Coastal/Bay – Inland River	-6.10	**0.014**
	Far North Coastal – Inland River	5.33	0.079

Table 21 presents the results of MANOVA tests of female femoral TA, CA, MA, I_x, I_y, and J. The null hypothesis of all comparisons is that there is no significant difference in the given variable between site types.

TA. Results of the Coastal/Bay – Far North Coastal ($p \leq 0.001$) and the Far North Coastal – Inland River ($p \leq 0.001$) analyses are significant. The null hypothesis is rejected in these cases, indicating that Far North Coastal female femoral TA is significantly greater than the Inland River and Coastal/Bay groups. There is no

significant difference in TA between the Coastal/Bay and Inland River samples

(p = 0.974); the null hypothesis is supported in that comparison.

CA. The results of the Coastal/Bay – Far North Coastal (p = 0.196), the

Coastal/Bay – Inland River (p = 0.748), and the Far North Coastal – Inland River

(p = 0.354) comparisons are all non-significant. The null hypothesis is supported in all

comparisons. There are no significant differences in female femoral CA between site

types.

MA. The only significant result is between the Far North Coastal and Inland River

samples (p = 0.011). The null hypothesis is rejected in this case, and Far North Coastal

MA is significantly greater than Inland River MA. The Coastal/Bay comparison with

both the Far North Coastal (p = 0.081) and Inland River (p = 0.790) samples did not

generate significant results, indicating support for the null hypothesis.

I_x. Results of the Coastal/Bay – Far North Coastal (p = 0.011) and the Far North

Coastal – Inland River (p = 0.003) analyses are significant. In these instances, the null

hypothesis is rejected; Far North Coastal female femoral I_x is significantly greater than

both Inland River and Coastal/Bay I_x. The null hypothesis is supported between the

Coastal/Bay and Inland River samples because MANOVA results are non-significant

(p = 0.945).

I_y. MANOVA analysis found significant results between the Coastal/Bay and Far

North Coastal samples (p = 0.014) and between the Far North Coastal and Inland River

samples (p = 0.022). The null hypothesis is thus rejected; Far North Coastal I_y is

significantly greater than that of the Coastal/Bay and Inland River groups. There is no

significant difference in female femoral I_y between the Coastal/Bay and Inland River samples (p = 0.837).

J. Results are significant in the Coastal/Bay – Far North Coastal (p = 0.006) and the Far North Coastal – Inland River (p = 0.004) comparisons. Female femoral J is significantly greater among the Far North Coastal sample than both the Inland River and Coastal/Bay samples, and the null hypothesis is rejected in these instances. However, the null hypothesis is supported between the Coastal/Bay and Inland River groups because MANOVA results were non-significant (p = 0.995).

Table 21. MANOVA Results, Female Femora

Variable	Site Type Comparison	Mean Difference	Sig. (p)
TA	Coastal/Bay – Far North Coastal	-104.77	**0.000**
	Coastal/Bay – Inland River	-3.74	0.974
	Far North Coastal – Inland River	101.03	**0.000**
CA	Coastal/Bay – Far North Coastal	-47.46	0.196
	Coastal/Bay – Inland River	-16.54	0.748
	Far North Coastal – Inland River	30.91	0.354
MA	Coastal/Bay – Far North Coastal	-57.31	0.081
	Coastal/Bay – Inland River	12.79	0.790
	Far North Coastal – Inland River	70.11	**0.011**
I_x	Coastal/Bay – Far North Coastal	-3.95	**0.011**
	Coastal/Bay – Inland River	0.28	0.945
	Far North Coastal – Inland River	4.23	**0.003**
I_y	Coastal/Bay – Far North Coastal	-3.43	**0.014**
	Coastal/Bay – Inland River	-0.42	0.837
	Far North Coastal – Inland River	3.00	**0.022**
J	Coastal/Bay – Far North Coastal	-7.38	**0.006**
	Coastal/Bay – Inland River	-0.14	0.995
	Far North Coastal – Inland River	7.24	**0.004**

Table 22 presents the results of MANOVA tests of male tibial TA, CA, MA, I_x, I_y, and J. The null hypothesis of all comparisons is that there is no significant difference in the given variable between site types.

TA. Results of the Coastal/Bay – Far North Coastal, (p = 0.736), Coastal/Bay – Inland River (p = 0.984), and Far North Coastal – Inland River (p = 0.702) analyses are all non-significant. The null hypothesis is supported in all cases, indicating no significant differences in male tibial TA between site categories.

CA. Only results of the Far North Coastal – Inland River analysis are significant (p = 0.003). The null hypothesis is rejected, and Far North Coastal CA is significantly less than Inland River CA. The Coastal/Bay – Far North Coastal (p = 0.071) and Coastal/Bay – Inland River (p = 0.158) analyses both generated non-significant results, indicating no significant difference in CA between the Coastal/Bay and other samples.

MA. As with CA, the only significant results are between the Far North Coastal and Inland River groups (p ≤ 0.001). The null hypothesis is again rejected, although in this case Far North Coastal MA is significantly greater than Inland River MA. Analyses between the Coastal/Bay and Far North Coastal and between the Coastal/Bay and Inland River groups produced nonsignificant results (p = 0.071 and p = 0.554, respectively).

I_x. Results of the Coastal/Bay – Far North Coastal (p = 1.000), Coastal/Bay – Inland River (p = 0.615), and Far North Coastal – Inland River (p = 0.464) analyses are all non-significant. The null hypothesis is supported in all cases, indicating no significant differences in male tibial I_x between site categories.

I$_y$. Results of the Coastal/Bay – Far North Coastal (p = 0.738), Coastal/Bay –

Inland River (p = 0.993), and Far North Coastal – Inland River (p = 0.768) analyses are

all non-significant. The null hypothesis is supported in all cases, indicating no significant

differences in male tibial I_y between site categories.

J. Results of the Coastal/Bay – Far North Coastal (p = 0.973), Coastal/Bay –

Inland River (p = 0.754), and Far North Coastal – Inland River (p = 0.503) analyses are

all non-significant. The null hypothesis is supported in all cases, indicating no significant

differences in male tibial J between site categories.

Table 22. MANOVA Results, Male Tibiae

Variable	Site Type Comparison	Mean Difference	Sig. (p)
TA	Coastal/Bay – Far North Coastal	-20.62	0.736
	Coastal/Bay – Inland River	-4.10	0.984
	Far North Coastal – Inland River	16.52	0.702
CA	Coastal/Bay – Far North Coastal	31.69	0.071
	Coastal/Bay – Inland River	-23.40	0.158
	Far North Coastal – Inland River	-55.10	**0.003**
MA	Coastal/Bay – Far North Coastal	-52.31	0.071
	Coastal/Bay – Inland River	19.30	0.554
	Far North Coastal – Inland River	71.62	**0.000**
I_x	Coastal/Bay – Far North Coastal	-0.0012	1.000
	Coastal/Bay – Inland River	-1.70	0.615
	Far North Coastal – Inland River	-1.70	0.464
I_y	Coastal/Bay – Far North Coastal	0.54	0.738
	Coastal/Bay – Inland River	0.07	0.993
	Far North Coastal – Inland River	-0.46	0.768
J	Coastal/Bay – Far North Coastal	0.54	0.973
	Coastal/Bay – Inland River	-1.63	0.754
	Far North Coastal – Inland River	-2.17	0.503

Table 23 presents the results of MANOVA tests of female tibial TA, CA, MA, I_x, I_y, and J. The null hypothesis of all comparisons is that there is no significant difference in the given variable between site types.

TA, CA, MA, I_x, I_y, and J. MANOVA analyses found no significant results (p ≤ 0.05) between site categories among any variable. The null hypothesis is supported in all instances. There are no significant differences in female tibial TA, CA, MA, I_x, I_y, or J between site types.

Table 23. MANOVA Results, Female Tibiae

Variable	Site Type Comparison	Mean Difference	Sig. (p)
TA	Coastal/Bay – Far North Coastal	-29.13	0.574
	Coastal/Bay – Inland River	23.33	0.265
	Far North Coastal – Inland River	52.46	0.165
CA	Coastal/Bay – Far North Coastal	-30.02	0.423
	Coastal/Bay – Inland River	-16.66	0.651
	Far North Coastal – Inland River	13.35	0.770
MA	Coastal/Bay – Far North Coastal	0.88	0.999
	Coastal/Bay – Inland River	39.99	0.079
	Far North Coastal – Inland River	39.10	0.163
I_x	Coastal/Bay – Far North Coastal	-1.42	0.708
	Coastal/Bay – Inland River	0.55	0.873
	Far North Coastal – Inland River	1.97	0.466
I_y	Coastal/Bay – Far North Coastal	-0.10	0.993
	Coastal/Bay – Inland River	0.86	0.338
	Far North Coastal – Inland River	0.96	0.433
J	Coastal/Bay – Far North Coastal	-1.52	0.824
	Coastal/Bay – Inland River	1.41	0.648
	Far North Coastal – Inland River	2.94	0.437

Table 24 presents the results of MANOVA tests of male humeral TA, CA, MA, I_x, I_y, and J. The null hypothesis of all comparisons is that there is no significant difference in the given variable between site types.

MA. Results of the Far North Coastal – Inland River analysis ($p \leq 0.001$) are the only significant results among male humeri. In this case, the null hypothesis is rejected, and Far North Coastal MA is significantly greater than Inland River MA. Analysis of MA between the Coastal/Bay and Far North Coastal ($p = 0.218$) and between the Coastal/Bay and Inland River ($p = 0.205$) groups produced non-significant results.

TA, CA, I_x, I_y, and J. MANOVA analysis found no significant results ($p \leq 0.05$) between site categories among these variables. The null hypothesis is supported in these instances. There are no significant differences in male humeral TA, CA, I_x, I_y, or J between site categories.

Table 24. MANOVA Results, Male Humeri

Variable	Site Type Comparison	Mean Difference	Sig. (p)
TA	Coastal/Bay – Far North Coastal	18.87	0.919
	Coastal/Bay – Inland River	103.04	0.146
	Far North Coastal – Inland River	84.16	0.082
CA	Coastal/Bay – Far North Coastal	85.87	0.128
	Coastal/Bay – Inland River	39.44	0.629
	Far North Coastal – Inland River	-46.42	0.251
MA	Coastal/Bay – Far North Coastal	-66.99	0.218
	Coastal/Bay – Inland River	63.59	0.205
	Far North Coastal – Inland River	130.59	**0.000**
I_x	Coastal/Bay – Far North Coastal	239.32	0.747
	Coastal/Bay – Inland River	416.81	0.490
	Far North Coastal – Inland River	177.48	0.763
I_y	Coastal/Bay – Far North Coastal	336.72	0.541
	Coastal/Bay – Inland River	596.45	0.208
	Far North Coastal – Inland River	259.72	0.489
J	Coastal/Bay – Far North Coastal	576.05	0.621
	Coastal/Bay – Inland River	1013.26	0.310
	Far North Coastal – Inland River	437.20	0.623

Table 25 presents the results of MANOVA tests of female humeral TA, CA, MA, I_x, I_y, and J. The null hypothesis of all comparisons is that there is no significant difference in the given variable between site types.

TA. Results of the Far North Coastal – Inland River analysis are significant ($p = 0.028$). The null hypothesis is thus rejected in this instance; Far North Coastal TA is significantly greater than that of the Inland River sample. Results of the Coastal/Bay and Far North Coastal ($p = 0.255$) and the Coastal/Bay – Inland River ($p = 0.677$) analyses are non-significant, prompting support for the null hypothesis.

MA. As with TA, results of the Far North Coastal – Inland River comparison are significant (p = 0.001). The null hypothesis is again rejected, and Far North Coastal MA is significantly greater than Inland River MA. The comparison of MA between the Coastal/Bay sample and both the Far North Coastal (p = 0.180) and the Inland River (p = 0.229) samples are not significant.

CA, I_x, I_y, and J. MANOVA analysis found no significant results ($p \leq 0.05$) between site categories among these variables. The null hypothesis is supported in these instances. There are no significant differences in female humeral CA, I_x, I_y, or J between site categories.

Table 25. MANOVA Results, Female Humeri

Variable	Site Type Comparison	Mean Difference	Sig. (p)
TA	Coastal/Bay – Far North Coastal	-71.68	0.255
	Coastal/Bay – Inland River	29.66	0.677
	Far North Coastal – Inland River	101.35	**0.028**
CA	Coastal/Bay – Far North Coastal	-0.35	1.000
	Coastal/Bay – Inland River	-23.20	0.740
	Far North Coastal – Inland River	-22.85	0.592
MA	Coastal/Bay – Far North Coastal	-71.33	0.180
	Coastal/Bay – Inland River	52.87	0.229
	Far North Coastal – Inland River	124.20	**0.001**
I_x	Coastal/Bay – Far North Coastal	-243.71	0.623
	Coastal/Bay – Inland River	127.29	0.819
	Far North Coastal – Inland River	371.00	0.189
I_y	Coastal/Bay – Far North Coastal	-330.53	0.228
	Coastal/Bay – Inland River	-49.67	0.952
	Far North Coastal – Inland River	280.85	0.238
J	Coastal/Bay – Far North Coastal	-574.24	0.397
	Coastal/Bay – Inland River	77.61	0.975
	Far North Coastal – Inland River	651.86	0.183

Table 26 presents the results of MANOVA tests of male radial TA, CA, MA, I_x, I_y, and J. The null hypothesis of all comparisons is that there is no significant difference in the given variable between site types.

TA. Results of the Coastal/Bay – Far North Coastal analysis are significant ($p = 0.022$). The null hypothesis is thus rejected; Coastal/Bay TA is significantly larger than Far North Coastal TA. The Coastal/Bay – Inland River ($p = 0.074$) and the Far North Coastal – Inland River ($p = 0.582$) comparisons are not significant, indicating no significant differences in TA between the Inland River and other samples.

CA. The Coastal/Bay – Far North Coastal ($p = 0.003$) and the Far North Coastal – Inland River ($p = 0.031$) analyses are significant. The null hypothesis is rejected, and Far North Coastal CA is significantly less than both the Inland River and Coastal/Bay samples. The Coastal/Bay – Inland River analysis is not significant ($p = 0.154$), indicating no significant difference in CA between these groups.

MA. The Far North Coastal – Inland River comparison produced significant results ($p = 0.018$). The null hypothesis is thus rejected; Far North Coastal MA is significantly greater than that of the Inland River group. Neither the Coastal/Bay – Far North Coastal ($p = 0.998$) or the Coastal/Bay – Inland River ($p = 0.278$) analyses are significant; Coastal/Bay male radial MA does not significantly differ from either Far North Coastal or Inland River MA.

I_x. None of the MANOVA analyses of male radial I_x produced significant ($p \leq 0.05$) results. The null hypothesis is supported; there are no significant differences in male radial I_x between site types.

I_y. Results of the Coastal/Bay – Far North Coastal analysis are significant (p = 0.007). The null hypothesis is thus rejected; Coastal/Bay Iy is significantly greater than Far North Coastal I_y. The Coastal/Bay – Inland River (p = 0.103) and the Far North Coastal – Inland River (p = 0.089) comparisons are not significant; Inland River I_y does not significantly differ from either Coastal/Bay or Far North Coastal I_y.

J. Results of the Coastal/Bay – Far North Coastal analysis are significant (p = 0.011). The null hypothesis is thus rejected; Coastal/Bay J is significantly greater than Far North Coastal J. The Coastal/Bay – Inland River (p = 0.101) and the Far North Coastal – Inland River (p = 0.229) comparisons are not significant, suggesting that Inland River J does not significantly differ from either Far North Coastal or Coastal/Bay J.

Table 26. MANOVA Results, Male Radii

Variable	Site Type Comparison	Mean Difference	Sig. (p)
TA	Coastal/Bay – Far North Coastal	160.45	**0.022**
	Coastal/Bay – Inland River	122.61	0.074
	Far North Coastal – Inland River	-37.83	0.582
CA	Coastal/Bay – Far North Coastal	162.29	**0.003**
	Coastal/Bay – Inland River	75.34	0.154
	Far North Coastal – Inland River	-86.95	**0.031**
MA	Coastal/Bay – Far North Coastal	-1.84	0.998
	Coastal/Bay – Inland River	47.27	0.278
	Far North Coastal – Inland River	49.11	**0.018**
I_x	Coastal/Bay – Far North Coastal	482.22	0.076
	Coastal/Bay – Inland River	357.83	0.172
	Far North Coastal – Inland River	-124.38	0.735
I_y	Coastal/Bay – Far North Coastal	1489.88	**0.007**
	Coastal/Bay – Inland River	917.93	0.103
	Far North Coastal – Inland River	-571.94	0.089
J	Coastal/Bay – Far North Coastal	1972.10	**0.011**
	Coastal/Bay – Inland River	1275.77	0.101
	Far North Coastal – Inland River	-696.33	0.229

Table 27 presents the results of MANOVA tests of female radial TA, CA, MA, I_x, I_y, and J. The null hypothesis of all comparisons is that there is no significant difference in the given variable between site types.

TA, CA, MA, I_x, I_y, and J. MANOVA analysis found no significant results ($p \leq 0.05$) between site categories among any variable. The null hypothesis is supported in all instances. There are no significant differences in female radial TA, CA, MA, I_x, I_y, or J between site types.

Table 27. MANOVA Results, Female Radii

Variable	Site Type Comparison	Mean Difference	Sig. (p)
TA	Coastal/Bay – Far North Coastal	-6.82	0.995
	Coastal/Bay – Inland River	10.42	0.987
	Far North Coastal – Inland River	17.24	0.931
CA	Coastal/Bay – Far North Coastal	-20.98	0.933
	Coastal/Bay – Inland River	-40.32	0.751
	Far North Coastal – Inland River	-19.33	0.877
MA	Coastal/Bay – Far North Coastal	14.16	0.949
	Coastal/Bay – Inland River	50.74	0.417
	Far North Coastal – Inland River	36.58	0.531
I_x	Coastal/Bay – Far North Coastal	24.23	0.995
	Coastal/Bay – Inland River	-36.07	0.988
	Far North Coastal – Inland River	-60.31	0.932
I_y	Coastal/Bay – Far North Coastal	-108.84	0.976
	Coastal/Bay – Inland River	106.91	0.969
	Far North Coastal – Inland River	215.76	0.815
J	Coastal/Bay – Far North Coastal	-84.60	0.993
	Coastal/Bay – Inland River	70.84	0.994
	Far North Coastal – Inland River	155.44	0.950

Unilateral Statistical Analyses – Nonparametric Tests

Table 28 shows the results of nonparametric Kruskal-Wallis tests used to identify any significant differences in the ratio of I_x to I_y (I_x/I_y) between site types of each bone by sex. The null hypothesis of all tests assumes that the distribution of I_x/I_y is the same across site categories.

Results of the Kruskal-Wallis test for male femora are significant (H = 6.787; p = 0.034). The null hypothesis in this case is rejected, signifying significant differences in the distribution of male femoral I_x/I_y between site types. A breakdown of male femoral

results shows significant differences between the Coastal/Bay and Inland River

(H = -15.689; p = 0.030) and between the Coastal/Bay and Far North Coastal

(H = -20.735; p = 0.011) samples. The null hypothesis is rejected in these cases, and

Coastal/Bay I_x/I_y is significantly less than both Far North Coastal and Inland River I_x/I_y.

However, there is no significant difference between the Inland River and Far North

Coastal samples (H = 5.046; p = 0.412), and the null hypothesis in this comparison is

supported.

The only other significant difference in I_x/I_y is within the male radial sample

(H = 10.004; p = 0.007). The null hypothesis is rejected; there are significant differences

in the distribution of male radial I_x/I_y between site types. A breakdown of these results

finds significant differences between the Coastal/Bay and Far North Coastal

(H = -23.409; p = 0.004) and between the Inland River and Far North Coastal

(H = 13.714; p = 0.014) samples. The null hypothesis is thus rejected; Far North Coastal

I_x/I_y is significantly greater than both Inland River and Coastal/Bay I_x/I_y. Results between

the Coastal/Bay and Inland River samples are not significant (H = -9.695; p= 0.195),

prompting support for the null hypothesis.

Results of the nonparametric Kruskal-Wallis tests for the distribution of I_x/I_y

between site types of female femora (H = 3.070; p = 0.215), male tibiae (H = 2.100;

p = 0.350), female tibiae (H = 0.820; p = 0.664), male humeri (H = 1.124; p = 0.570),

female humeri (H = 1.406; p = 0.495), and female radii (H = 3.611; p = 0.164) are all

nonsignificant. In these cases, the null hypothesis of equal distribution is supported.

There is no significant difference in the distribution of I_x/I_y among these samples.

Table 28. Kruskal-Wallis Results, Femoral, Tibial, Humeral, and Radial I_x/I_y

Variable	Test Statistic (H)	Sig. (p)	Pairwise Comparison[1]	Test Statistic (H)	Sig. (p)
Male Femoral I_x/I_y	6.787	**0.034**			
	---	---	Coastal/Bay – Inland River	-15.689	**0.030**
	---	---	Coastal/Bay – Far North Coastal	-20.735	**0.011**
	---	---	Inland River – Far North Coastal	5.046	0.412
Female Femoral I_x/I_y	3.070	0.215		---	---
Male Tibial I_x/I_y	2.100	0.350		---	---
Female Tibial I_x/I_y	0.820	0.664		---	---
Male Humeral I_x/I_y	1.124	0.570		---	---
Female Humeral I_x/I_y	1.406	0.495		---	---
Male Radial I_x/I_y	10.004	**0.007**		---	---
	---	---	Coastal/Bay – Inland River	-9.695	0.195
	---	---	Coastal/Bay – Far North Coastal	-23.409	**0.004**
	---	---	Inland River – Far North Coastal	13.714	**0.014**
Female Radial I_x/I_y	3.611	0.164		---	---

Descriptive Statistics: Analyses of Bilateral Asymmetry

Male Humeri. Summary statistics of male humeral bilateral asymmetry analyses are shown in Table 29, and Figures 42-48 present box plots of male humeral TA, CA, MA, I_x, I_y, J, and I_x/I_y asymmetry percentages. The highest median value of male humeral TA asymmetry is among the Far North Coastal sample while the lowest is among the Coastal/Bay sample (Figure 42). The Coastal/Bay IQR has the greatest range of all IQRs, completely enveloping both the Inland River and Far North Coastal IQRs. Only the upper portion of the Inland River IQR overlaps with the lower portion of the Far North Coastal IQR. The Coastal/Bay IQR is distributed towards the 10th percentile while those of the Far North Coastal and Inland River groups are centrally positioned between whiskers. No outliers are present.

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[1] Pairwise comparisons are only performed if the initial Kruskal-Wallis test indicates a significant difference in distribution between site types.

The Far North Coastal sample shows the highest value and the Coastal/Bay sample the lowest value of male humeral CA asymmetry (Figure 43). The Coastal/Bay IQR has the greatest range of all IQRs and overlaps the Far North Coastal and Inland River IQRs, which have similar ranges and values. While the Inland River and Far North Coastal IQRs are centrally-distributed between the 10th and 90th percentiles, that of the Coastal/Bay group is skewed towards the 10th percentile. No outliers are observed.

Median male humeral MA asymmetry is greatest among the Far North Coastal group and lowest among the Coastal/Bay group (Figure 44). The Far North Coastal IQR demonstrates the greatest range and only overlaps with the upper portion of the Inland River IQR. The Inland River IQR in turn only overlaps with a portion of the Coastal/Bay IQR. All IQRs are relatively centrally positioned between upper and lower whiskers. The Inland River sample contains two outliers – one below and one above the whiskers.

The greatest median value of male humeral I_x asymmetry is found among the Far North Coastal group while the lowest is among the Coastal/Bay group (Figure 45). The IQR of the Coastal/Bay group displays the largest IQR, which completely overlaps the Inland River and Far North Coastal IQRs. The Coastal/Bay and Far North Coastal IQRs are skewed towards the lower whisker while the Inland River IQR is centrally distributed between whiskers. A single outlier below the 10th percentile is present within the Far North Coastal sample.

Median male humeral I_y asymmetry is lowest among the Coastal/Bay and highest among the Far North Coastal group (Figure 46). The Coastal/Bay group also demonstrates the greatest IQR range which overlaps substantially with the Inland River

and Far North Coastal IQRs. Both the Inland River and Coastal/Bay IQRs show some skewing towards the 10th percentile. No outliers are present.

The Far North Coastal sample demonstrates the highest median value of male humeral J asymmetry while the Coastal/Bay sample demonstrates the lowest median value (Figure 47). The IQR of the Coastal/Bay group has the greatest range and overlaps both the Inland River and Far North Coastal IQRs. The Inland River and Far North Coastal IQRs in turn overlap with approximately half of one another. The Inland River IQR is centrally distributed between whiskers, but the Coastal/Bay IQR is skewed towards the lower whisker while the Far North Coastal IQR is skewed towards the upper whisker.

Median male humeral I_x/I_y asymmetry is roughly equivalent between samples, although the Far North Coastal sample is slightly greater than the other two samples (Figure 48). The IQR of the Coastal/Bay group has the greatest range, which overlaps the Far North Coastal IQR, which in turn overlaps the Inland River IQR. The Inland River and Coastal/Bay IQRs are centrally distributed between whiskers while the Far North Coastal IQR is skewed towards the upper whisker. A single outlier is present among the Inland River sample above the 90th percentile.

Female Humeri. Summary statistics of female humeral bilateral asymmetry analyses are shown in Table 30, and Figures 42-48 present box plots of female humeral TA, CA, MA, I_x, I_y, J, and I_x/I_y asymmetry percentages. Median female humeral TA asymmetry is approximately equal between groups, with the Inland River sample appearing slightly below that of the other site types (Figure 42). All IQRs show

substantial overlap, although the Far North Coastal IQR has a lower range than either the Coastal/Bay or Inland River IQRs. Both the Far North Coastal and Coastal/Bay IQRs are heavily skewed towards the 90th percentile, and the Inland River IQR is more centrally positioned between whiskers. No outliers are present.

The Coastal/Bay group shows the greatest median value of female humeral CA asymmetry while the median values of the Far North Coastal and Inland River groups appear similar (Figure 43). The Coastal/Bay group also has the IQR with the greatest range, which completely overlaps both the Inland River and Far North Coastal IQRs. All IQRs appear centrally distributed between the 10th and 90th percentiles. Two outliers are present above the 90th percentile among the Inland River group.

The highest median value of female humeral MA asymmetry is found in the Far North Coastal sample, although median values of all site types appear roughly equivalent (Figure 44). All IQRs have similar ranges, although the Coastal/Bay IQR has lower numerical value than either the Inland River or Far North Coastal IQRs. Both the Inland River and Far North Coastal IQRs are centrally positioned between whiskers while the Coastal/Bay IQR is skewed towards the upper whisker. The Coastal/Bay sample shows one outlier above and one outlier below the whiskers, and the Inland River sample contains two outliers above and one outlier below the whiskers.

Median female humeral I$_x$ asymmetry is highest in the Coastal/Bay group and lowest in the Inland River group (Figure 45). IQR range is greatest within the Coastal/Bay group and lowest within the Far North Coastal group. All IQRs overlap to some extent, with the Coastal/Bay IQR enveloping the Inland River IQR, which in turn

envelops the Far North Coastal IQR. The Coastal/Bay and Far North Coastal IQRs show skewing towards the 90th percentile, and the Inland River IQR shows skewing towards the 10th percentile. No outliers are present.

The Coastal/Bay group shows the highest median value of female humeral I_y asymmetry, and the Inland River group shows the lowest value (Figure 46). All site IQRs have approximately similar ranges which all show substantial overlap. Furthermore, the Far North Coastal and Inland River IQRs are both centrally distributed between the upper and lower whiskers while that of the Coastal/Bay sample appears skewed towards the upper whisker. Two outliers above the 90th percentile are present – one in the Coastal/Bay and another in the Inland River sample.

The highest median value of female humeral J asymmetry is present in the Coastal/Bay sample, and median values are approximately equal between the Far North Coastal and Inland River groups (Figure 47). The IQR of the Far North Coastal group has the lowest range, which is overlapped by the Inland River IQR, which is in turn overlapped by the Coastal/Bay IQR, which demonstrates the greatest range. While both the Far North Coastal and Inland River IQRs are centrally positioned between the upper and lower whiskers, that of the Coastal/Bay sample is heavily skewed towards the 10th percentile. No outliers are observed.

Median values of female humeral I_x/I_y asymmetry are approximately equal between the Far North Coastal and Inland River groups and greatest within the Coastal/Bay sample (Figure 48). While all IQRs show substantial overlap, that of the Inland River sample has a smaller range than that of the Coastal/Bay and Far North

Coastal groups. None of the IQRs appear centrally distributed between whiskers; instead

the Coastal/Bay and Far North Coastal IQRs are skewed towards the upper whisker while

the Inland River IQR is skewed towards the lower whisker. The Inland River sample

contains one outlier above the 90th percentile.

Table 29. Bilateral Analysis Summary Statistics, Male Humeri

Site Type		TA	CA	MA	I_x	I_y	J	I_x/I_y
Coastal/Bay	N	4	4	4	4	4	4	4
	Mean	-3.52	-2.54	-12.26	-7.19	-5.67	-6.29	-1.50
	Std. Deviation	15.74	20.65	5.72	42.15	26.63	34.64	21.61
	Std. Error of Mean	7.87	10.32	2.86	21.07	13.31	17.32	10.80
	Variance	247.77	426.59	32.76	1777.07	709.63	1200.57	467.11
Far North Coastal	N	15	15	15	15	15	15	15
	Mean	6.74	5.15	10.58	11.97	12.67	12.23	-0.73
	Std. Deviation	7.28	8.24	15.37	13.86	15.87	13.89	10.26
	Std. Error of Mean	1.88	2.12	3.97	3.57	4.09	3.58	2.65
	Variance	53.12	67.90	236.46	192.20	252.07	193.19	105.47
Inland River	N	30	30	30	30	30	30	30
	Mean	0.84	3.22	-5.41	2.82	2.55	2.64	0.26
	Std. Deviation	4.50	5.80	11.17	8.84	11.33	9.19	8.49
	Std. Error of Mean	0.82	1.05	2.04	1.61	2.06	1.67	1.55
	Variance	20.29	33.66	124.91	78.28	128.40	84.62	72.10
Total	N	49	49	49	49	49	49	49
	Mean	2.29	3.34	-1.07	4.80	4.98	4.85	-0.18
	Std. Deviation	7.31	8.41	14.53	15.65	15.06	14.59	10.19
	Std. Error of Mean	1.04	1.20	2.07	2.23	2.15	2.08	1.45
	Variance	53.54	70.73	211.21	244.95	227.09	212.94	103.88

Table 30. Bilateral Analysis Summary Statistics, Female Humeri

| Site Type		TA	CA	MA	I_x	I_y	J	I_x/I_y
Coastal/Bay	N	10	10	10	10	10	10	10
	Mean	3.46	5.32	0.53	6.44	9.57	7.78	-3.15
	Std. Deviation	8.90	12.36	14.07	20.65	19.95	19.23	13.37
	Std. Error of Mean	2.81	3.91	4.44	6.53	6.31	6.08	4.23
	Variance	79.33	152.98	197.98	426.59	398.37	370.14	178.95
Far North Coastal	N	8	8	8	8	8	8	8
	Mean	2.78	0.81	4.50	1.92	6.49	4.03	-4.56
	Std. Deviation	3.02	4.09	7.84	7.43	7.24	5.04	10.95
	Std. Error of Mean	1.06	1.44	2.77	2.62	2.56	1.78	3.87
	Variance	9.14	16.76	61.54	55.25	52.52	25.50	120.01
Inland River	N	31	31	31	31	31	31	31
	Mean	1.89	1.96	2.99	3.42	4.77	4.01	-1.36
	Std. Deviation	5.81	8.77	11.18	14.42	13.20	12.88	10.28
	Std. Error of Mean	1.04	1.57	2.00	2.59	2.37	2.31	1.847
	Variance	33.75	76.96	125.12	208.17	174.34	165.94	105.82
Total	N	49	49	49	49	49	49	49
	Mean	2.36	2.46	2.73	3.79	6.03	4.78	-2.25
	Std. Deviation	6.14	9.03	11.21	14.84	13.96	13.38	10.89
	Std. Error of Mean	0.87	1.29	1.60	2.12	1.99	1.91	1.55
	Variance	37.72	81.56	125.87	220.29	194.99	179.18	118.76
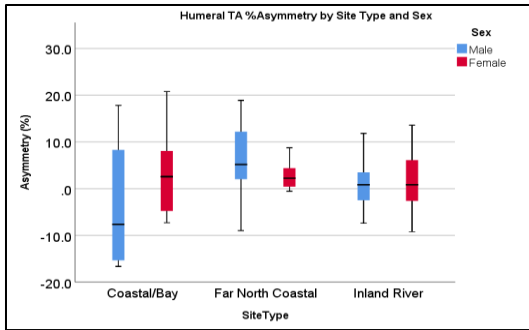
Figure 42. Humeral TA
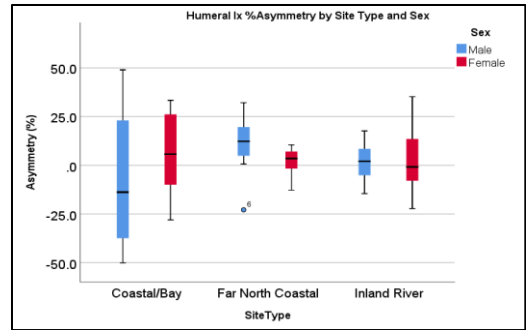
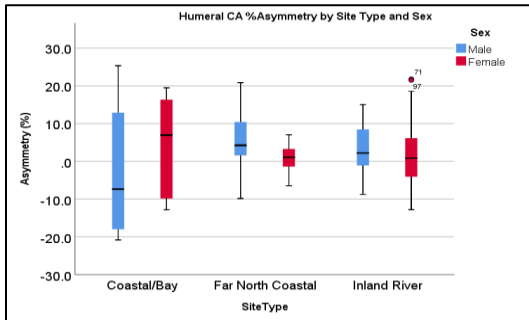*Figure 45. Humeral I_x*

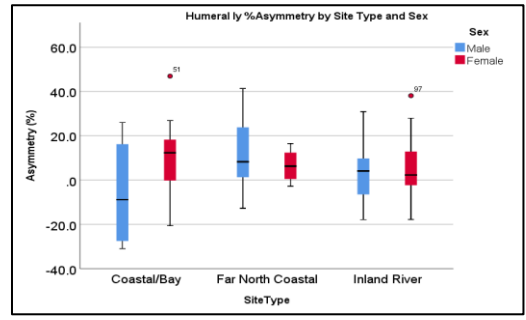*Figure 43. Humeral CA*

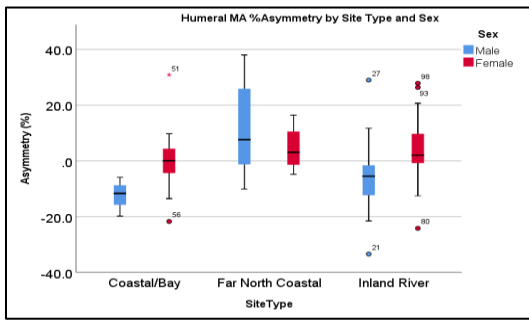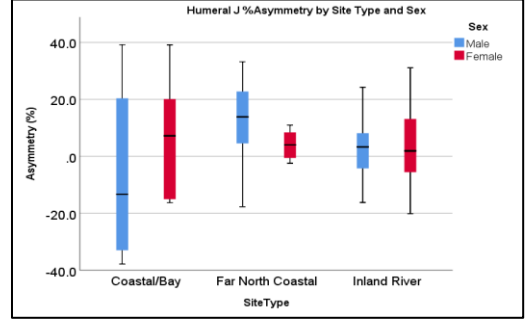*Figure 46. Humeral I_y*

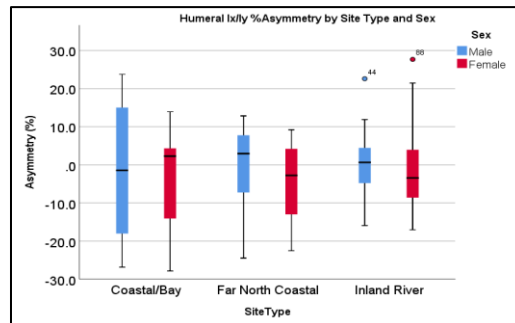*Figure 44. Humeral MA*

Figure 47. Humeral J

Figure 48. Humeral I_x/I_y

Figures 42-48. Humeral Bilateral Asymmetry Percentages by Site Type and Sex

Male Radii. Summary statistics of male radial bilateral asymmetry analyses are shown in Table 31, and Figures 49-55 present box plots of male radial TA, CA, MA, I_x, I_y, J, and I_x/I_y asymmetry percentages. Median male radial TA asymmetry is highest among the Coastal/Bay sample and lowest among the Inland River sample (Figure 49). The Far North Coastal and Inland River samples show IQRs with greater ranges than the Coastal/Bay IQR, although all IQRs overlap to some extent. Both the Inland River and Far North Coastal IQRs are skewed towards the upper whisker while the Coastal/Bay IQR appears centrally positioned between whiskers. The Far North Coastal sample contains two outliers above the 90th percentile, and the Inland River sample has one outlier above the 90th percentile.

The highest median value of male radial CA asymmetry is within the Coastal/Bay group, and the Far North Coastal and Inland River groups have approximately equivalent median values (Figure 50). The IQRs of the Coastal/Bay and Far North Coastal groups have smaller ranges than that of the Inland River group, and Far North Coastal and Coastal/Bay IQRs do not overlap with one another. Both the Inland River and Coastal/Bay IQRs are skewed towards the 10th percentile while the Far North Coastal IQR appear centrally positioned between whiskers. Two outliers above the 90th percentile are present within the Far North Coastal group.

The Far North Coastal sample has the greatest median value of male radial MA asymmetry (Figure 51). Although both the Coastal/Bay and Far North Coastal IQRs overlap with the Inland River IQR, they do not overlap with one another and each have smaller ranges than the Inland River IQR. All IQRs appear roughly centrally distributed

between the 10th and 90th percentiles, although the Far North Coastal IQR shows a slight skew towards the 10th percentile. An outlier below the 10th percentile is present in the Far North Coastal sample, and an outlier above the 90th percentile is present in the Inland River sample.

Median male radial I_x asymmetry values appear roughly equivalent between site types (Figure 52). The Coastal/Bay IQR has approximately only half the range of the Inland River and Far North Coastal IQRs, but the three IQRs all overlap with one another to some extent. Additionally, both the Far North Coastal and Inland River IQRs are centrally distributed between whiskers while the Coastal/Bay IQR appears skewed towards the lower whisker. A single outlier above the 90th percentile is present in the Far North Coastal group.

The Far North Coastal and Inland River samples have similar median values of male radial I_y asymmetry, which are less than that of the Coastal/Bay sample (Figure 53). The IQR ranges of the Coastal/Bay and Far North Coastal samples are less than that of the Inland River sample, although all IQRs do overlap to some degree. The Inland River and Coastal/Bay IQRs appear skewed towards the 90th percentile while the Far North Coastal IQR appears skewed towards the 10th percentile. The Far North Coastal sample contains two outliers above the 90th percentile, and the Inland River sample contains a single outlier above the upper whisker.

The greatest value of median male radial J asymmetry is found among the Coastal/Bay group, and the lowest is among the Inland River group (Figure 54). The greatest IQR range is found within the Inland River sample while the Coastal/Bay sample

IQR demonstrates the smallest range. However, all IQRs do overlap to some extent. All IQRs additionally show some degree of skewing towards the upper whisker; this is least pronounced within the Far North Coastal sample. Three outliers above the 90th percentile are observed – two among the Far North Coastal and one among the Inland River sample.

Median male radial I_x/I_y asymmetry is greatest in the Inland River sample and appears equal between the Far North Coastal and Coastal/Bay groups (Figure 55). The Coastal/Bay and Inland River IQRs show different values but a similar range, and both overlap with the Far North Coastal IQR. All IQRs appear relatively centrally distributed between the upper and lower whiskers. Both the Far North Coastal and Inland River groups contain a single outlier each – the former above the 90th percentile and the latter below the 10th percentile.

Female Radii. Summary statistics of female radial bilateral asymmetry analyses are shown in Table 32, and Figures 49-55 present box plots of female radial TA, CA, MA, I_x, I_y, J, and I_x/I_y asymmetry percentages. Median female radial TA asymmetry is greatest among the Coastal/Bay and lowest among the Far North Coastal group (Figure 49). Although all IQRs show similar ranges, that of the Coastal/Bay group has higher numerical values than either the Inland River or Far North Coastal IQR. However, all IQRs overlap to some extent. Additionally, all IQRs appear centrally distributed between the upper and lower whisker. The Inland River group contains one outlier below and one outlier above the whiskers.

The Coastal/Bay sample has the greatest value of median female radial CA asymmetry (Figure 50). Although all IQRs appear to overlap, the range of the Inland

River IQR is smaller than those of either the Coastal/Bay or Far North Coastal sample. Furthermore, the Coastal/Bay and Far North Coastal IQRs appear skewed towards the 10th percentile to some extent, while that of the Inland River sample is centrally positioned between whiskers. The Inland River sample contains one outlier below the 10th percentile and one outlier above the 90th percentile.

Median female radial MA asymmetry is approximately equal between site types (Figure 51). The Inland River and Far North Coastal IQRs have similar ranges and values, which are both overlapped by the Coastal/Bay IQR. The Inland River and Coastal/Bay IQRs appear centrally distributed between whiskers, and that of the Far North Coastal sample is skewed towards the 90th percentile. The Inland River group contains three outliers, all of which are above the 90th percentile.

The highest value of median female radial I_x asymmetry is among the Coastal/Bay sample while the lowest is among the Far North Coastal sample (Figure 52). The IQRs of the Coastal/Bay and Far North Coastal groups show similar ranges while that of the Inland River sample has a smaller range. However, all IQRs show some overlap. No IQRs appear centrally positioned between whiskers; that of the Coastal/Bay sample is skewed towards the lower whisker, and those of the Far North Coastal and Inland River samples are skewed towards the upper whisker. The Inland River sample contains two outliers: one above the 90th percentile and one below the 10th percentile.

The Far North Coastal group demonstrates the lowest median value of female radial I_y asymmetry, while the Coastal/Bay group demonstrates the highest median value (Figure 53). Although all IQRs have similar ranges, the Coastal/Bay IQR has greater

value than, and does not overlap with, the Far North Coastal IQR. The Inland River IQR is centrally positioned between whiskers, the Far North Coastal IQR is skewed towards the lower whisker, and the Coastal/Bay IQR is skewed towards the upper whisker. The Inland River sample contains two outliers – one above and one below the whiskers.

Median female radial J asymmetry is highest within the Coastal/Bay group and lowest within the Far North Coastal group (Figure 54). The Coastal/Bay group also demonstrates the IQR with the largest range and greatest numerical value. This IQR only overlaps with the Inland River IQR, not with the Far North Coastal IQR. Both the Coastal/Bay and Far North Coastal IQRs are skewed in favor of the 90th percentiles, while that of the Inland River sample is more centrally positioned. Once again, the Inland River sample contains one outlier above and one outlier below the whiskers.

Finally, median female radial I_x/I_y asymmetry is slightly greater in the Far North Coastal sample than either the Coastal/Bay or Inland River samples (Figure 55). The IQR of the Coastal/Bay group has a greater range than either the Far North Coastal or Inland River groups, although all IQRs do overlap to some degree. Both the Inland River and Far North Coastal IQRs appear centrally positioned between the 10th and 90th percentiles, while the Coastal/Bay IQR is skewed closer to the 10th percentile. Three outliers are present; the Far North Coastal sample contains one above and one below the whiskers while the Inland River sample contains one below the lower whisker.

Table 31. Bilateral Analysis Summary Statistics, Male Radii

Site Type		TA	CA	MA	I_x	I_y	J	I_x/I_y
Coastal/Bay	N	4	4	4	4	4	4	4
	Mean	3.69	5.87	-4.33	4.82	12.41	9.53	-7.60
	Std. Deviation	3.27	1.67	6.88	3.50	9.49	6.28	9.60
	Std. Error of Mean	1.63	0.83	3.44	1.75	4.74	3.14	4.80
	Variance	10.73	2.81	47.45	12.27	90.19	39.49	92.24
Far North Coastal	N	14	14	14	14	14	14	14
	Mean	4.64	3.90	6.24	7.34	11.47	9.79	-3.55
	Std. Deviation	13.24	16.54	11.06	32.28	22.86	25.68	18.11
	Std. Error of Mean	3.53	4.42	2.95	8.62	6.11	6.86	4.84
	Variance	175.41	273.68	122.44	1042.26	522.69	659.69	328.03
Inland River	N	32	32	32	32	32	32	32
	Mean	2.07	1.59	3.68	3.51	4.44	4.04	-0.98
	Std. Deviation	6.92	8.77	13.10	14.12	16.40	14.66	10.60
	Std. Error of Mean	1.22	1.55	2.31	2.49	2.89	2.59	1.87
	Variance	48.00	77.02	171.76	199.43	269.01	214.96	112.50
Total	N	50	50	50	50	50	50	50
	Mean	2.92	2.58	3.76	4.69	7.05	6.09	-2.23
	Std. Deviation	8.88	11.11	12.29	20.15	18.07	17.91	12.95
	Std. Error of Mean	1.25	1.57	1.73	2.85	2.55	2.53	1.83
	Variance	78.92	123.53	151.17	406.35	326.75	321.06	167.71

Table 32. Bilateral Analysis Summary Statistics, Female Radii

| Site Type		TA	CA	MA	I_x	I_y	J	I_x/I_y
Coastal/Bay	N	8	8	8	8	8	8	8
	Mean	7.04	8.23	10.06	13.96	16.68	15.66	-2.66
	Std. Deviation	5.27	10.72	15.63	17.86	13.81	12.68	18.41
	Std. Error of Mean	1.86	3.79	5.52	6.31	4.88	4.48	6.51
	Variance	27.87	115.03	244.43	319.13	190.98	160.96	339.18
Far North	N	6	6	6	6	6	6	6
Coastal	Mean	-0.99	-.092	2.77	-3.33	0.68	-.054	-3.98
	Std. Deviation	4.26	6.59	10.23	14.47	11.27	8.66	18.65
	Std. Error of Mean	1.74	2.69	4.17	5.90	4.60	3.53	7.61
	Variance	18.17	43.52	104.78	209.43	127.16	75.16	348.05
Inland River	N	30	30	30	30	30	30	30
	Mean	4.05	3.32	7.71	3.90	11.90	8.85	-8.02
	Std. Deviation	6.95	10.56	15.40	16.06	17.47	15.44	14.12
	Std. Error of Mean	1.27	1.92	2.81	2.93	3.19	2.81	2.57
	Variance	48.41	111.53	237.44	258.08	305.47	238.50	199.60
Total	N	44	44	44	44	44	44	44
	Mean	3.90	3.63	7.47	4.74	11.24	8.81	-6.49
	Std. Deviation	6.67	10.29	14.71	16.60	16.53	14.72	15.34
	Std. Error of Mean	1.00	1.55	2.21	2.50	2.49	2.21	2.31
	Variance	44.48	105.92	216.48	275.78	273.25	216.75	235.54
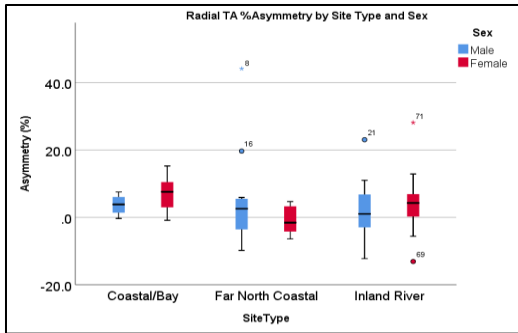
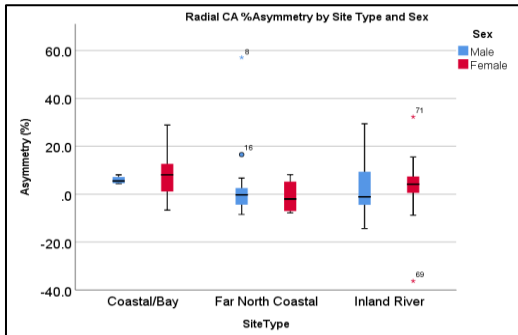*Figure 49. Radial TA*
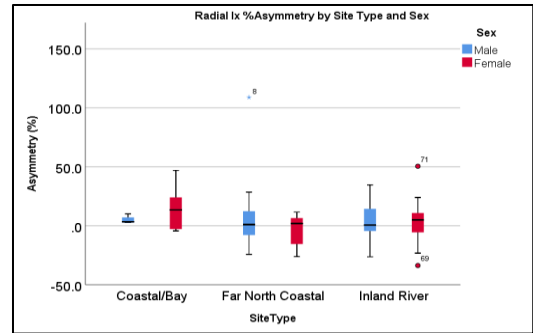
Figure 52. Radial I_x
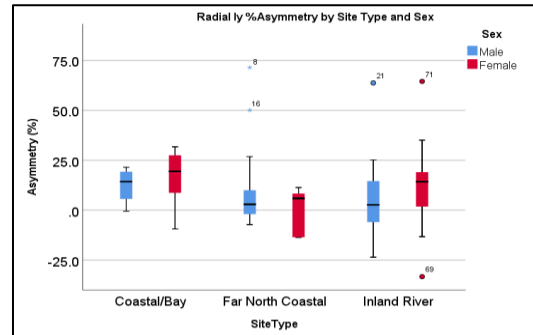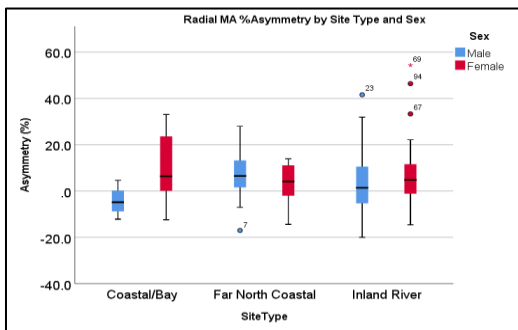

Figure 50. Radial CA

Figure 53. Radial I_y
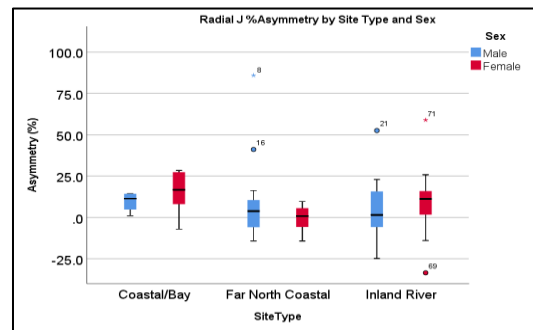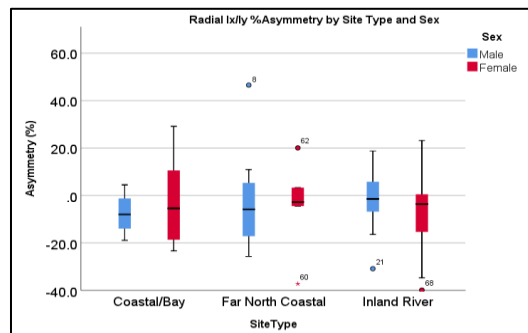

Figure 51. Radial MA

Figure 54. Radial J

Figure 55. Radial I_x/I

Figures 49-55. Radial Bilateral Asymmetry Percentages by Site Type and Sex

Bilateral Statistical Analyses – Nonparametric Tests

Table 33 presents the results of nonparametric Kruskal-Wallis tests for differences in bilateral asymmetry of male humeral TA, CA, MA, I_x, I_y, J, and I_x/I_y. The null hypothesis of each test assumes no significant difference in the distribution of asymmetry percentages between site types.

TA. Results of the Kruskal-Wallis test of male humeral TA are significant ($H = 8.608$; $p = 0.014$). The null hypothesis is rejected; there is a significant difference in the distribution of male humeral TA bilateral asymmetry between site types. A pairwise comparison of the TA test finds significant results in both the Coastal/Bay – Far North Coastal ($H = -17.483$; $p = 0.030$) and the Inland River – Far North Coastal ($H = 11.933$; $p = 0.008$) comparisons. This indicates that Far North Coastal TA asymmetry is significantly greater than that of both the Inland River and Coastal/Bay samples. Results of the Inland River – Coastal/Bay analysis are not significant ($H = -5.55$; $p = 0.466$), signifying no significant differences in TA asymmetry between these groups.

CA. Results of the Kruskal-Wallis test of male humeral CA asymmetry are not significant ($H = 2.192$; $p = 0.334$). The null hypothesis is supported, and there are no significant differences in the distribution of male humeral CA bilateral asymmetry between site categories.

MA. Results of the Kruskal-Wallis test of male humeral MA asymmetry are significant ($H = 15.251$; $p \leq 0.001$). The null hypothesis is thus rejected. There is a significant difference in the distribution of male humeral MA bilateral asymmetry between site types. Pairwise comparisons reveal significant differences in the

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Coastal/Bay – Far North Coastal analysis (H = -25.267; p = 0.002) and in the Inland

River – Far North Coastal analysis (H = 15.033; p = 0.001). Far North Coastal MA

asymmetry is significantly greater than the Inland River and Coastal/Bay samples.

Results of the Inland River – Coastal/Bay analysis are not significant (H = -10.233;

p = 0.178), indicating no significant difference in MA asymmetry between these samples.

I_x. Results of the Kruskal-Wallis test of male humeral I_x asymmetry are

significant (H = 7.870; p = 0.020). The null hypothesis is rejected; there are significant

differences in the distribution of male humeral I_x bilateral asymmetry between site types.

Pairwise analysis reveals significant results of the Coastal/Bay – Far North Coastal

(H = -16.833; p = 0.036) and the Inland River – Far North Coastal

(H = 11.367; p = 0.012) comparisons. Thus, Far North Coastal I_x asymmetry is

significantly greater than that of the other site categories. The Inland River – Coastal/Bay

analysis is nonsignificant (H = -5.417; p = 0.472); I_x asymmetry does not significantly

differ between these samples.

I_y. Results of the Kruskal-Wallis test of male humeral I_y asymmetry are not

significant (H = 4.026; p = 0.134). The null hypothesis is supported. There is no

significant difference in male humeral I_y bilateral asymmetry between site categories.

J. Results of the Kruskal-Wallis test of male humeral J asymmetry are significant

(H = 6.196; p = 0.045). Thus, the null hypothesis is rejected, and there is a significant

difference in the distribution of humeral J asymmetry between groups. Pairwise

comparison reveals a significant result of the Inland River – Far North Coastal (H = 10.1;

p = 0.025) analysis, indicating that Inland River J asymmetry is significantly less than

that of the Far North Coastal group. Comparisons of the Coastal/Bay sample with both

the Far North Coastal (H = -14.9; p = 0.064) and Inland River (H = -4.8; p = 0.528)

samples are nonsignificant, indicating no significant differences in J asymmetry between

these groups.

   I_x/I_y. Results of the Kruskal-Wall test of male humeral I_x/I_y asymmetry are not

significant (H = 0.048; p = 0.976). The null hypothesis is supported, and there is no

significant difference in the distribution of male humeral I_x/I_y bilateral asymmetry

between site types.

Table 33. Kruskal-Wallis Results, Male Humeri

Variable	Test Statistic (H)	Sig. (p)	Pairwise Comparison[2]	Test Statistic (H)	Sig. (p)
TA	8.608	**0.014**	---	---	---
---	---	---	Coastal/Bay – Far North Coastal	-17.483	**0.030**
---	---	---	Inland River – Far North Coastal	11.933	**0.008**
---	---	---	Coastal/Bay – Inland River	-5.550	0.466
CA	2.192	0.334		---	---
MA	15.251	**0.000**	---	---	---
---	---	---	Coastal/Bay – Far North Coastal	-25.267	**0.002**
---	---	---	Inland River – Far North Coastal	15.033	**0.001**
---	---	---	Coastal/Bay – Inland River	-10.233	0.178
I_x	7.870	**0.020**	---	---	---
---	---	---	Coastal/Bay – Far North Coastal	-16.833	**0.036**
---	---	---	Inland River – Far North Coastal	11.367	**0.012**
---	---	---	Coastal/Bay – Inland River	-5.467	0.472
I_y	4.026	0.134		---	---
J	6.196	**0.045**	---	---	---
---	---	---	Inland River – Far North Coastal	10.100	**0.025**
---	---	---	Coastal/Bay – Inland River	-4.800	0.528
---	---	---	Coastal/Bay – Far North Coastal	-14.900	0.064
I_x/I_y	0.048	0.976		---	---

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[2] Pairwise comparisons are only performed if the initial Kruskal-Wallis test indicates a significant difference in distribution between site types.

Table 34 presents results of nonparametric Kruskal-Wallis tests for differences in bilateral asymmetry of female humeral TA, CA, MA, I_x, I_y, J, and I_x/I_y. The null hypothesis of each test assumes no significant difference in the distribution of asymmetry percentages between site types.

TA, CA, MA, I_x, I_y, J and, I_x/I_y. Results of the Kruskal-Wallis tests of female humeral TA (H = 0.360; p = 0.835), CA (H = 1.100; p = 0.577), MA (H = 0.855; p = 0.652), I_x (H = 0.223; p = 0.895), I_y (H = 1.133; p = 0.567), J (H = 0.458; p = 0.795), and I_x/I_y (H = 0.245; p = 0.885) are all nonsignificant. The null hypothesis is supported in all cases; there is no significant difference in the distribution of female humeral bilateral asymmetry among any variable.

Table 34. Kruskal-Wallis Results, Female Humeri

Variable	Test Statistic (H)	Sig. (p)
TA	0.360	0.835
CA	1.100	0.577
MA	0.855	0.652
I_x	0.223	0.895
I_y	1.133	0.567
J	0.458	0.795
I_x/I_y	0.245	0.885

Table 35 presents results of nonparametric Kruskal-Wallis tests for differences in bilateral asymmetry of male radial TA, CA, MA, I_x, I_y, J, and I_x/I_y. The null hypothesis of each test assumes no significant difference in the distribution of asymmetry percentages between site types.

TA, CA, MA, I_x, I_y, J and, I_x/I_y. Results of the Kruskal-Wallis tests of male radial

TA (H = 0.677; p = 0.713), CA (H = 0.945; p = 0.378), MA (H = 3.763; p = 0.152), I_x

(H = 0.681; p = 0.712), I_y (H = 2.051; p = 0.359), J (H = 0.854; p = 0.653), and I_x/I_y

(H = 2.714; p = 0.257) are all nonsignificant. The null hypothesis is supported. There is

no significant difference in the distribution of male radial bilateral asymmetry among any

variable.

Table 35. Kruskal-Wallis Results, Male Radii

Variable	Test Statistic (H)	Sig. (p)
TA	0.677	0.713
CA	0.945	0.378
MA	3.763	0.152
I_x	0.681	0.712
I_y	2.051	0.359
J	0.854	0.653
I_x/I_y	2.714	0.257

Table 36 presents results of nonparametric Kruskal-Wallis tests for differences in

bilateral asymmetry of female radial TA, CA, MA, I_x, I_y, J, and I_x/I_y. The null hypothesis

of each test assumes no significant difference in the distribution of asymmetry

percentages between site types.

TA. Results of the Kruskal-Wallis test of female radial TA bilateral asymmetry

are significant (H = 6.961; p = 0.031). The null hypothesis is thus rejected, signifying a

significant difference in the distribution of TA bilateral asymmetry between site types.

Pairwise analysis reveals significant results of the Far North Coastal – Inland River

(H = -11.267; p = 0.050) and the Far North Coastal – Coastal/Bay (H = 18.250; p = 0.009) comparisons. This indicates that Far North Coastal TA asymmetry is significantly less than that of the other two samples. The pairwise comparison between Coastal/Bay and Inland River is nonsignificant (H = 6.983; p = 0.172) signifying no significant difference in female radial TA between these groups.

CA, MA, I_x, I_y, J, and I_x/I_y. Results of the Kruskal-Wallis tests of female radial CA (H = 3.573; p = 0.168), MA (H = 0.366; p = 0.833), I_x (H = 3.052; p = 0.217), I_y (H = 5.734; p = 0.057), J (H = 5.9000; p = 0.052), and I_x/I_y (H = 0.574; p = 0.075) are all nonsignificant. The null hypothesis is supported. There is no significant difference in the distribution of female radial bilateral asymmetry among these variables.

Table 36. Kruskal-Wallis Results, Female Radii

Variable	Test Statistic (H)	Sig. (p)	Pairwise Comparison	Test Statistic (H)	Sig. (p)
TA	6.961	**0.031**		---	---
	---	---	Far North Coastal – Inland River	-11.267	**0.050**
	---	---	Far North Coastal – Coastal/Bay	18.250	**0.009**
			Inland River – Coastal/Bay	6.983	0.172
CA	3.573	0.168		---	---
MA	0.366	0.833		---	---
Ix	3.052	0.217		---	---
Iy	5.734	0.057		---	---
J	5.900	0.052		---	---
Ix/Iy	0.574	0.075		---	---

DISCUSSION

Unilateral Analyses

Femora. Based on the information presented in Chapters 1 and 2, it was predicted that the Far North Coastal sample would demonstrate the highest, and the Coastal/Bay sample the lowest, measurements of femoral robusticity and ratios of A-P to M-L loading, likely due to differences in mobility associated with different hunting and gathering techniques. The Inland River sample was predicted to have intermediate robusticity and diaphyseal shape measurements. This hypothesis is widely supported within each sex.

Among male femora, the Far North Coastal sample demonstrates significantly greater total subperiosteal area (TA) than both the Coastal/Bay and Inland River samples, with the Coastal/Bay group showing the lowest TA measurement. This implies that Far North Coastal male femoral midshafts are larger than those of the other site types. However, TA is not a direct measure of bone robusticity. More relevant is the amount and distribution of cortical bone and medullary space (MA) within the total subperiosteal area.

Male femoral cortical area (CA) among the Inland River sample is significantly greater than either the Far North Coastal or Coastal/Bay groups, which do not statistically differ. Despite having smaller overall femoral diaphyses, the Inland River group

possesses more cortical bone within the femoral diaphysis than the Far North Coastal sample. In contrast, male femoral MA is significantly greater among the Far North Coastal sample than both the Inland River and Coastal/Bay site types.

Areal measurements thus indicate that among male femora, the Far North Coastal sample demonstrates the largest overall femoral diaphyses, inside of which are significantly larger medullary cavities relative to other site types. Despite having significantly less CA than the Inland River sample, the Far North Coastal group shows orientation of bone material further from the center of the diaphyseal cross-section. As stated in Chapter 1, during bending or torsional stress, the magnitude of such stress is proportional to the distance from a neutral axis. Therefore, bone material oriented further from a neutral plane or axis should be stronger than that which is closer to a neutral point. Since Far North Coastal male femora demonstrate such an orientation, the sample should have greater bending and torsional robusticity.

Comparisons of male femoral A-P bending rigidity (I_x), M-L bending rigidity (I_y), and torsional rigidity (J) between site types tentatively support the above prediction. The Coastal/Bay sample demonstrates I_x measurements significantly lower than both the Far North Coastal and Inland River samples, and the Far North Coastal sample is non-significantly greater than the intermediate Inland River sample. However, Far North Coastal male femoral I_y is significantly greater than both the Coastal/Bay and Inland River groups. As with I_x, the Coastal/Bay sample demonstrates significantly smaller J values than both the Inland River and Far North Coastal groups, and the Far North Coastal group is non-significantly greater than the intermediate Inland River sample.

Although only differences in I_y are significant, Far North Coastal male femora demonstrate consistently greater values of bending and torsional robusticity, while the Coastal/Bay group demonstrates consistently, and often significantly, lower values of femoral midshaft robusticity.

Besides greater femoral robusticity, it was also predicted that Far North Coastal femora would demonstrate more anteroposteriorly-reinforced diaphyses, manifest in an increased ratio of A-P/M-L bending rigidities (I_x/I_y). I_x/I_y refers the overall shape of a cross-section and reflects the type of loading (anteroposterior-dominant, mediolateral-dominant, or proportional) to which a bone has been adapted over time. Within this study, I_x/I_y of the Coastal/Bay sample is significantly lower than both the Inland River and Far North Coastal ratios. The Coastal/Bay mean is close to 1.0, suggesting that the femora of this population have been subjected to relatively proportional A-P and M-L loading. Far North Coastal and Inland River mean values are not significantly different, and are near 1.2, suggesting greater A-P bending over time. However, given the nonsignificant difference in I_x/I_y between the Far North Coastal and Inland River samples, the original hypothesis cannot be fully supported. Far North Coastal male femoral I_x/I_y is only significantly greater than the Coastal/Bay, not the Inland River, sample.

A similar pattern of robusticity emerges among female femoral diaphyses, despite likely differences in habitual activities due to sexual divisions of labor. Far North Coastal female femora display consistent and significant differences in measurements of

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robusticity from the Inland River and Coastal/Bay site types. However, there is no significant difference in female femoral I_x/I_y between sites.

Far North Coastal female femoral TA is significantly greater than the Inland River or Coastal/Bay samples, and Coastal/Bay TA is non-significantly smaller than that of the intermediate Inland River group. But as noted above, TA is not a strength-related measurement. While there are no significant differences in female femoral CA between site types, the Far North Coastal sample does demonstrate the highest measure of MA, differing significantly from the Inland River and non-significantly from the Coastal/Bay sample. This again suggests that Far North Coastal females are strengthening femora during bending and torsional stresses by orienting bone further from the neutral axis or plane.

This suggestion is supported by measurements of female femoral bending and torsional rigidities. The Far North Coastal sample shows significantly greater I_x, I_y, and J than either the Inland River or Coastal/Bay groups. In all analyses, the Coastal/Bay sample demonstrates values non-significantly less than or nearly equivalent to the intermediate Inland River sample. Far North Coastal females thus have consistently, significantly greater femoral diaphyseal rigidity, both bending and torsional. However, as noted above, there are no significant differences in I_x/I_y between site types; all groups demonstrate median I_x/I_y values just above 1.0, suggesting relatively proportional amounts of A-P and M-L loading. This corresponds to previous research finding less variation in female I_x/I_y ratios related to reduced variation in mobility compared to males (Ruff 1987).

Overall, the above discussion provides tentative, if not always significant, support for the original hypothesis that Far North Coastal femora will display the greatest measures of robusticity while the Coastal/Bay sample will demonstrate the lowest measures. Additionally, the Coastal/Bay sample demonstrates the lowest ratio of A-P/M-L bending rigidity. The results correlate with behavioral expectations regarding femoral diaphyseal robusticity and shape. Despite both the Far North Coastal and Coastal/Bay samples representing hunter-gatherers, habitual subsistence activities differed markedly (Clark 1984, Clark 1998, Gillispie 2018, Mason 2014, and Stanford 1976). The former group consistently participated in high-intensity hunting of big game mammals such as caribou, seals, and whales. In contrast, coastal populations relied more heavily on the harvesting of fish, an activity requiring reduced terrestrial mobility. Given the habitual nature of food collection, it is unsurprising that the femora reflect these differences.

Previous research also supports the results of the current study. As noted in Chapter 1, Stock and Pfeiffer (2001) found that populations with high terrestrial mobility demonstrate exaggerated measures of femoral robusticity and that those with increased marine mobility (either via rowing or swimming) have reduced or limited terrestrial mobility and therefore exhibit reduced measures of femoral robusticity.

Increased femoral robusticity among arctic hunter-gatherers is not unique to the current study. Shackleford (2014) compared femoral and humeral cross-sectional properties of Tigara and Inupiat hunter-gatherers from Point Hope, Alaska with those of

five Holocene populations[3] with differing subsistence strategies to determine if the effects of a high-intensity artic lifestyle are discernable on the postcranial skeleton. The author found that, relative to other Holocene samples, both male and female Inuits demonstrate high levels of femoral midshaft robusticity, even when compared to the hyper-robust Jōmon population. Shackleford attributes the robust femora of male and female Inuits to the increased mobility of this group relative to other Holocene populations. The Inuits of Shackleford's study and the Far North Coastal sample of the current study lived in similar climatic conditions and practiced similar high-intensity subsistence strategies, so the correlation between results is unsurprising.

Shackleford (2014), Stock and Pfeiffer (2001), and the current study each identified significant differences in female femoral robusticity between populations. This is unusual because in most hunter-gatherer societies, females did not regularly participate in high-intensity and highly mobile hunting. However, research suggests that individuals who are not habitually highly mobile (females) may still demonstrate high degrees of robusticity associated with mobility in males. This is suggestive that a factor other than subsistence-related mobility is at least partially responsible for femoral robusticity.

Terrain may represent such a factor. As noted in Chapter 1, Holt et al. (2018) found that across geographic and temporal ranges of Europe, populations residing in more rugged terrain demonstrate more robust femora and increased loading along the A-P plane. Additionally, in an analysis of midshaft femoral robusticity, Ruff (1999) found that among a combined sample of pre-agricultural and agricultural Amerindians from the

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[3] Late to Final period Jōmon, Andaman Islanders, Semi-nomadic Libyan Sahara herders, sedentary agricultural Egyptians, and contemporary Kenyans

Great Basin, Pecos Pueblo, northern Great Plains, and Georgia coast regions, diaphyseal cross-sectional properties significantly differed with respect to local terrain. Populations residing in mountainous regions (Great Basin and Pecos Pueblo) showed significantly greater CA and J than plain or coastal samples, which did not significantly differ from one another.

Similarly, Marchi (2008) compared femoral and tibial cross-sectional measurements of a Middle Neolithic Ligurian population to 94 European individuals ranging from the Late Upper Paleolithic to the Neolithic Age. Neolithic humans are in general characterized by decreased long bone robusticity relative to Late Upper Paleolithic humans due largely to the adoption of sedentary agriculture in place of hunting and gathering. However, the Ligurian sample did not follow this trend; rather the population showed levels of femoral and tibial robusticity similar to highly mobile Late Upper Paleolithic and Mesolithic humans. Since the Ligurian region demonstrates exaggerated rugged and hilly terrain, the author contends that such terrain may influence lower limb robusticity to the point of masking the effects of reduced mobility related to an agricultural subsistence. The practice of transhumance, the seasonal movement of livestock, may have also contributed to increased robusticity among Ligurians (Stagno 2018). This study and that of Ruff (1999) suggest that terrain may play just as significant a role in lower limb robusticity as mobility and could explain why in the current study Far North Coastal females demonstrate significantly more robust femora than populations inhabiting less rugged terrain.

Tibiae. Compared to the femora, the distal portion of the lower limb demonstrates limited significant differences in any variable measured in this study. Among male tibiae, there are no differences in bending or torsional rigidities or in diaphyseal shape between site types; only two areal properties differ. The Inland River sample demonstrates significantly greater CA than the Far North Coastal sample and non-significantly greater CA than the intermediate Coastal/Bay sample. In contrast, Far North Coastal male tibial MA is significantly greater than the Inland River but non-significantly greater than the intermediate Coastal/Bay group. These results indicate that the Far North Coastal sample has decreased axial robusticity, resulting from decreased CA and increased MA, compared to the Inland River group. But as stated before, axial robusticity is less relevant to long bones than are bending and torsional robusticity. The female tibial analysis found no significant differences in any variable measured.

Given the differences between site types in male and female femoral robusticity, the significant difference in male femoral shape between sites, and the high degree of individual overlap between elements within the femoral and tibial samples[4], the lack of significant differences in the tibiae of both sexes is unexpected. For one, Marchi (2008) found that, in addition to femora, the tibiae of Ligurian populations exhibited increased robusticity in response to rugged terrain. Stock (2006) additionally identified a strong correlation between tibial diaphyseal robusticity and mobility patterns, with more mobile populations exhibiting more robust tibial diaphyses. Finally, Macdonald et al. (2009) and

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[4] Out of 79 male femora used in this study, 72 (91.1%) had a corresponding tibia from the same individual, and out of 91 female femora used in this study, 82 (90.1%) had a corresponding tibia from the same individual.

Shaw and Stock (2009b) found that tibial cross-sectional shape (I_x/I_y) is also responsive to differing types of loading in contemporary populations. As these studies prove that the tibia is capable of adapting to differing levels of mechanical strain, the apparent lack of such adaptation in the current study is surprising.

The lack of significant differences in tibial robusticity between site categories may be due to increased selective pressure for structural optimization in distal segments of locomotory limbs. The concept of symmorphosis assumes that a given biological system adheres to an "economy of structural design" (Weibel 1998, 3) in which each component of that system is structurally capable of performing a respective function with no excess capacity to do so. In the case of an ambulatory limb like a human leg, symmorphosis would assume that both proximal and distal portions of the leg are equally capable of withstanding forces generated by walking and running.

However, studies of quadrupedal mammals have suggested that the skeletal system does not necessarily adhere to the theory of symmorphosis. For example, veterinary observations have found that a greater percentage of racehorse fractures occur in the distal portion of the leg (cannon bone) compared to the proximal portion (Vaughan and Mason 1975). Skedros et al. (2003) additionally found a progressive decrease in bone mineral content from the humerus to the phalanx in wild mule deer, possibly as an adaption for regional loading conditions.

Although increased robusticity is beneficial in preventing structural failure, it is also costly in the lower segment of a limb (Alexander 1998). During locomotion, the distal portion of a limb must accelerate and decelerate through a larger range of motion

than the proximal portion. Any excess bone within the lower limb, beyond what is necessary for weight support and fracture prevention, increases energy expenditure during locomotion. Lower limb segments must therefore strike a balance between enough robusticity to maintain structure yet not impede movement. It is thus possible that the lack of significant differences in tibial robusticity in this study, despite differences in the femora, reflects a strategy to balance energy efficiency and structural optimization.

In contrast, ecogeographical adaptation may also explain the lack of significant differences in tibial diaphyseal shape between site categories. Humans now inhabit regions with climatic extremes, and the human body shows a high degree of plasticity in its ability to adapt to such environments. In hot regions, it is advantageous to increase bodily surface area so as to increase areas from which heat can dissipate. Conversely, an advantage in cold environments is reduction of surface area to retain as much body heat as possible.

The surface area of the human body may be altered through changes in length (often represented through the brachial and crural indices) and/or changes in width (often measured in bi-iliac breadth [BIB]). Studies of extant and extinct humans have found that human populations adapted to cold environments tend to demonstrate shortened limb lengths and increased BIB, while those residing in hot climates exhibit lengthened limbs and reduced BIB (Ruff 1994).

Given the relationship between climate and body proportions, Shaw and Stock (2011) tested whether limb length, limb segment length, or BIB have any significant influence on femoral and tibial diaphyseal shape. The authors analyzed 136 femora and

159 tibiae from populations of nine unique geographic origins[5] and predicted that 1) populations with longer limbs relative to body weight would have greater I_x/I_y ratios and 2) that populations demonstrating greater BIB would show reduced I_x/I_y ratios.

Although the first hypothesis was not supported, Shaw and Stock (2011) found that populations with greater BIB had reduced I_x/I_y values. The results were significant for both male and female femoral shape and for pooled tibial shape. The authors contend that wider hips lead to mediolaterally-reinforced lower limb bones. Such M-L reinforcement would increase the denominator of the I_x/I_y ratio, thus lowering the overall ratio. Native Eskimo populations are demonstrated to have classic adaptations to cold environments (short limbs and wide bodies), so in the current study, the ecogeographic adaptations of Alaskan populations may be influencing tibial diaphyseal shape and preventing significant differences between sites. The current study did not calculate the brachial and crural indices or bi-iliac breadth for the samples used. Further research regarding these factors within the current sample may shed light on whether ecogeographic adaptations influence functional adaptation in the distal portion of the lower limb of Native Alaskans.

Humeri. Predictions for the upper limb hypothesized that the Far North Coastal sample should demonstrate lower levels of humeral robusticity than either the Coastal/Bay or Inland River groups, based on differences in aquatic mobility. However, within each sex, male and female humeri demonstrate few differences in cross-sectional

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[5] Andaman Islands, Late Archaic Great Lakes of North America, Predynastic Egypt, Protohistoric Yahgan, Later Stone Age South Africa, post-Neolithic Sudan, Late Pleistocene North Africa, Late Pleistocene Levant, and Mesolithic France

properties between site types. Only one significant difference is found among male humeri. Inland River male humeral MA is significantly lower than the Far North Coastal and non-significantly lower than the Coastal/Bay sample. This indicates that of all groups, the Inland River sample has the smallest amount of medullary space in the humerus. The Far North Coastal group has the greatest medullary area, but this is not significantly greater than the intermediate Coastal/Bay medullary area. Male humeri do not significantly differ in any other areal property, measures of bending or torsional rigidity, or humeral shape.

Female humeri demonstrate a similar lack of differences between site types; the sample only shows significant differences in areal measurements, not in measures of bending or torsional rigidity or the I_x/I_y ratio. Far North Coastal female humeral TA and MA are both significantly greater than the corresponding variable in the Inland River sample. In both cases, the Far North Coastal sample is non-significantly greater than the intermediate Coastal/Bay group. These results suggest that Far North Coastal female humeri have larger overall diaphyseal area and larger relative medullary cavities. Although this would suggest an increase in bending and/or torsional strength through the orientation of bone further from a neutral plane, no significant increase in Far North Coastal I_x, I_y, or J is present.

As indicated above, humeri in the current study show minimal differences between site types, and the small number of differences are in areal measurements not directly related to bending or torsional robusticity. These results are unexpected, especially in light of the increased robusticity of Far North Coastal femora, which is

attributed to mechanical loading induced by mobility and rugged terrain. However, since the upper limb in humans is not responsible for locomotion, the same patterns should not necessarily be expected.

The lack of significant differences in humeral geometric properties between the Coastal/Bay and Inland River samples is not entirely unexpected. Both samples are believed to have had similar levels of aquatic mobility. These populations were likely engaging in rowing of limited geographic regions – that is, within rivers or coastal areas. There is no evidence of the groups engaging in open-ocean rowing like Alaskan Aleuts. Weiss (2003) found similar levels of humeral robusticity among non-ocean rowing populations, so the similarity between the two non-ocean rowing samples concurs with these results.

Weiss (2003) and Stock and Pfeiffer (2001) both found support for reduced humeral robusticity among non-rowing populations compared to rowing populations, and the similarity in this study of the Far North Coastal sample to the Inland River and Coastal/Bay samples does not correspond to these findings. However, there is likely more affecting humeral cross-sectional robusticity than mobility alone. Shackleford (2014), mentioned previously, found evidence of increased humeral as well as femoral robusticity in a population from Point Hope, Alaska. Compared to other populations of similar antiquity, Point Hope humeri were robust, with males demonstrating humeral robusticity approaching that of populations with high marine mobility. Point Hope female humeral robusticity was also high, although not as exaggerated as that of males. Shackleford

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attributes Point Hope humeral robusticity to the high-intensity subsistence practices of the population, which includes caribou, seal, and walrus hunting as well as whaling.

Archaeological evidence suggests that the Far North Coastal sample in the current study participated in a subsistence pattern similar to that of the Point Hope group, although with a decreased dependence on whales. The results of the current study may thus be reflecting an equalizing effect between aquatic mobility and high-intensity subsistence strategies. Despite the Coastal/Bay and Inland River groups likely having greater habitual aquatic mobility in the form of rowing, these groups likely had less intense subsistence practices related to the harvesting of fish and occasional caribou hunts. Despite seasonal sea ice likely preventing habitual marine mobility, the high-intensity subsistence patterns and related activities of the Far North Coastal sample may increase overall humeral robusticity to approximate that of the other groups. It may be useful in future research to compare the three Alaskan groups of the current study to populations with diverse mobility and subsistence patterns to determine the relative humeral robusticity of Alaskan hunter-gatherers in greater context.

Radii. Given how few differences are present in the proximal portion of the upper limb, male radii in the current study demonstrate a surprisingly high level of variation in cross-sectional parameters between site types. In accordance with predictions concerning the upper limb, radial analyses suggest that the Coastal/Bay sample has more robust radii, at least among males. TA in the Coastal/Bay group is significantly greater than the Far North Coastal and non-significantly greater than the Inland River group. In contrast, the Far North Coastal sample shows significantly smaller CA than both the Inland River and

Coastal/Bay groups, and the Far North Coastal sample also shows significantly greater MA than the Inland River and non-significantly greater MA than the Coastal/Bay sample. These results demonstrate that the Far North Coastal sample has the smallest overall diaphyseal size, lowest amount of cortical bone, and greatest amount of medullary space. Compared to the other groups, the Far North Coastal sample thus exhibits the lowest axial robusticity.

There are no significant differences between site types in male radial I_x, possibly due to morphological limitations of the radius. Since I_x reflects A-P bending rigidity, and the radius is anteroposteriorly narrow, there may be functional constraints acting on radial I_x. In contrast, both Coastal/Bay male radial I_y and J are significantly greater than the Far North Coastal group and non-significantly greater than the Inland River group, indicating that Coastal/Bay male radii are adapted to higher levels of M-L bending and diaphyseal torsion. Lastly, the shape of male radii differs between sites. Due to the shape of the radius, radial I_x/I_y values are in general below 1.0; nonpathological adult radii are mediolaterally elongated and anteroposteriorly narrow. However, Coastal/Bay I_x/I_y is significantly lower than that of the Far North Coastal group and non-significantly lower than the Inland River sample. Thus, the Far North Coastal ratio is closer to 1.0, indicating more proportional loading, while the Coastal/Bay ratio is further from 1.0, indicating more mediolateral loading.

In contrast, female radii show no significant differences in any cross-sectional parameters between site categories; the limited significant differences in female humeral properties makes this result less surprising. However, this begs the question of why

Coastal/Bay male radii exhibit greater robusticity when the corresponding humeri do not. Compared to the humerus, research concerning functional adaptation in the human radius is lacking. A number of studies have sought to understand the effects of mechanical strain on the radii of quadrupedal mammals including sheep, pigs, dogs, and horses (Rubin and Lanyon 1982, Lee et al. 1999, and Goodship et al. 1979). However, since human bipedality relieves the radius from locomotory and weight-bearing roles, such comparisons are not appropriate here.

The limited research which has studied the effect of mechanical strain on the radius have found conflicting results. For example, Ashizawa et al. (1999) compared bone mineral content, bone mineral density, periosteal area, cortical area, endocortical area, and cortical thickness of the radii of adult tennis players to age-matched controls. Information was collected from several points along the length of the radius, including mid-diaphysis (50% of bone length), mid-distal diaphysis (20% bone length from the distal end), and distal regions (4% bone length from the distal end).

At the mid-radius, the authors found that the playing arm of athletes demonstrates increased total bone mineral content, periosteal area, cortical BMC, and cortical bone area and decreased cortical volumetric density relative to the nonplaying arm (Ashizawa et al. 1999). Additionally, playing arms exhibit significantly greater strength strain index (SSI), a measure of stability against bending and torsion. The authors conclude that "physical activity induces cortical drift toward periosteal direction, resulting in a significant increase in mechanical strength despite lower volumetric density" (Ashizawa et al. 1999, 1350) in the mid-radius of playing arms. The results of this study suggest that

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high-intensity repetitive loading can induce structural adaptations in radial morphology, which is supported in the current study. Heinonen et al. (2002) found similar support for changes in radial shape without changes in density of the radii of female weight lifters.

In contrast, in a study of the effect of age on cross-sectional parameters of the mid-diaphyseal radius and distal humerus in female tennis and squash players, Kontulainen et al. (2003) found that, in the humerus, exercise-induced periosteal expansion of bone was present in athletes who began habitually playing prior to menarche and those who began playing after the onset of puberty. However, in the distal radius, exercise-induced cortical bone enlargement was not clear, and there was more evidence of changes in trabecular density in response to loading. This would suggest that, in the distal portion of the upper limb, bone material property, rather than cross-sectional morphology, is more responsive to mechanical strain. However, this study examined radial properties only in the distal portion (4% bone length from the distal end) of the bone, an area with more trabecular bone than the midshaft. So, this may not be indicative of the adaptive properties of the radial diaphysis.

The above research and results of the current study support the adaptive capabilities of the radius, but do not address why, in the current study, male radii demonstrate significant differences in cross-sectional parameters while male humeri do not. A possible explanation is the specific mechanics utilized during habitual activity like rowing. Hosea and Hannafin (2012) found that among contemporary collegiate rowers, issues with the upper limb comprised 14% of overall injuries acquired during the activity. A common injury found in the upper limb of rowers is extensor tenosynovitis, an overuse

injury caused when specific motions during rowing cause the *extensor pollicis brevis* and *abductor pollicus longus* tendons to cross over and compress the *extensor carpi radialis longus* and *brevis* muscles, which are responsible for radial abduction.

That such an overuse injury is relatively common among collegiate rowers indicates that the muscles of the forearm are subject to substantial mechanical loading during rowing. This could potentially explain why the Coastal/Bay sample, who have higher predicted marine mobility, would have significantly higher measures of radial robusticity than either the Inland River or Far North Coastal groups. However, contemporary collegiate rowing style likely differs from riverine and coastal rowing practiced by prehistoric Alaskans, so this comparison may not be entirely appropriate. Results of the current study call for additional analyses of radial cross-sectional geometry in general and of the relationship between the humerus and radius during high-intensity activities to reach a definitive explanation for the results obtained here.

Analyses of Bilateral Asymmetry

As discussed in Chapter 3, bilateral asymmetry in this study was calculated by converting differences between the left and right humeri and radii into a percentage of directional asymmetry with the following formula:

$$\%DA = (right - left)/((right - left)/2) *100$$

Since the formula subtracts left-side measurements from those of the right side, positive results indicate a right-side bias, while negative results reflect a left-bias. Analyses of male and female humeral and radial bilateral asymmetry in the current study found significant differences between site types almost exclusively among male humeri. A

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single additional significant difference in female radii was identified, but as will be discussed below, this difference is not believed to be significant regarding diaphyseal robusticity.

Among the male humeri, overall results suggest that the Far North Coastal sample has greater percentages of bilateral asymmetry than both the Inland River and Coastal/Bay groups. Far North Coastal TA asymmetry is significantly greater than both the Coastal/Bay and Inland River groups; Far North Coastal mean asymmetry is about 6.0%, Inland River about 0.8%, and Coastal/Bay about -3.5%. Male humeral CA asymmetry is non-significantly different between site types and averages between -2.5% to 5.1%. Far North Coastal MA (averaging about 10.6%) asymmetry is significantly greater than both the Coastal/Bay (about -12%) and Inland River (-5.4%) samples.

Far North Coastal male humeral I_x asymmetry significantly differs from that of the Coastal/Bay and Inland River groups. Median Far North Coastal I_x asymmetry is about 12%, Inland River is about 2.8%, and Coastal/Bay is about -7.2%. However, asymmetry of male humeral I_y does not significantly differ between sites, and mean values range between -5.7% to 12.7%. Asymmetry of Far North Coastal male humeral J is significantly greater than that of the other sites; Far North Coastal asymmetry is about 12.2%, Inland River is near 2.6%, and Coastal/Bay is -6.3%. Finally, there is no significant difference in I_x/I_y between sites; average asymmetry values fall between -1.5-0.2%.

In contrast, female humeri demonstrate no significant differences in bilateral asymmetry of any variable between site categories. The mean value of most variables

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falls between -4.5-9.6%. Additionally, most median values are positive, suggesting an overall right bias among female humeri. Similarly, male radial asymmetry shows no significant differences between site categories in cross-sectional properties. Mean values range between -7.6-12.4%, with most properties falling near or just above 0%. Female radial asymmetry demonstrates a significant difference between sites in just one property. Far North Coastal female radial TA asymmetry (mean value about -0.9%) is significantly less than that of the Coastal/Bay (average 7.0%) and Inland River (average 4.0%) groups. However, since TA does not reflect diaphyseal strength or rigidity, this significant difference may not be indicative of adaptation to loading among female radii.

Overall, analysis of upper limb bilateral asymmetry indicates that Far North Coastal male humeri have significantly different levels of bilateral asymmetry in total subperiosteal area, medullary area, A-P bending rigidity, and torsional rigidity compared to the Coastal/Bay and Inland River site types. Furthermore, the median values of all Far North Coastal variables (even those which are non-significantly different) are positive, indicating a right bias within this group. Inland River asymmetry values tend to fall around 0%, suggesting an approximately equal adaptation to stress between sides. Coastal/Bay median values are consistently negative, reflecting a bias towards the left limb among this sample.

Humans preferentially use one upper limb, and that preferential use has been shown to increase measures of long bone robusticity in the dominant hand (Roy et al. 1994). Because of the preferential use of one limb, some level of bilateral asymmetry is anticipated, at least within the humerus. As described in Chapter 1, Trinkaus et al. (1994)

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found that among industrial EuroAmericans and non-specialized prehistoric hunter-gatherer samples, bilateral asymmetry of median humeral robusticity is moderate (5-14%). Only in populations with unique patterns of exaggerated unilateral upper limb loading, such as contemporary tennis players and Neandertals, did humeral asymmetry reach higher levels (from 28-101%). However, as noted earlier, the measurements obtained in the work of Trinkaus et al. differ from those used in this study, so these percentages should not be considered baselines against which to compare the current results.

Mean asymmetry of any Far North Coastal male humeral cross-sectional variable does not exceed 13% (either left or right bias). While this degree of asymmetry does not reach exaggerated levels, asymmetry of Far North Coastal male humeral TA, MA, I_x, and J is significantly different from those of the other samples. There is therefore evidence that the habitual activities of Far North Coastal males place greater mechanical strain on one upper limb relative to the other, resulting in significantly greater humeral bilateral asymmetry than in inland riverine or coastal samples. Far North Coastal populations are known to have hunted large mammals including caribou and seals (Mason 2014 and Jensen 2014), activities that required the use of harpoons and spears, which can induce disproportional strain on one upper limb (Schmitt et al. 2003).

The lack of significant differences in female humeral bilateral asymmetry supports this inference, as big game hunting is usually performed by males. Additionally, the lack of humeral asymmetry between the Inland River and Coastal/Bay sites suggests that these populations tended to utilize the upper limbs proportionally, possibly because

habitual subsistence activities like rowing and harvesting fish do not induce

disproportionate strain on the arms. Finally, the absence of significant differences in male

radial asymmetry between sites, despite significant differences in male humeral

asymmetry between sites, suggests that the distal portion of the upper limb responds

differently to disproportionate loading than does the proximal portion of the arm.

SUMMARY AND CONCLUSION

This work compared cross-sectional geometric measures of femoral, tibial, humeral, and radial diaphyseal robusticity and compared humeral and radial bilateral asymmetry between three samples of native Alaskan hunter-gatherers. Since the publication of Julius Wolff's "law" of bone transformation, clinical research has supported the functional adaptation of bone in response to external stress, in which osteoblasts deposit new bone and osteoclasts resorb bone to maintain structural optimization during habitual activity. This process thus alters the amount and distribution of bone within a diaphysis to reflect the degree and type of loading to which a bone has been subjected over time. Engineering beam theory provides an objective method through which to analyze functional adaptation and has been used to generate hypotheses regarding habitual activity of prehistoric human populations. This research has revealed some of the factors most likely to impact long bone robusticity of past populations, such as terrain, mobility, and subsistence strategy.

The samples used in the current study were all comprised of prehistoric Alaskan hunter-gatherers who were differentiated based on geographic location and access to aquatic resources. The Far North Coastal sample is comprised of populations residing on far northern Alaskan coasts who primarily hunted large sea mammals and caribou and are believed to have had relatively high terrestrial mobility. The Coastal/Bay sample consists

of individuals residing on the more southerly Kodiak Island as well as those residing at estuaries in southwestern Alaska. Archaeological evidence suggests these groups established semi-permanent settlements, relied primarily on harvested fish for subsistence, and may have had at least some degree of aquatic mobility. The Inland River sample is comprised of riverine populations residing in inland regions of southwestern Alaska, primarily along the Yukon and Kuskokwim Rivers. Such populations likely had relatively high aquatic mobility and demonstrate split subsistence between harvested fish and caribou.

Following standard sex and age estimation, long bone measurement, and body mass calculation, computed tomography (CT) images were taken of all useable femora, tibiae, humeri, and radii diaphyses at prescribed lengths. Unilateral analyses utilized 170 femora, 154 tibiae, 167 humeri, and 147 radii while comparisons of bilateral asymmetry used 98 left-right pairs of humeri and 188 pairs of radii. Cross-sectional geometric variables were calculated directly from CT scan images and include measurements of total subperiosteal area, cortical area, medullary area, A-P bending rigidity, M-L bending rigidity, torsional rigidity, and the ratio of A-P to M-L bending rigidity.

Results of unilateral comparisons found that most significant differences between site samples were among male and female femora as well as male radii. Femoral comparisons indicate that the Far North Coastal group demonstrates significantly higher measurements of diaphyseal robusticity than the other samples. This result correlates to behavioral expectations based on differences in terrestrial mobility between samples and concurs with other research identifying hyper-robust femora among artic populations.

Tibiae, in contrast, show few significant differences between site categories in either sex, possibly due to structural optimization adaptations for the distal portion of the lower limb or the effects of ecogeographical adaptations among artic populations. Further research concerning the role of the upper and lower portion of the leg during locomotion may provide insight as to why the tibiae in this study show limited significant differences despite the numerous significant differences found among femora.

Unilateral humeral comparisons also found few significant differences in robusticity between site categories, likely because differing habitual activities between samples produced approximately equal degrees of mechanical strain. In other words, although the hunting of large mammals by the Far North Coastal sample differs from the at least occasional aquatic mobility of the Inland River and Coastal/Bay samples, these activities resulted in a similar level of strain placed on the upper arm. It may be more beneficial to compare these combined samples to other hunter-gatherer populations of similar antiquity to determine how robust Alaskan hunter-gatherers were within a larger prehistoric context.

Surprisingly, unilateral radial analyses found significant differences in male radial robusticity despite no such differences in male humeri, with the Coastal/Bay sample showing consistently and often significantly more robust radial midshafts. The radius is relatively underutilized in studies of long bone functional adaptation, so there is little literature against which to compare these results. However, clinical studies of collegiate athletes have found that rowing places strain on the muscles and tendons of the forearm rather than the upper arm. As the Coastal/Bay sample was likely rowing at least

occasionally, this may partially explain the differences in radial robusticity. These results call for more general research on radial robusticity in prehistoric human populations and for explorations of the relationship of the humerus and radius during mechanical loading of the upper limb.

The final analysis of upper limb bilateral asymmetry found significant differences in torsional and bending rigidities only among male humeri. The Far North Coastal sample demonstrates significantly greater percentages of bilateral asymmetry than the Inland River and Coastal/Bay groups. This suggests that the habitual activities, possibly related to hunting of large mammals, of male Arctic Coast hunter-gatherers placed disproportionate strain on one upper limb more so than the activities of other populations. The same pattern was not identified in analyses of male radial asymmetry, indicating different responses to disproportionate strain in the proximal and distal portions of the upper limb.

In summary, the current study finds evidence of functional adaptation to mechanical strain in prehistoric Alaskan populations. Because significant differences are concentrated on the femora of both sexes and male radii, it appears that mobility – both terrestrial and aquatic – may be the factor most strongly affecting the long bones of these populations. Additionally, while overall levels of upper limb bilateral asymmetry are relatively low, there is evidence of disproportionate loading of the upper limb consistent with strenuous sea mammal hunting in far north populations. Although additional research may contextualize these results, this study provides further insight into the activity patterns of prehistoric populations residing in a challenging arctic environment.

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