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The impact of mobility and climate on the cross-sectional geometry of long bones:
Comparing preindustrial Euro-Canadians and Inuit to other archaeological populations

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The impact of mobility and climate on the cross-sectional geometry of long bones: Comparing preindustrial Euro-Canadians and Inuit to other archaeological populations

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Résumé

L'analyse biomécanique peut être utilisée pour comprendre et interpréter l'impact de la mobilité et du climat sur la morphologie squelettique des populations humaines préhistoriques en mesurant les propriétés mécaniques des os longs. Le comportement et le climat font parties de plusieurs facteurs non-génétiques qui peuvent avoir un impact sur l'adaptation fonctionnelle osseuse en influençant les charges mécaniques sur le squelette et déclenchant le processus de modelage osseux. Cette étude se concentre sur les changements au niveau macrostructural des os longs : les propriétés mécaniques sont ainsi calculées sur plusieurs sections en coupe afin de mesurer la robustesse et la géométrie diaphysaire. Mon projet consiste à développer une collection de référence incluant quatre populations holocènes du Nord du Canada dont les Inuit Sadlermiut et trois échantillons d'Euro-Canadiens venant de Notre-Dame, Pointe-aux-Trembles et Sainte-Marie. L'objectif est de contrôler pour différents facteurs environnementaux afin de mieux comprendre l'effet de la mobilité et le climat sur la morphologie squelettique humaine. Les propriétés mécaniques d'os longs incluant l'humérus, le fémur et le tibia sont mesurées par tomodensitométrie quantitative périphérique (pQCT). Ces données sont ensuite incluses dans une méta-analyse dont les données sont tirées de la littérature scientifique, comparant d'autres populations archéologiques qui avaient différents modes de subsistance et habitaient diverses zones climatiques. Les données démontrent que les Inuit Sadlermiut ont des membres supérieurs et inférieurs plus robustes que trois échantillons de populations d'Euro-Canadiens qui ne diffèrent pas l'un de l'autre. La robustesse squelettique chez les Sadlermiut proviendrait de leur haut niveau d'activité physique nécessité par leur mode de vie de chasseur-cueilleur dans un climat rude et froid. De plus, la méta-analyse portant sur la mobilité a déterminé que le type et l'intensité des charges mécaniques habituelles ont une influence importante sur la morphologie des membres supérieurs et inférieurs tandis que celle portant sur le climat démontre qu'une relation est significative avec l'humérus. Ainsi, ce projet atteste que le processus de modelage osseux est multifactoriel et que le degré d'influence des facteurs comportementaux et environnementaux n'est pas uniforme sur le squelette.

Mots-clés: Morphologie postcrânienne humaine, géométrie de coupe transversale, robustesse, mobilité, climat, mode de subsistance

Abstract

Biomechanical analyses have been used to study the impact of mobility and climate on the skeletal morphology of past human populations through the measure of the cross-sectional geometry of long bones. Behavior and climate are one of the many non-genetic factors that can impact bone functional adaptation by influencing mechanical loads on the skeleton and triggering the bone modeling process. The present study focuses on the structural changes occurring at the macrolevel of long bones, more specifically robusticity and shape, by calculating mechanical properties at several cross-sectional locations. This project consists of creating a reference collection using four Holocene populations from northern Canada including Sadlermiut Inuit and three Euro-Canadian samples from Notre-Dame, Pointe-aux-Trembles and Sainte-Marie. The objective is to control for different environmental factors to better understand the impact of mobility and climate on human postcranial morphology. Cross-sectional properties were measured in the humerus, femur and tibia using a portable peripheral quantitative computed tomography (pQCT). These data were then input into a meta-analysis that included data, drawn from the scientific literature, from other archaeological populations with different modes of subsistence and inhabiting various climate types. The results showed that Sadlermiut Inuit had more robust upper and lower limbs than all three samples of Euro-Canadians who did not differ significantly from one another. The high measures of robusticity among Sadlermiut were attributed to the strenuous physical activity demanded by their hunting and gathering mode of subsistence in cold and harsh environmental conditions. Furthermore, the meta-analysis on mobility demonstrated that the type and intensity of habitual mechanical loading on the skeleton has a significant influence on the upper and lower limbs whereas the meta-analysis pertaining to climate only had a significant relationship with the humerus. Essentially, this project highlights the multifactorial nature of the bone modeling process and that the level of influence of behavioral versus climatic factors is not uniform throughout the skeleton.

Keywords: Human postcranial morphology, cross-sectional geometry, robusticity, mobility, climate, subsistence mode

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List of abbreviations

Second moments of area: SMAs

Polar moment of areas: PMAs

Cortical area: CA

Torsional rigidity: J

Maximum second moment of area: I_{max}

Minimum second moment of area: I_{min}

Diaphyseal shape: I_{max}/I_{min} and I_x/I_y

Second moment of area about the M-L axis: I_x

Second moment of area about the A-P axis: I_y

Euro-Canadians: EC

Hunter-gatherer: HG

Transitional: TR

Intermediate: INT

Intensive agriculturalist: IA

Tropical/Subtropical: TROP

Sami-arid/Desert: ARID

Temperate continental/oceanic: TEMP

Polar/Subarctic tundra: POL

Tardiglacial: TG

Last glacial maximum: LGM

I would like to dedicate this project to my mother, who through showing class, strength and determination to fight in the face of adversity has become a role model I will cherish for a lifetime.

Acknowledgements

1. Introduction

Biomechanical analyses are used to understand and interpret variations in human postcranial morphology. There are genetic and non-genetic factors that contribute to micro- and macrostructural changes in bone by influencing the body's bone cell response processes (Lieberman and Crompton 1998; Martin et al. 1998; Pearson and Lieberman 2004; Ruff 2007; Ruff, Holt, and Trinkaus 2006). Research has focused on examining human skeletal variation at the macrolevel, including bone size and shape, through measuring the cross-sectional geometry of long bones to explore the relationship between bone structure and changes in mechanical loading. Several factors can lead to changes in mechanical stimuli including behavioral factors such as mobility and subsistence strategy as well as environmental factors like climate and terrain. Previous studies have attempted to disentangle the role of external factors in bone functional adaptation which have differential degrees of influence depending on the environmental context (Bridges 1985; Bridges, Blitz, and Solano 2000; Churchill et al. 2000; Davies and Stock 2014; Holt 2003; Larsen and Ruff 2011; Mummert et al. 2011; Pearson 2000; Ruff 1999; Ruff 2017; Shackelford 2005; Stock 2002; Stock and Pfeiffer 2001). Although, the lack of consensus in the results of these studies suggests that more research is needed to better understand the complexity of the bone modeling process and that multiple factors may need to be explored in combination to explain morphological variations.

The main objective of this thesis is to gain insight on how factors such as mobility and climate impact bone structure through changing mechanical stimuli. This will be achieved by creating a reference collection that will contribute to existing knowledge on bone modeling processes. Results for these populations will then be included into a larger meta-analysis to contribute in building a comprehensive model for interpreting human skeletal variation that is applicable across populations. A peripheral quantitative computed tomography scanner was used to scan five locations along the length of the humerus, femur and tibia of Sadlermiut Inuit and three Euro-Canadian samples from Notre-Dame, Pointe-aux-Trembles and Sainte-Marie and measure cross-sectional geometry.

In this project, the level of mobility of a population will be based on the mode of subsistence. The assumption is that hunter-gatherers are generally more mobile than agriculturalists given the high physical demands of acquiring seasonally dependent wild resources.

Current evidence suggests that higher levels of mobility or habitual physical activity impose greater mechanical loads on the skeleton (Pearson and Lieberman 2004; Ruff 2007; Ruff, Holt, and Trinkaus 2006). Since the body must balance between maximizing bone strength and the metabolic costs of bone, changing mechanical stimuli will trigger the bone modeling process to redistribute bone where loads have increased or remove bone where loads have decreased and less tissue is needed (Bertram and Swartz 1991; Martin et al. 1998; Ruff 2007). Therefore, having a more active lifestyle, hunter-gatherers are subject to greater mechanical loads on a daily basis and are expected to have more robust morphology compared to agriculturalists. This is corroborated by studies comparing the bone structure of hunter-gatherers to populations with a more sedentary mode of subsistence that generally found greater postcranial robusticity in the former as expected (Churchill et al. 2000; Holt 2003; Ruff and Hayes 1983; Ruff 1999; Stock 2006; Shackelford 2005).

Furthermore, the bone structure of populations will be examined according to the climate zone of the geographical area and period in which they inhabited. Climate can impact skeletal morphology directly through natural selection based on Allen's and Bergman's Rules, and indirectly through changing environmental conditions, topography and diet which is dependent on the availability and abundance of resources. Based on Allen's and Bergman's rules, populations living in extremely cold climates tend to have a small and stocky body shape with shorter extremities as well as greater bone girth than individuals living in warmer environments (Allen 1877 and Bergmann 1848 in Pearson 2000; Weiss 2003). Previous studies have found contradicting results with respect to body mass, however, they consistently observed high correlations between body proportions and climate including temperature and humidity. Results showed that populations living in colder conditions had smaller stature and shorter bone lengths as well as more robust morphology in some cases than populations from warmer climates (Pearson 2000; Ruff 1994; Stock 2002). Therefore, the samples from polar/subarctic tundra climates in this study are expected to have the heaviest body mass, shortest long bone lengths and greatest bone robusticity than all other climate groups.

A comparison between Inuit and Euro-Canadians will provide insight into whether their distinct levels of mobility based on the mode of subsistence (hunter-gatherer vs. intermediate/intensive agriculturalists) and climate types (polar/subarctic tundra vs. temperate

continental/oceanic) determined morphological differences. It is expected that the Sadlermiut Inuit are predisposed to shorter limbs and heavier body mass due to their extreme polar/subarctic tundra climate based on Allen's and Bergmann's rules, and will have greater measures of robusticity in the lower limbs than Euro-Canadians as a result of their mobile hunting and gathering mode of subsistence that demands higher levels of physical activity (Hypothesis 1.1). Subsequently, Inuit will have more elliptical shaped diaphyses due to their highly active lifestyle that imposes strain in stereotypical directions causing elongation along the A-P axis, thus creating more resistance (Hypothesis 1.2). When examining the upper limbs, it is expected that the high marine mobility of Sadlermiut Inuit will be compounded by their climate-related small body proportions and result in larger cross-sectional properties indicating more robust upper limbs compared to Euro-Canadians (Hypothesis 2.1). Moreover, the strenuous physical activities on the upper limbs involved in hunting and processing game which represent an important dietary source for Inuit impose stress along the anteroposterior axis causing lengthening of that plane and more elliptical shaped diaphyses (Hypothesis 2.2).

For the meta-analysis pertaining to mobility, populations with a hunting and gathering mode of subsistence are more active and thus, will have more robust lower limbs and more oval long bone diaphyses than transitional, intermediate and intensive agriculturalists (Hypothesis 3.1). Moreover, the bone structure of transitional, intermediate and intensive agriculturalists is expected to reflect increasingly sedentary behavior through gracilization (Hypothesis 3.2). With regards to the upper limbs, hunter-gatherers will be more robust than intermediate populations due to the introduction of mechanized tools with agricultural development that alleviated loading on the upper limbs (Hypothesis 4.1). Also, diaphyseal shape will be significantly more oval in hunter-gatherers than any other subsistence division as a result of differences in the type of habitual activities such as hide scraping in foragers and plowing among agriculturalists (Hypothesis 4.2). For the meta-analysis about climate, populations from extremely cold climates such as polar/subarctic tundra are predicted to have the highest measures of lower limb (Hypothesis 5.1) and upper limb (Hypothesis 5.2) robusticity compared to all other climate categories.

The present project is divided into five parts: theoretical framework (chapter 2), literature review (chapter 3), materials and methods (chapter 4), results (chapter 5), and discussion and conclusion (chapter 6). The theoretical framework will outline the underlying principles of

biomechanical analyses such as Wolff's law and Beam theory. The literature review provides an overview of current knowledge on the relationships between postcranial robusticity, mobility and climate, which are the focus of this project, and develops the research hypotheses. The results and discussion/conclusion chapters will be subdivided into three parts; the first presents the biomechanical analysis of Sadlermiut Inuit and Euro-Canadians, the second addresses the meta-analysis in relation to mobility and the third discusses the meta-analysis according to climate. The interpretations will be made in light of ethnohistorical, bioarchaeological and biomechanical research.

2. Theoretical framework

2.1. Underlying theory: From Wolff's law to bone functional adaptation

Biomechanics employs mechanical principles to the study of skeletal remains in order to examine the factors that affect the development of bone structure and function. This approach was initially founded on the notion of *Wolff's law* which subsequent researchers framed as the process of bone functional adaptation under rigid mathematical rules (Bertram and Swartz 1991). The modern concept of *Wolff's law* is composed of three underlying principles. The first is that bone strength and rigidity must be optimized relative to tissue weight. For instance, the trabecular structure at a specific location of bone will have to compromise between the amount of tissue used to support mechanical loads and maintaining flexibility for shock absorption. This maximization of bone strength is limited by the expensive metabolic cost of bone which has double the density of other bodily tissues and, thus, is balanced by minimizing bone mass to decrease the energetic demands of physical activity (Martin et al. 1998). The second concept, derived from drawing comparisons between the human femur and a crane like beam, stresses that the internal trabecular architecture will be aligned with principal stress directions. Essentially, long bones have trabeculae oriented according to the stress trajectories imposed by different mechanical forces (Martin et al. 1998; Ruff 2007). The third concept explains that the skeleton adapts through a physiological self-regulating system of bone cells that sense and respond to mechanical stimuli (Bertram and Swartz 1991; Martin et al. 1998) and it is the magnitude and orientation of mechanical loadings that influence the location of bone cell response.

Wolff's law was criticized for its strict mathematical reasoning and its underlying premise that equated long bones with homogenous beam like structures (Bertram and Swartz 1991; Ruff, Holt, and Trinkaus 2006). Developments in our knowledge of skeletal biology have since led to a replacement of the strict version of *Wolff's law* with a more generalised model of bone functional adaptation underlined by two key principles. First, bone has a certain degree of plasticity which

allows organisms to respond to changes in living conditions through structural modifications. Second, bone cells can respond locally to mechanical stresses acting on specific region's of the skeleton (Ruff, Holt, and Trinkaus 2006). A bone's ability to remain both stiff and flexible in response to mechanical loads derives from its internal structure and composition (Figure 1). Therefore, bone functional adaptation suggests that bone tissue adapts both in the trabecular architecture and in the distribution of the cortical bone to mechanical forces imposed by physical activity during an individual's lifetime. Changes in bone structure as a result of strain from mechanical loading occur at both the micro and macrostructural level (Lieberman and Crompton 1998). Examples of microstructural changes are collagen organisation and
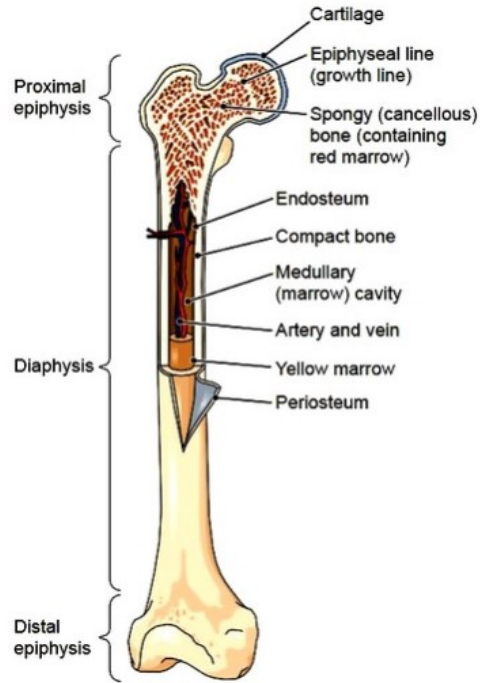
Figure 1:The internal structure of a long bone. Image by http://15.race.boldhighend.de/long-bone-structure.html.

density as well as mineralisation whereas macrolevel changes include bone size and shape to redistribute stress (Lieberman and Crompton 1998; Pearson and Lieberman 2004). It is important to acknowledge, however, the limitations of applying a simplistic model to the complex processes involved in bone adaptation (Bertram and Swartz 1991; Martin et al. 1998; Ruff 2007).

2.2. Bone functional adaptation

The adaptation of bone to its mechanical environment occurs via a complex process of bone cell response (Figure 2). Bone is synthesised by osteoblasts, a type of skeletogenic cell, that produces collagen and bone mineral crystals. Bone mineral is the principal component of bone and serves to resist against compressive stresses by providing stiffness. Collagen, the second component of bone, organises bone mineral crystals and is responsible for
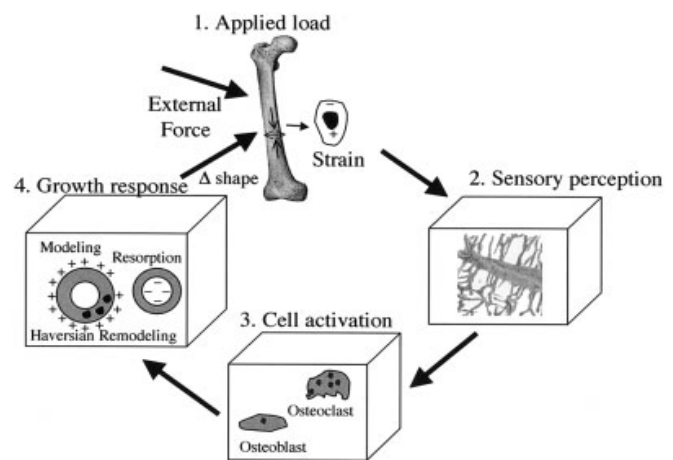
Figure 2: The bone response to mechanical loading (Pearson and Lieberman 2004).

elasticity in response to tension stresses. Bone functional adaptation occurs when applied mechanical loads are higher or lower than a bone's strain magnitude. Consequently, bone cells sense mechanical stimuli and then transduce the signal, whether bone forming or bone resorbing, to other affected areas throughout the bone, thereby activating a response in osteogenic cells to adapt to new stresses (Pearson and Lieberman 2004). Depending on the signal, osteoblasts are activated for bone modeling, or deposition, to grow new bone whereas osteoclasts are deployed for bone remodeling, or resorption where bone tissue is removed, and new tissue is formed. Although, for the remodeling of intracortical bone (i.e. the replacement of existing bone within the cortex), known as Haversian remodeling, both osteoclasts and osteoblasts are recruited consecutively (Martin and Burr 1989 in Pearson and Lieberman 2004). Thus, communication between skeletogenic cells allows bone to customize adaptations to variations in mechanical stimuli. Bone functional adaptation has been described as a compromise between modeling and remodeling where certain properties such as density, bone mass, shape, and flexibility are favoured (Lieberman and Crompton 1998).

A simplified model adapted by Ruff (2007) illustrates the feedback involved in the process of bone remodeling, the final phase of bone cell response (Figure 3). This process includes activation, resorption and formation (ARF) for remodeling or formation and resorption for modeling (Martin et al. 1998; Ruff 2007). Bone functional adaption is activated when tissue has been deformed or damaged by the strain of mechanical loads and can occur at the
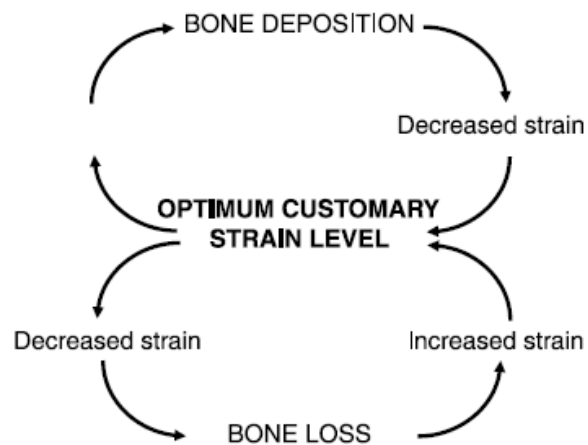
Figure 3: A feedback model of bone functional adaptation (Ruff 2007).

periosteal, endosteal and trabecular surfaces. For instance, bone deposition will be activated when bone is under higher strain due to increased body mass or physical activity to repair microcracks and strengthen bone, thereby decreasing strain to optimum levels. On the other hand, when strain has decreased, either from weight loss or inactivity, bone resorption is stimulated to adjust the metabolic cost by weakening the bone to return to an "optimum customary strain level (Ruff 2007, 184)." This strain threshold changes depending on the skeletal location, genetics, age, disease and

hormonal status of the individual (Pearson and Lieberman 2004; Ruff 2007; Ruff, Holt, and Trinkaus 2006). Ruff and colleagues acknowledge the limitations of applying a simplistic model to such a complex physiological process, however, the model maintains its validity when comparing across genetically or morphologically similar populations and species (Ruff, Holt, and Trinkaus 2006).

Mechanical strain becomes recorded in the skeleton through this self-regulating system of bone remodeling and modeling that serves to repair damaged tissues and modify bone to suit new physical demands (Ruff 2007). The intensity of the skeletal response is determined by the frequency and magnitude of strain, the loading history as well as genetic and non-genetic factors such as diet (Ruff, Holt, and Trinkaus 2006). Modeling occurs most frequently during ontogeny and only in mature skeletons when under extreme mechanical loads that cause permanent fractures and require bone deposition. In contrast, the bone remodeling process is mainly responsible for the maintenance and repair of bone tissue in adulthood at the microstructural level (Martin et al. 1998; Ruff, Walker, and Trinkaus 1994). For this reason, biomechanical analyses of macrostructural changes in mature skeletons result from bone modeling that occurred during development and thus, reflect activity patterns during youth.

2.3. Cross-sectional geometry

2.3.1. Types of mechanical loading

A popular niche of biomechanics involves examining the cross-sectional geometry of long bone diaphyses through a beam model. The properties are measured perpendicular to the bone's longitudinal axis and are hypothesized to reflect the stress imposed from external mechanical loads. Mechanical properties reflect bone strength, meaning resistance to breakage, and rigidity, referring to a bone's ability to resist deformation. Strength and rigidity are measured either from an axis going across the section or a centroid marking the center of mass of the cross-section as illustrated in Figure 4 (Ruff 2007).
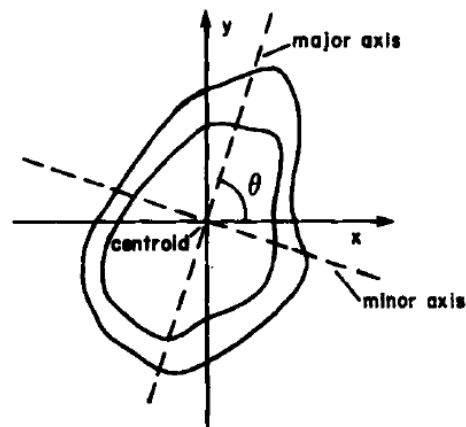
Figure 4:The neutral axes of a long bone cross-section (Ruff and Hayes 1983)

Loads applied to a given area of material create stress and strain. Stress refers to the pressures building inside the bone and strain is the measure of deformation of bone tissue under stress. There are five types of mechanical loads or forces: axial compression and tension, bending, shear and torsion (Figure 5). Axial compression occurs when forces are compressing the bone along its longitudinal axis, for example body weight acting on the skeleton, creating compressive stress and strain. In contrast, tension occurs with pulling forces along the same axis, namely when muscle contracts and pulls the attached bone, producing tensile stress and strain. Tensile and compressive stress can each be defined as normal stress, varying in direction (+ or -). Bending occurs when a force or moment is applied to the bone, causing the element to bend in activities like running and jumping. Bending loads are a combination of compressive and tensile stress separated by the neutral axis. Shear loading involves two parallel forces coming from opposite directions that displace one portion of bone from

Figure 5: Types of mechanical loading on bone: Axial compression and tension, bending, shear and torsion. Image from https://www.slideshare.net/NabapallabDeka/introduction-to-analysis-of-strain-and-strain-in-human-bone.

another causing friction, or shearing stress, and is experienced in activities such as walking and squatting. A bone is under torsional loadings when it is twisted along its longitudinal axis making the bone tissue that compose it susceptible to shearing, bending as well as tensile stresses. This type of loading occurs in the humerus when throwing objects for example (Pearson and Lieberman 2004; Ruff 2007; Ruff and Hayes 1983; Ruff, Holt, and Trinkaus 2006).

2.3.2. Cross-sectional geometric properties

Cross-sectional geometric properties of bones trace changes in mechanical loading, or the amount of force applied to an element, during an individual's life. Biomechanical studies examining the relationship between mobility and postcranial morphology have focused on the properties that reflect diaphyseal robusticity in long bones such as bending and torsional rigidity and strength. Bending and torsional rigidity refer to the bone's ability to resist against deformation from bending and torsional loads, while bending and torsional strength reflects the ability of a long

bone to resist against breakage. Diaphyseal geometry pertains to the shape of the long bone diaphysis whereas robusticity refers to the thickness of bone relative to its length and body mass as a measure of strength. Moment areas are properties that provide information on the relative distribution of bone within a cross-section as well as the cortical thickness. Moment areas are important in the interpretation of bone structure because their distribution relative to the centroid influences the measure of strength and rigidity against compressive and tensile loads (Ruff 2007; Ruff and Hayes 1983; Stock 2002).

Second moments of area (SMAs) are properties that measure the strength and rigidity of long bones against bending stresses along an axis, whereas polar moment of areas (PMAs) are measured about the centroid for torsional stresses (Ruff 2007). The mechanical properties that estimate bending and torsional strength are known as section moduli. The bone fibers that lie at the most external part of a section experience the greatest bending and torsional stress, therefore section moduli is the bending rigidity that can account for the distance from a section's outermost surface to an axis (Ruff and Hayes 1983). Cross-sectional geometric properties shed light on the resistance of long bones to changes in mechanical stimuli. There are other characteristics of bone involved in estimating rigidity and strength such as bone density. However, this information is limited in archaeological samples due to alterations from taphonomic processes. Furthermore, research has found that mechanical rather than material properties are more susceptible to change in response to variation in loads and thus, are a better measure of bone functional adaptation. Although cross-sectional properties have proved useful in examining bone functional adaptation, it is important to remember that they represent a simplified measure of the mechanical loading history of a bone (Ruff 2007).

2.4. Obtaining cross-sectional data

Biomechanical analyses can be conducted using imaging technology or external measurements. Imaging techniques such as computed tomography (Ct-scan), peripheral quantitative computed tomography (pQCT) and radiography produce 2D images of long bone cross-sections and represent non-invasive methods of acquiring cross-sectional slices. Another technique involves direct sectioning of long bone diaphyses and digitizing slices using an optical scanner. Once 2D images of cross sections are produced, there are several programs such as ImageJ or NIH image that are used to extract the cross-sectional properties of these images (Ruff 2007). There are limitations, however, to using imaging techniques because of differences in machine

calibration, handling experience and the location where research is conducted. When this technology is not available or too costly, researchers have developed a series of external measurements that can be used to calculate mechanical properties (Stock and Shaw 2007).

2.5. Factors impacting long bone morphology

The development of bone form and function is influenced by several genetic and non-genetic factors. Genetic, or intrinsic, factors are especially relevant during ontogeny and contribute to variations in morphology between individuals. Furthermore, genetics play a role in determining the target strain level (Ruff 2007). Research has examined genetic influence on skeletal features such as bone mass and density, bone mineral content, length and volume, however, there remains a lot of uncertainty in the level of control of genetic compared to environmental factors in determining skeletal morphology, particularly cross-sectional geometry (Ruff, Holt, and Trinkaus 2006).

The endocrine system is another factor that regulates bone formation. Hormones such as estrogen and leptin impact the bone modeling process through their influence on osteogenic cells such as osteoblasts and osteoclasts. In this way, hormones impact the bone cell response to strain through activating or inhibiting osteoblasts and in consequence, bone mineral density and content. Furthermore, certain hormones, such as parathyroid hormone (PTH), can impact the threshold required for the activation of bone cell response to changes in mechanical stimuli. The role of hormones in modulating cell production raises the importance of considering differences between sexes when examining long bone morphology. For instance, changes in the concentration of estrogen among females or testosterone among males occurring with age lead to alterations in the rate of bone deposition and resorption for endosteal and subperiosteal surfaces (Pearson and Lieberman 2004), resulting in variation in cross-sectional properties between the sexes that are unrelated to mechanical stimuli. Moreover, sex is relevant when considering differences in gender roles and the sexual division of labor which influences an individual's daily activities. Consequently, the sexual dimorphism in body form resulting from hormonal differences can be compounded by discrepancies in the type and intensity of physical activities according to sex that further differentiate the morphological patterns between males and females.

Age is an important aspect to consider during biomechanical studies because bone functional adaptation is different between juveniles and mature individuals. Since bone growth

stops around young adulthood, modeling usually significantly increases bone mass solely in youth whereas in mature individuals' bone is mainly conserved. For this reason, bone functional adaptation is more sensitive to mechanical stimuli during development than during adulthood, where change will be more subtle. Therefore, in adulthood, contrary to macrostructural changes, microstructural changes in bone accumulate over the long-term and are a reflection of activity (Bertram and Swartz 1991; Ruff, Holt, and Trinkaus 2006). Subsequently, age affects the composition of bone, meaning bone mineral and collagen, thereby reducing the strength and resistance to applied loads (Pearson and Lieberman 2004). Age is associated with processes like endosteal and subperiosteal surface expansion that alter the distribution and quantity of bone in a cross-section and influence mechanical properties. The endosteum and periosteum are vascular membranes in which the former lines the medullary cavity and the latter lines the area beneath the outer surface of bone (Ruff 2007; Ruff and Hayes 1982; Ruff and Hayes 1983). Moreover, age is associated with pathologies such as osteoporosis, which occurs when there is excessive bone resorption due to hormonal changes which, as described above, moderate the balance between bone deposition and resorption. Aging can impact a cell's ability to react to mechanical stimuli (Pearson and Lieberman 2004).

Health and nutrition impact postcranial morphology by regulating bone growth. Adequate nutrition, complete with nutrients like vitamins and essential amino acids as well as a sufficient caloric intake, is necessary for normal development and overall bone health. Malnourished individuals have stunted growth and brittle bones that are more susceptible to breakage due to the role of diet in maintaining bone health. Certain types of infectious, chronic or metabolic diseases over the short and long term interfere with bone cell response and can result in modifications of long bone morphology. Subsistence strategies impact bone by influencing the level of mobility of populations depending on the resources and technology used to sustain themselves (Larsen et al. 2015; Mummert et al. 2011).

Long bone morphology is also impacted by climate through long-term genetic adaptation and its influence on other factors such as subsistence. There are body proportions that are typical of specific climatic conditions. Individual's in colder climates tend to be smaller in stature and have shorter limbs than those from warmer climates (Ruff 1994; Stock 2002). The assumption is that smaller body proportions provide better thermoregulation, hence heat retention to survive in cold conditions. Furthermore, colder environments tend to have sparsely distributed and clustered

resources that require higher levels of mobility than warm environments with densely rich resources (Stock 2002).

Mobility is a key factor involved in bone functional adaptation by altering the mechanical loading regime of long bones. Its effect can be mediated by variations in topography and types of physical activity. For instance, flat compared to mountainous terrain changes the direction and magnitude of loading forces during walking and running. Terrestrial mobility involves greater loading on the lower limbs whereas marine mobility involves loading of the upper limbs, which will translate into morphological differences between the types of limbs (Ruff 2007).

Biomechanical analyses investigating the relationship between postcranial morphology and mobility must consider the complexity of bone functional adaptation and the factors that control the bone cell response when drawing conclusions about past human behavior. With a better understanding of the relationship between bone structure and physical activity, scientists can improve their interpretation of past daily life based on patterns identified in bone.

Chapter 3: Literature review

The following chapter aims to provide an overview of current knowledge on the impact of mobility and climate on human postcranial morphology and forms the basis of hypotheses proposed in the present project. Research has tended to investigate mobility and climate in connection with a population's mode of subsistence because these external factors interact and influence one another.

3.1. Mobility

Biomechanical analyses have shown that the bone modeling process occurs as a result of alterations in mechanical loading imposed during changes in habitual physical activity which affects the cross-sectional properties of bone (Ogilvie 2000). As a consequence, the type and intensity of physical activity will differentially impact upper and lower limbs, thus the two types must be treated separately. It is hypothesised that decreasing levels of habitual physical activity lead to a reduction in postcranial robusticity and rounder diaphyseal shape by influencing mechanical stimuli (hypothesis of gracilization). Research investigating this hypothesis has focused on examining changes in bone functional adaptation through temporal analyses of increased sedentism or in relation to subsistence transitions in past human populations (Bridges 1989; Bridges, Blitz, and Solano 2000; Churchill et al. 2000; Holt 1999; Knobbe 2010; Larsen and Ruff 2011; Ogilvie 2000; Marchi et al. 2006; Pearson et al. 2014; Ruff 1999; 2007; Ruff et al. 1984; Shackelford 2005; Stock 2002; Wescott and Cunningham 2006; Zaleski 2013). Both of these avenues predict that increased sedentism leads to gracilization and involve comparing the morphology of hunter-gatherer and agriculturalist populations. The assumption is that hunter-gatherers are generally more mobile than agriculturalists given the high physical demands of acquiring seasonally dependent wild resources. Consequently, having a more active lifestyle, hunter-gatherers would have a more robust morphology compared to agriculturalists (Holt 2003; Shackelford 2005; Ruff 2007; Stock 2006; Zaleski 2013).

3.1.1. Subsistence

3.1.1.1. The impact of mobility on the lower limbs

Based on the gracilization hypothesis, hunter-gatherers are expected to have greater skeletal robusticity and more oval diaphyseal shape than agriculturalists. A foraging lifestyle

involves strenuous physical activity which imposes heavy mechanical loads on the lower limbs. Consequently, the bone modeling process will redistribute bone to resist against this intense loading regime and prevent deformation by increasing bone rigidity and cortical thickness. Subsequently, engaging in activities such as walking, running and climbing require contraction of the quadricep and hamstring muscles causing high bending strain along the A-P axis. Therefore, the femur is extended along the A-P plane and becomes more oval in shape. Based on this reasoning, hunter-gatherers, who habitually engage in these types of activities, should have more robust lower limbs and elliptical shaped diaphyses compared to more sedentary populations, typically agriculturalists (Ruff 2007; Ruff et al. 1984; Stock 2002; Zaleski 2013).

The morphology of each skeletal element will cause differential impacts on bone structure in relation to the type and intensity of the activity, such as repetitive low-impact loading (running) compared to high impact loading (jumping) (Pearson et al. 2014). Since bone adapts locally to changes in mechanical loads, there can be conflicting evidence between cross sections of the same element that reflect different kinds of loading regimes. For instance, it is suggested that the femur midshaft is a better indicator of terrestrial mobility, meaning the distance traveled while walking or running, which impacts A-P/M-L bending strength. In contrast, the impact of terrestrial mobility at the subtrochanteric region is lessened by the fixed position of the hip joint that follows the body's center of gravity and involves only minor changes in the flexion and extension of the hip (Ruff 1987; 1999). Consequently, the subtrochanteric section is suggested to be an indicator of habitual behavior patterns since it is closest to the hip joint which receives all weight-bearing activities (Zaleski 2013). Based on this reasoning, section locations of a skeletal element provide different information on an individual's mobility patterns such as terrestrial mobility or general levels of physical activity.

There is a general consensus that hunter-gatherers tend to be more robust than agriculturalists based on evidence of reduced skeletal robusticity and increased diaphyseal circularity when shifting from a hunting and gathering mode of subsistence to food production (Churchill et al. 2000; Holt 1999; Holt et al. 2017; Larsen et al. 1995; Marchi et al. 2006; Ogilvie 2000; Pearson 2000; Ruff 1999; Ruff et al. 1984; Shackelford 2005; Stock 2002). These results were interpreted as indicative of changes in physical activity or mobility attributed to either growing dependence on semi-sedentary settlements and food production (Holt 1999; Holt et al.

2017; Larsen et al. 1995; Marchi et al. 2006; Ogilvie 2000; Pearson 2000; Ruff 1999; Ruff et al. 1984; Shackelford 2005; Stock 2002), technological innovations (Holt et al. 2017; Shackelford 2005) or climate change and shifts in resource availability and abundance (Churchill et al. 2000; Holt 1999; Pearson 2000; Shackelford 2005; Stock 2002).

On the other hand, there is significant variation in research investigating the impact of the Neolithic transition on lower limb morphology. Studies have shown evidence of stable (Bridges, Blitz, and Solano 2000; Holt 2003; Marchi et al. 2006; Shackelford 2005; Wescott and Cunningham 2006) or even increased (Bridges 1989; Bridges, Blitz, and Solano 2000; Holt et al. 2017; Larsen and Ruff 2011; Pearson 2000; Shackelford 2005; Wescott and Cunningham 2006) skeletal robusticity with reduced mobility which conflicts with subsistence-related predictions in cross-sectional geometry. These results were interpreted as reflecting either similar loading patterns and levels of physical activity (Bridges, Blitz, and Solano 2000; Holt 2003; Shackelford 2005), agricultural introduction or intensification (Bridges 1989; Bridges, Blitz, and Solano 2000; Wescott and Cunningham 2006), poor health (Wescott and Cunningham 2006; Zaleski 2013), the result of variability in the accuracy of cross-section locations for representing habitual behavior (Shackelford 2005), differences in the type of habitual activity that have not yet been explored (Shackelford 2005) or the influence of a confounding factor associated with a specific situational context (Holt et al. 2017; Marchi et al. 2006; Larsen and Ruff 2011; Pearson 2000; Wescott and Cunningham 2006).

3.1.1.2. The impact of mobility on the upper limbs

Morphology in the upper limbs is impacted by general activity levels rather than variations in the level of terrestrial mobility because its functions are non-locomotor in nature (Ruff 2007). It is hypothesised that a decrease in physical activity involving the upper limbs will lead to similar patterns of increased gracilization as observed in the lower limbs by altering the magnitude and orientation of mechanical loads. Research investigating gracilization in the upper limbs through temporal analyses or subsistence transitions predict that hunter-gatherers will have more robust upper limbs than agriculturalists due to their physically strenuous lifestyle that imposes drastically different mechanical stresses (Churchill et al. 2000; Shackelford 2005; Wescott 2001).

Cross-sectional properties of the upper limbs did not show a consistent pattern, with studies indicating either decreased (Bridges, Blitz, and Solano 2000; Holt et al. 2017; Larsen and Ruff

2011; Marchi et al. 2006; Shackelford 2005; Stock et al. 2011; Wescott 2001), stable (Bridges 1989; Wescott 2001; Wescott and Cunningham 2006) or even increased (Bridges 1989; Bridges, Blitz, and Solano 2000; Churchill et al. 2000; Holt et al. 2017; Larsen and Ruff 2011; Marchi et al. 2006; Ogilvie and Hilton 2011; Shackelford 2005; Wescott 2001) skeletal robusticity with reduced mobility. Studies demonstrating a general reduction in upper limb robusticity and increased diaphyseal circularity were interpreted as evidence of subsistence-related variations in upper limb loading regimes through either a change in mobility and/or food procurement techniques (Holt et al. 2017; Larsen and Ruff 2011; Marchi et al. 2006; Shackelford 2005; Stock et al. 2011; Wescott 2001) or technological innovations (Bridges, Blitz, and Solano 2000; Holt et al. 2017; Shackelford 2005). However, studies demonstrating stable measures of upper limb robusticity and diaphyseal shape between hunter-gatherers and agriculturalists were attributed to either similar patterns in the type and intensity of physical activity (Bridges 1989; Wescott 2001; Wescott and Cunningham 2006), the intensification of food production (Bridges 1989; Bridges, Blitz, and Solano 2000; Holt et al. 2017), strenuous agricultural techniques (Bridges 1989; Bridges, Blitz, and Solano 2000; Holt et al. 2017; Marchi et al. 2006; Ogilvie and Hilton 2011), harsher environmental conditions (Churchill et al. 2000; Shackelford 2005) or regionally specific socioeconomic factors (Holt et al. 2017; Larsen and Ruff 2011).

An overview of research investigating bone functional adaptation in the upper and lower limbs in relation to subsistence yielded inconsistent results. This demonstrates the sensitivity of cross-sectional properties to changes in mechanical stimuli and reflects the plasticity of bone (Holt 1999). Therefore, the relationship between mobility, subsistence and diaphyseal geometry is more complex than the simple correlation proposed in the gracilization hypothesis. Moreover, subsistence divisions are inherently problematic given their subjectivity and the behavioral variation within groups. Hunter-gatherers specifically exhibit considerable variation in bone structure which attests to the diversity in the level of mobility and food acquisition techniques that exists among foraging groups (Kelly 1983; Stock 2002). Despite apparent discrepancies in results pertaining to subsistence, studies tend to support the broader notion that physical activity influences bone functional adaptation when local socioenvironmental factors are considered. Subsistence shifts bring different behavioral changes relative to a region's socio-ecological conditions and thus, lead to regionally specific morphological adaptations (Larsen and Ruff 2011; Ruff 1999). Essentially, multiple contextually specific factors are operating together to moderate

the process of bone cell response to external stressors (Churchill et al. 2000; Pearson 2000; Ruff 1999).

3.1.2. Terrestrial versus marine mobility

Terrestrial mobility involves more frequent loading of the lower limbs while marine mobility relies on upper body strength. Research on marine and terrestrial mobility typically focuses on comparing hunting and gathering populations. Based on the gracilization hypothesis, populations with a terrestrial subsistence economy are expected to have greater bending and torsional rigidity, meaning higher skeletal robusticity, in the lower limbs than predominantly maritime populations. In turn, populations that move around by watercraft (i.e. canoe or kayak) for subsistence-related activities are predicted to have more gracile lower limbs but more robust upper limbs (Churchill 1994; Shackelford 2005; Stock 2002; Stock and Pfeiffer 2001; Weiss 2003; Zaleski 2013).

Studies examining marine and terrestrial-based economies have demonstrated that groups with high marine mobility tend to have greater upper limb robusticity while terrestrially mobile populations have the highest measures of robusticity in the lower limbs (Churchill 1994; Knobbe 2010; Stock 2002; Stock and Pfeiffer 2001; Weiss 2003). The results were interpreted as evidence that behavioral patterns differ significantly when inland versus offshore resources are exploited despite general similarities in subsistence strategy. There were variations in diaphyseal shape within mobility groups that provided an indication of how different types of activities differentially impact bone. Activities such as rowing or casting nets exert higher shearing stresses that radiate on all planes to the external surface of the bone, thereby creating a rounder diaphyseal shape in populations that regularly engage in this behavior (Shackelford 2005, 2014; Knobbe 2010 in Zaleski 2013). In contrast, populations that repeatedly participate in whaling or hunting will have more elliptical diaphyses due to the thrusting movement that requires more resistance on the anteroposterior axis than on the mediolateral axis (Shackelford 2005, 2014).

On the other hand, comparisons between the effects of marine and terrestrial mobility do not consistently follow predictions. An individual's daily life is not a direct reflection of their subsistence economy, rather habitual activities are influenced by factors such as environmental conditions and sexual division of labor. Also, different activities can engender similar cross-sectional geometry when they involve the same movements, or loading regime (Davies and Stock

2014; Weiss 2003; Zaleski 2013). For instance, certain marine foragers lead a highly active lifestyle on land that involves intense loading of the lower limbs resulting in similar or even greater cross-sectional properties compared to primarily terrestrial groups. Populations with strict sexual division of labor within each economy have shown similar levels of skeletal robusticity in both sexes despite females rarely participating in hunting trips or rowing watercrafts (Davies and Stock 2014; Knobbe 2010; Shackleford 2014; Weiss 2003; Zaleski 2013). The mode of subsistence does not necessarily reflect the magnitude of marine and terrestrial mobility since various habitual activities contribute to upper and lower limb robusticity. This suggests that the categorisation of populations under a marine or terrestrial subsistence economy may be an oversimplification because it omits habitual behaviors unrelated to subsistence that have the potential to impact bone functional adaptation (Davies and Stock 2014; Stock 2006; Weiss 2003).

3.2. Climate

Previous research investigating the role of climate in influencing skeletal morphology initially examined morphological differences according Bergmann's and Allen's rules. Bergmann hypothesised that populations from cold environments will have heavier body mass and consequently, greater bone girth for structural support than warmer climates (Bergmann 1848 in Pearson 2000). Allen stipulated that individuals living in colder climates will have shorter limbs and stockier body proportions than those living in warmer environments for better thermoregulation (Allen 1877 in Pearson 2000; Weiss 2003). Subsequently, biomechanical analyses incorporated these rules to compliment cross-sectional data when comparing skeletal robusticity in populations from different climate types. Bergmann's and Allen's rules were applied by measuring body size indices such as body mass, limb length, crural and brachial indices as well as body breadth.

Biomechanical studies have mainly compared populations from extremely cold and hot climates. The idea being that inhabiting opposing environmental conditions imposes drastically different selective pressures on the body that will translate into divergent cross-sectional geometry. Based on this notion, it is hypothesised that there will be a negative correlation between climate and skeletal robusticity in which the colder the conditions the more robust the morphology (Churchill et al. 2000; Pearson 2000; Ruff 1994; Stock 2002, 2006; Stock et al. 2011). Studies have shown evidence of climate mediated bone functional adaptation between polar versus tropical

climates by demonstrating higher skeletal robusticity in populations from colder environments whereas warmer climates were more gracile (Pearson 2000; Stock 2006). There may be differential bone functional adaptation between the upper and lower limbs in response to climate, meaning that the degree of influence of climate varies depending on the skeletal element and its orientation. The proximal elements of the lower limb and the distal elements of the upper limb showed the most significant correlations with climate. In turn, the distal portion of the lower limb and proximal portion of the upper limb were largely determined by mechanical stimuli. These results indicate that limbs may have different adaptive constraints on bone modeling associated with balancing the metabolic costs for optimal bone distribution to resist against mechanical loads and thermoregulatory selective pressures (Shackelford 2005; Stock 2002, 2006).

Studies have suggested that climate does not directly impact bone structure. Rather, it is through its affect on the ratio of body mass relative to stature which alters loading on the limbs that climate influences diaphyseal robusticity (Pearson 2000; Stock 2002, 2006). Therefore, despite evidence of a climatic component in cross-sectional geometry, climate seems to play a larger role in determining body shape/size indices than skeletal robusticity. This is corroborated by evidence of the presence of several morphological adaptations in response to cold climates such as increased body mass and stature which produce more metabolic heat, low crural and brachial indices which better retain heat, and high bi-iliac breadth which is effective for thermoregulation (Churchill et al. 2000; Pearson 2000; Ruff 1994; Stock 2002; Stock et al. 2011). For this reason, including measurements for body size in biomechanical analyses on climate will provide a better indication of whether a confounding factor and/or long-term genetic adaptation is responsible for a correlation between environment and postcranial morphology.

3.3 Interaction between mobility and climate: Hypotheses

The present literature review demonstrated that the aforementioned factors do not act independently but may interact to determine bone functional adaptation. Climate can indirectly influence skeletal morphology by mediating mobility, nutrition and subsistence-related activity patterns through determining the availability and abundance of resources. For instance, climate change may cause shrinking territory size and resource scarcity thereby reducing mobility and increasing risk of malnutrition while also diversifying behavior (Churchill et al. 2000; Holt 2003; Pearson 2000; Shackelford 2005; Stock 2002; Wescott 2001; Zaleski 2013). Inhabiting harsh

climatic conditions is associated with a physically demanding lifestyle that may consequently lead to more robust morphology and a greater risk of developing pathologies (Merbs 1983; Pearson 2000; Stock 2002). Moreover, certain climate types pose a higher risk of poor health. For instance, populations living in hot and humid environments tend to have a higher incidence of parasitic infections and disease-carrying insects. This means that low measures of robusticity characteristic of populations from warm climates may be caused, in part, by poor health conditions that led to the loss of bone mass or prevented bone growth (Zaleski 2013). Essentially, climate can influence behavioral patterns and health through environmental stress and subsistence transitions. Since behavior and health are factors that directly affect the bone modeling process, climate indirectly influences cross-sectional geometry (Holt 2003; Shackelford 2005).

Terrain is another environmental factor suggested to impact the magnitude and orientation of mechanical loading associated with terrestrial mobility in which high levels of ruggedness in topography put greater demands on the lower limbs. The plane or axis where the mechanical load is received will alter the direction of bending stresses and may result in different morphological patterns for the same activity when considering terrain (Ruff 1999; Ruff 2007). However, environmental differences in topography do not always translate into variations in diaphyseal size and shape (Shackelford 2005). Therefore, the influence of topographical differences on skeletal morphology may be minimal or not straightforward.

While there is sufficient evidence supporting the impact of mobility or climate on bone structure, the current project aims to contribute to understanding the possible interaction between these two variables in affecting the bone modeling process. The research hypotheses were formed based on this literature review. For the samples from this study, it is expected that the Sadlermiut Inuit will have shorter limbs and heavier body mass (part of Hypothesis 1.1 and 2.1) based on evidence that climate influences body size indices (Churchill et al. 2000; Pearson 2000; Ruff 1994; Stock 2002; Stock et al. 2011). On the other hand, Sadlermiut are predicted to have greater diaphyseal robusticity as a result of their active lifestyle as hunter-gatherers. According to research on mobility, the lower limbs should be more robust due to higher levels of habitual physical activity (part of Hypothesis 1.1) (Holt 1999; Holt et al. 2017; Larsen et al. 1995; Marchi et al. 2006; Ogilvie 2000; Pearson 2000; Ruff 1999; Ruff et al. 1984; Shackelford 2005; Stock 2002) while robusticity in the upper limbs would be a factor of high marine mobility (part of Hypothesis

2.1) (Churchill 1994; Knobbe 2010; Stock 2002; Stock and Pfeiffer 2001; Weiss 2003). Diaphyseal shape was shown to be influenced by the type and intensity of activity (Knobbe 2010; Ruff 2007; Ruff et al. 1984; Shackelford 2005, 2014; Stock 2002; Zaleski 2013). Therefore, Sadlermiut are expected to have more elliptical shaped diaphyses as a consequence of their strenuous daily life imposing strain in stereotypical directions causing elongation along the A-P axis for resistance (Hypothesis 1.2 and 2.2).

Previous studies have demonstrated that hunter gatherers are habitually more active and thus, tend to have more robust morphology than agriculturalists. Correspondingly, differences in the type of habitual activities such as hide scraping in foragers and plowing among agriculturalists imposed strain in different directions causing variances in diaphyseal shape (Holt 1999; Holt et al. 2017; Larsen et al. 1995; Marchi et al. 2006; Ogilvie 2000; Pearson 2000; Ruff 1999, 2007; Ruff et al. 1984; Shackelford 2005; Stock 2002). Therefore, for the meta-analysis pertaining to mobility, hunter-gatherers are predicted to have the highest measures of cross-sectional geometry and more oval-shaped diaphyses than any food producing subsistence group (Hypothesis 3.1, part of 4.1 and 4.2). Also, diaphyseal robusticity in the lower limbs of transitional, intermediate and intensive agriculturalists should reflect gradual gracilization since these groups represent different intensities in agricultural practices (Hypothesis 3.2). On the other hand, differences in the upper limbs may only be significant between hunter-gatherers and intermediate populations since transitional groups were not yet introduced to mechanized tools which facilitated agricultural work (part of Hypothesis 4.1) (Holt et al. 2017; Wescott 2001).

Biomechanical analyses have shown a negative correlation between climate and robusticity in which warmer conditions were associated with increased gracility while colder environments led to more robust morphology (Pearson 2000; Ruff 1994; Stock 2006). For the meta-analysis about climate, the highest measures of cross-sectional geometry in the upper and lower limbs are anticipated for populations from extremely cold climates such as polar/subarctic tundra than any other climate category (Hypothesis 5.1 and 5.2). The present study will highlight the benefits of conducting a biomechanical analysis both within a population, subsistence group or, in this case, geographical region and on a larger spatial and temporal scale. A small scale analysis has greater potential for removing confounding factors (Bridges, Blitz, and Solano 2000; Stock 2002) while the meta-analysis provides a broad view of what past research can tell us and insight on

overarching trends in bone functional adaptation (Churchill et al. 2000; Holt 2003; Shackelford 2005).

3.4. Limitations in biomechanical research: Methodological differences

The rapidly growing interest in the field of biomechanics has created an influx of data, however, methodological differences in the acquisition and analysis of cross-sectional geometric properties cause discrepancies in results and prevent comparisons between studies (Friedl, Eisová, and Holliday 2016). Contradictory results may reflect differences in the method of data acquisition, whether by imaging technique or using external measurements. Although this debate is beyond the scope of this paper, a strong correlation was found between measures of robusticity obtained by external methods and imaging techniques but there were considerable prediction errors (Stock and Shaw 2007). More research is needed to investigate the compatibility of data derived from these methods to allow for easier cross comparison between biomechanical analyses. Comparisons across studies are further limited by data collection involving different measures of robusticity, such as second moments versus section moduli, or different measures of diaphyseal shape, like Imax/Imin or I_x/I_y (Ruff 1987 in Churchill et al. 2000). Subsequently, given the difficulty of acquiring human remains in optimal condition, small sample size is often listed as an explanation for unexpected results in postcranial morphology (Zaleski 2013).

The method of body size standardization applied to cross-sectional geometry was shown to contribute to variation between biomechanical studies based on research demonstrating that patterns in bone functional adaptation sometimes disappeared when a different scaling method was used (Churchill et al. 2000; Friedl, Eisová, and Holliday 2016; Ruff 2000). Standardizing for body size using body mass and bone length results in cross-sectional properties for the upper and lower limbs that best reflect mechanical loading. In contrast, standardizing by powers of bone length does not account for changes in body proportions through time and assumes that body shapes are similar which can be problematic for temporal analyses or heterogeneous samples (Holt 2003; Ruff 2000; Weiss 2003; Zaleski 2013). However, the method of powers of bone length is useful when access to osteometric data on body size and shape is limited, a fairly common issue in biomechanical studies (Ruff 2000).

Differences in population grouping categories such as mobility, subsistence strategy or climate also limit comparisons between biomechanical studies since the grouping criteria are subjective. Dividing populations according to subsistence can be problematic because subsistence strategies are not definitive but rather, are on a spectrum. Therefore, examining differences in cross-sectional properties by lumping populations into large subsistence groups employs rigid categorization to a dimension that is highly variable in terms of behavior and environment. Moreover, the samples included in each group may not be representative of the patterns for the entire population, especially when analysing early human populations where specimens are chosen based on availability.

The problems caused by broad categorization may be circumvented by creating smaller, more defined subsistence categories, for instance, separating samples into 4 groups (hunter-gatherer, transitional, intermediate, and intensive agriculturist) instead of 2 groups (hunter-gatherer and agriculturalist) (Ruff 2007; Zaleski 2013). The mode of subsistence is most commonly used as a grouping variable when researching mobility since it greatly influences behavioral patterns. Also, data on subsistence strategy is more accessible than other measures of mobility such as kilometers travelled annually or number of moves per year which are typically scarce (Davies and Stock 2014; Holt 2003). Overall, the lack of methodological standardization of biomechanical analyses in the form of data acquisition, including data collection and the variables examined, and data analysis, including body size standardization methods and the grouping categories, has created compatibility issues between studies and contributes to discrepancies in patterns of bone functional adaptation.

Chapter 4: Materials and methods

4.1. Materials

4.1.1. Materials: pQCT

The human remains used in the present study were obtained from collections available at Université de Montréal (Laboratoire de bioarchéologie humaine). The sample also included scans of specimens held at the ecomorphology laboratory of the aforementioned university and at the Canadian History Museum (CHM) that were previously scanned as part of a project by Dr. Olivia Alexandre De Carvalho.

4.1.1.1. Populations included in the study

The original data for four populations are included in this thesis: Sadlermiut from Southampton Island, Euro-Canadians from three historic cemeteries in Montreal (Notre-Dame), Pointe-aux-Trembles and Sainte-Marie (Beauce). The first sample corresponds to an urban population and the last two to rural ones.

Sadlermiut

The Sadlermiut (or Sallirmiut) are a proto-historic Inuit population from Southampton Island in northern Canada dating between the 13th and 19th century. The remains were recovered from excavations at the Native Point site between 1954 and 1959 by Taylor who worked at CHM, Dr. H.B. Collins, Dr. W. Laughlin and Dr. C. Merbs. Several reports were published on these archaeological interventions, however, access to these documents was limited. A total of 302 burials were recovered on site but only 184 were exhumed. There were 111 immature and 46 undetermined individuals, as well as 1 in poor condition that were excluded from the sample of the present study leaving 26 adults including 12 males and 14 females. The sample size reflects 9% of the entire skeletal collection, meaning that interpretations of bone functional adaptation among Sadlermiut will be fairly restricted (Collins 1956 and Merbs 1972 in De Carvalho 2015; Symchych 2016). The Sadlermiut Inuit are suspected to be the descendants of the Dorset people (Coltrain 2009). They were relatively genetically isolated and perished in 1903 as a result of a disease epidemic. The Sadlermiut were foragers with a diet mainly dependent on marine resources such as ringed seal and seabirds but, had no history of whaling and limited access to caribou (Coltrain 2009). This high latitude population practiced marine mobility and terrestrial mobility in

the context of a hunting and gathering mode of subsistence. Previous skeletal analyses of the collection from the Native Point site have demonstrated that patterns of pathology such as osteoarthritis correlate with the high physical demands of their active foraging lifestyle, most prominently in the upper limbs (Merbs 1983). The Sadlermiut are considered to have "hyper-arctic" body proportions given their high body mass, short stature, low intralimb indices and wide body breadth that create a generally massive build (Auerbach 2014).

Euro-Canadians

The three samples of Euro-Canadians represent various phases of the colonisation of New-France. The individuals from Notre Dame were part of the first wave of colonizers in Montreal and witnessed its development into an urban center (Arkéos 2008). Individuals from Pointe-aux-Trembles were new settlers in more rural areas east of Montreal (Arkéos 2008). The samples from Sainte-Marie are also rural, but more recent, representing people from established settlements with more stable patterns of behavior that were acclimatized to the new world (Ethnoscop 2006). It is important to note that both the populations from Notre Dame and Pointe-aux-Trembles were experiencing significant demographic growth because of the arrivals of artisans and soldiers to fortify the village against native Canadians and the British. These migrations brought disease epidemics and reoccurring famines that were characteristic of Montreal during the French colonial period. These factors were especially prevalent in urbanised areas like Notre Dame as demonstrated by their extremely high infant mortality rates (Amorevieta-Gentil 2010). In contrast, the village of Sainte-Marie was not as affected by the waves of migrations as urban centers like Montreal and represents a more stable point in the history of New-France (Ethnoscop 2006).

Notre Dame cemetery

The Euro-Canadians from Notre Dame cemetery in downtown Montreal were part of the first parish church established in 1683 and represent one of the earliest groups to colonise North America. The burials date between the end of the 17th century and the end of the 18th century after the cemetery closed due to overcrowding. Their state of conservation was highly variable, and most were incomplete or scattered out of context due to damage from infrastructure work or being reburied. A total of 180 individuals were excavated from the cemetery of which only 73 were identified as adult male (N=42) and female (N=31) after excluding juveniles and undetermined remains (Arkéos 2008). The sample of the current study consists of 6 out of 73 individuals

representing 3.3% of the total skeletal inventory retrieved from the cemetery. There were 67 individuals omitted from the sample for either missing long bones (humerus, femur and tibia), having signs of pathology or being in poor condition with cracks or taphonomic deformation. Interpretations of bone functional adaptation for Notre-Dame will be limited since the small sample size is not representative of the entire population. Isotopic evidence suggests that their diet kept with Old World European farming traditions (Vigeant et al 2017). The people of Notre Dame were agriculturalists subsisting largely on the food they produced and supplementing with small quantities of local resources such as moose and maize, and some aquatic resources like fish. The population of Notre Dame were highly active due to the demands involved in establishing themselves and shaping their environment in a new world (Arkéos 2008). Their centralised location in New France meant that they also participated in commercial exchanges and the population included artisans, carpenters, butchers and bakers reflective of an urban center (Crépin 2018).

Pointe-aux-Trembles

The samples from the Montreal borough of Rivière-des-Prairies-Pointe-aux-Trembles were found during excavations surrounding the fourth convent of the Sisters of the Congregation of Notre Dame built in 1912. The burials were recovered in a cemetery located south of the convent dating from the 18th to the mid-19th century. There were 63 burials exhumed and only 21 individuals including 8 males and 11 females were eligible for the current study after omitting juveniles and undetermined remains (Ethnoscop 2016; I. Ribot personal communication). The research sample consisted of 8 out of 21 adults because 14 were missing long bones, 5 had pathologies like arthritis and 2 were of undetermined sex. The sample size represents around 13% of the total skeletal inventory excavated from the Cemetery at Pointe-aux-Trembles. Consequently, interpretations of behavioral patterns will be limited to a small portion of the population. The rural village of Pointe-aux-Trembles was situated on the border of the Saint-Laurence river and served mainly for agricultural purposes. However, activities became more diversified after the construction of the "Chemin du Roy" in 1734 which established Pointe-aux-Trembles as an important travel post. Historically, rural populations from Quebec were very active which is supported by the high incidence of arthritis found among the adults of this sample (Ethnoscop 2016). Unfortunately, not much is known about the activities of the individuals from Pointe-aux-

Trembles. An objective of this biomechanical analysis is to gain more insight into the habitual behavior of this rural population.

Sainte-Marie-De-Beauce Cemetery

The remains from the Cemetery of Sainte-Marie-in Beauce date to the 19th century. A total of 62 burials were found during excavations with only 30 identified as mature individuals including 11 males and 19 females (Ethnoscope 2006; I. Ribot personal communication). There were 28 individuals eligible for the current study since 2 were excluded for being of undetermined sex. This sample represents 45% of the total skeletal inventory retrieved from the Cemetery of Sainte-Marie. The sample size is reflective of the entire population providing good support for interpretations of trends in postcranial morphology. The first colonizers of Sainte-Marie arrived in 1738, meaning that this sample represents individuals living after the establishment of the parish. Consequently, their daily life was much less laborious than the first colonizers who led a physically demanding lifestyle where both sexes engaged in strenuous tasks associated with settling in a new territory and preparing the soil for cultivation. Instead, the activities of the inhabitants of Sainte-Marie mainly revolved around agriculture and were far less diversified than in centralised villages such as Notre Dame in Montreal. The division of labor was more accentuated in rural areas with women restricted to domestic activities such as maintaining the household and child rearing while men had more rigorous demands involved in agricultural work (Crépin 2018).

4.1.1.2. Sampling methodology

For this project, skeletal elements including the humerus, femur and tibia were chosen based on previous studies demonstrating their significance in establishing past human behavioral patterns. The humerus provides information on activities involving the upper limbs which is especially relevant for marine mobile populations and when investigating changes in subsistence-related activities. The femur and tibia were both selected to measure the impact of mobility on the lower limbs, not only for being the most studied, but because they react differentially to changes in stress and strain and therefore, when examined together, best reflect activity patterns (Ruff 2007; Shackelford 2005; Stock 2002).

Only skeletons of mature individuals with fused long bone epiphyses were selected because the interpretation of cross-sectional geometric properties is different during ontogeny. Research has shown that habitual activity patterns are typically established during adolescence in prehistoric

societies and thus, determine adult skeletal morphology (Ruff, Holt, and Trinkaus 2006). Subsequently, adult skeletons may continue to gradually accumulate structural adaptations as a result of changes in mechanical stimuli, especially during strenuous physical activity or after behavioral differences from youth. For these reasons, cross-sectional properties in adult long bones reflect variations of behavior in adulthood (Pearson and Lieberman 2004; Ruff, Holt, and Trinkaus 2006).

Long bones showing signs of pathology or visible surface damage such as cracks were excluded from the sample. Studies have shown that certain pathologies influence the internal structure of bone, therefore its morphology may not be accurately reflective of habitual behavior. Also, surface damage on bone may distort measures of mechanical properties (Ruff and Hayes 1983).

4.1.1.3. Sample Size

The sample consists of 71 adults consisting of 29 males and 42 females from the four populations discussed previously and sample sizes for each element vary due to differential preservation (Table 1).

Table 1: Sample sizes of skeletal elements by side for each population.

Populations	Skeletal elements					
	Humerus		Femur		Tibia	
	Left	Right	Left	Right	Left	Right
Sadlermiut	26	26	26	26	24	25
Sainte-Marie	19	18	27	28	26	27
Notre Dame	5	5	1	6	5	6
Pointe-aux-Trembles	8	5	4	5	4	4
Total	58	54	58	65	59	62

4.1.2. Materials: Meta-analysis

An extensive review of research examining the role of non-genetic factors in human long bone cross-sectional variation was undertaken in the interest of understanding the extent of current knowledge on bone functional adaptation and gathering comparative samples for the present project. Studies that reported cross-sectional properties including the profile of the medullary canal were selected so that they could be directly compared with the data collected in this study (see Appendix 2).

4.1.2.1. Skeletal elements and section locations

From previous research, data were compiled for the cross-sectional geometric properties at the mid-distal portion (35%) of the humerus, at the midshaft (50%) and subtrochanteric (80%) region of the femur and the tibial midshaft (50%). The mid-distal humerus is generally preferred to avoid the deltoid tuberosity located near the midshaft whereas the favoured cross sections of the lower limbs are shown to best reflect the impact of mechanical loading on bone (Ruff and Hayes 1983; Ruff 2007). The femur midshaft receives anteroposterior bending loads which provides information about changes in gait, while the tibial midshaft receives anteroposterior loads (A-L) imposed during strenuous activities such as walking, running and climbing. However, the impact of terrestrial mobility is best reflected in the morphological differences of the femur midshaft and lesser in the tibia midshaft because of confounding effects associated with the fibula that shares the distribution of mechanical loads (Holt 2003; Ruff 1999). The femur subtrochanteric section reflects changes in general activity patterns and sexual dimorphism better than the midshaft, since it receives the highest mediolateral bending loads (M-L). M-L loading is imposed during most activities because the femur is positioned laterally in relation to the body's center of gravity (Holt 1999).

4.1.2.2. Population

The meta-analysis was restricted to studies examining skeletal variation in mature individuals that exhibited no signs of pathology and were identified by sex (pooled-sex data were excluded). Data was gathered on modern human populations from Asia, Europe and the Americas. Data from Australia was excluded because its populations may not have practiced agriculture (currently debated). Data from Africa was also excluded because individuals are generally more robust due to their large body proportions such as a tall stature and long limbs which are too different to compare to that of Inuit and Euro-Canadian samples from the present study (Ruff 1993; Stock 2002;). The ideal was to search for anatomically modern human samples from northern and southern latitudes with distinct levels of mobility to examine morphological differences based on climate and mobility. This project covered a period between the end of Last Glacial Maximum and contemporary populations of the 19th century (Holt 2003). A total of 83 different archaeological and extant populations were included and are listed in Appendix 2.

4.2. Methods

4.2.1. pQCT

4.2.1.1. Data acquisition

The specimens from the four Holocene populations sampled for this research were scanned using a semi-portable peripheral quantitative computed tomography (pQCT: Stratec XCT Research SA+) available in the ecomorphology laboratory at Université de Montréal (Figure 6). The pQCT scanner was selected because it offers a rapid non-invasive method to produce accurate 2-dimensional images of long bone cross-sections (Ruff 2007).
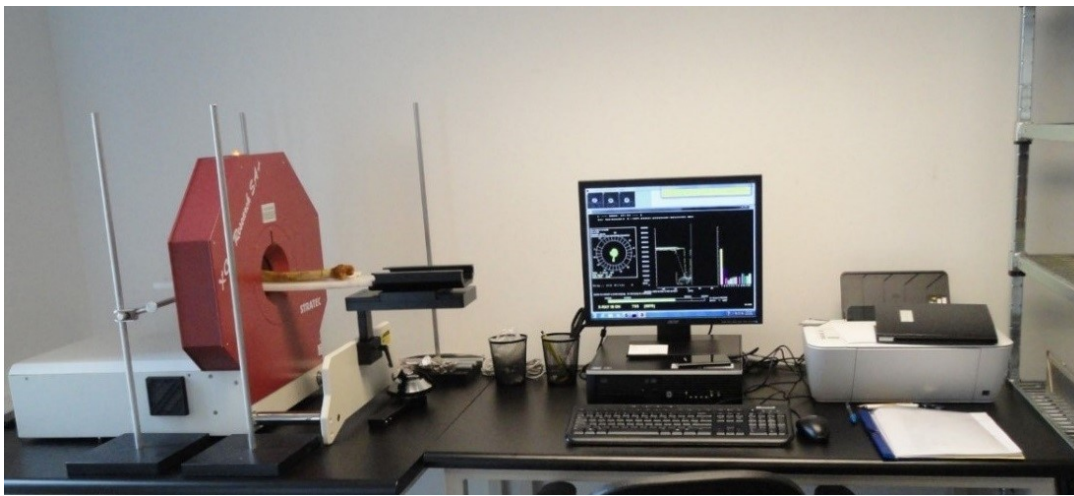
Figure 6: Semi-portable peripheral quantitative computed tomography (pQCT: Stratec XCT Research SA+) with bone positioned on radio-translucent low-density polyethylene foam for stability.

Scanning procedure

The samples from Sainte-Marie and the Sadlermiut were previously scanned as part of a project by Dr. Olivia Alexandre De Carvalho (De Carvalho 2015). The scanning procedure for the specimens from Notre Dame and Pointe-aux-Trembles was modeled according to Macintosh et al. (2013). The bones were oriented along the anteroposterior plane beginning from the proximal to the distal portion of the diaphyses. When bone

Figure 7: Clay block securing in place the proximal end of the femur.

length exceeded the distance covered by the scanner (175 mm), specimens were adjusted forward

on the holders to allow the distal portion to be scanned, rather than being reoriented from the distal portion to the proximal portion as was done by Dr. Carvalho. The humerus and tibia were scanned in anatomical position with the anterior portion facing upwards while the femur was placed with the posterior side up because its robustness prevented anatomical placement in the scanner. The extremities of each bone were supported by parallel metal bars and the Ct-scan holder was placed at the highest setting (Figure 6). Subsequently, specimens were secured with radio-translucent low-density polyethylene foam that was placed flat using a leveling device and had a paper ruler stuck on the surface to align the bones straight into the scanner (Macintosh et al. 2013). The specimens were stabilised using clay blocks that were placed under the distal end of the humerus, the greater trochanter and the distal condyles of the femur, and the proximal lateral portion and distal end of the tibia (Figure 7). These blocks served to elevate the bones so that they were positioned parallel to the supporting surface along the A-P (y) and M-L (x) planes, according to a leveling device. The same parameters set by Dr. Carvalho were utilised to ensure continuity in data acquisition between samples including a voxel size of 0.1 mm that was used for all long bones.

Section locations

Ct-scans were taken at various locations along the diaphysis based on maximum bone length: 20%, 35%, 50%, 65% and 80% starting from the distal portion to the proximal end of the bone as modeled after previous studies (Macintosh et al. 2013; Ruff 2007; Ruff and Hayes 1983). These standard section locations at 15% intervals of bone length were chosen because they sufficiently represent the variation in bone structure throughout long bone diaphyses (Ruff and Hayes 1983; Ruff 2007). The slices were taken on the transverse plane that is perpendicular to the sagittal and the frontal (coronal) planes (Figure 8) (Macintosh et al. 2013).
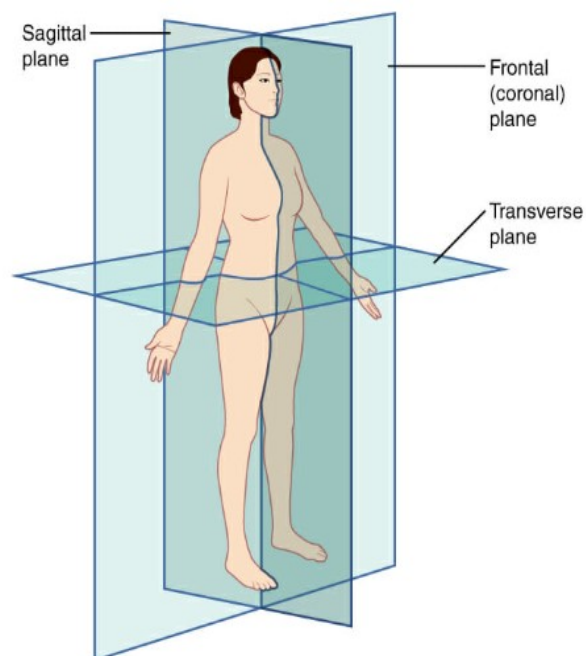
Figure 8: Body planes. Image from https://biologydictionary.net/sagittal-plane/

4.2.1.2. Data processing: Program

The scans were processed using the open-software program NIH image with the plugin BoneJ which calculates cross-sectional properties based on 2D images of long bone cross-sections by applying engineering principles (Doube et al. 2010). When the images are input into the software, a common threshold for cross-sectional analyses was found by averaging the threshold of a few images from each population for the relative skeletal element to ensure homogeneity. Additionally, the trabecular bone of the medullary cavity, when present, was included in the analysis. Once the properties for each scan are measured by the program, results were imported into Microsoft Excel.

4.2.1.3. Cross-sectional geometric properties

The mechanical properties that measure bending and torsional rigidity and strength include cortical area (CA), total subperiosteal area (TA), second moments of area or SMAs (I_x, I_y, I_{max} and I_{min}), and polar moments of area (J). The variables that calculate bone strength include maximum and minimum section modulus (Z_{max} and Z_{min}), polar section modulus (Z_p) as well as section modulus about the anteroposterior and mediolateral axis (Z_y and Z_x) (Ruff 2007; Ruff and Hayes 1983). The list of cross-sectional properties used in the present study is provided in Table 2: Cross-sectional properties utilised in the present study. Table 2. These mechanical properties were measured for all cross-sections of the humerus, femur and tibia.

Table 2: Cross-sectional properties utilised in the present study.

Symbol	Definition	Mechanical relevance
CA	The area of cortical bone	Strength and rigidity against axial compression and tension[1]
J	Polar moment of area	Torsional rigidity[2]
I_{max}	Maximum second moment of area	Greatest bending rigidity in the direction of a section's major axis
I_{min}	Minimum second moment of area	Lowest bending rigidity in the direction of a section's minor axis
I_{max}/I_{min}[3]	Ratio of maximum over minimum second moment of area	Diaphyseal geometry
I_x	Second moment of area along the mediolateral (M-L) plane	A-P bending rigidity
I_y	Second moment of area along the anteroposterior (A-P) axis	M-L bending rigidity
I_x/I_y[3]	Ratio of second moment of area along the M-L axis over the A-P axis	Diaphyseal geometry

[1] Axial compression and tension are less common for long bones than bending and torsional loads (Churchill et al. 2000).
[2] Polar moment of area is also often used as an average value of bending rigidities of the bone since it is equal to two perpendicular SMAs of a bone (Ruff 2007; Ruff and Hayes 1983; Stock 2002).
[3] For both shape indices, values close to 1.0 reflect a circular long bone shaft while those higher or lower than 1.0 reflect a more elliptical diaphysis (Ruff and Hayes 1983; Wescott and Cunningham 2006). In the meta-analysis, the shape index used for each cross section was determined based on the availability of data for archaeological populations from previous publications.

4.2.1.4. Body size standardization

There are two main methods employed to control for body size across populations including powers of bone length or body mass and bone length. Body size standardization is necessary when comparing populations with different body proportions because it impacts the mechanical loading of the skeleton and muscle size, and ensures that cross-sectional properties are representative of external factors rather than discrepancies in body size and shape (Ruff 2007). The same scaling methods for bone rigidity and strength are used in the upper and lower limbs (Ruff 2000). Standardizing for body size according to powers of bone length involves the following formula (Ruff 2007):

Standardized Areas= $(Areas \div Bone\ Length^3) \times 10^8$

Standardized SMAs= $(SMAs \div Bone\ Length^{5.33}) \times 10^{12}$

When using body mass and bone length to scale for body size this equation was used (Ruff 2007):

Standardized Areas= $(Areas \div Body\ Mass) \times 10^2$

Standardized SMAs= $(SMAs \div (Bone\ Length \times Body\ Mass)) \times 10^4$

The bone length applied in these formulas was the biomechanical length of the skeletal element particular to each specimen and the body mass was specific to the individual as well. This type of bone length is most typically used in biomechanical analyses because it best represents the distance between the center of articular surfaces when applying a beam model. Biomechanical length for the humerus refers to the distance from the top of the humeral head to the lateral lip of the trochlea (Mongle, Wallace, and Grine 2015a, b). Femur biomechanical length is the distance between the average end point of the distal condyles and the intersection where the femoral neck meets the greater trochanter. Tibia mechanical length pertains to the distance from the top of the medial condylar plateau and the midpoint of the distal articular surface (Mongle, Wallace, and Grine 2015b).

The body mass of the Sadlermiut and Euro-Canadian samples was calculated using femoral head breadth (FHB) and the following equation (Ruff, Scott, and Liu 1991):

Body Mass Males= $(2.741 \times FHB - 54.9) \times 0.90$

Body Mass Females= $(2.426 \times FHB - 35.1) \times 0.90$

Although estimations of body mass using stature (ST) and bi-iliac breadth (BIB) are more accurate, this information was not available for the specimens in our study (Holt 1999; Ruff, Trinkaus, and Holliday 1997). For the meta-analysis, some of the collected samples included osteometric measurements of ST and BIB in which case, body mass was calculated using (Holt 1999):

Body Mass Males= $(0.373 \times ST) + (3.033 \times (1.17 \times (BIB \div 10) - 3)) - 82.5$

Body Mass Females= $(0.522 \times ST) + (1.809 \times (1.17 \times (BIB \div 10) - 3)) - 75.5$

It is important to consider that comparing body mass data using two different methods leads to slightly lower or higher estimates depending on the population, however, this was necessary given the gaps in osteometric data between samples.

4.2.2. Meta-analysis

4.2.2.1. Data acquisition and processing

Several search engines, including google scholar and university libraries (McGill University and Université de Montréal), were used to find publications that examine the influence of external factors on human skeletal morphology. Key words such as mobility, climate, biomechanics and human postcranial morphology were used to narrow the search to articles pertaining to this topic. Subsequently, articles were input into a reference management software called *Zotero* and further filtered for articles including data on cross-sectional geometric properties of long bones.

4.2.2.2. Body size standardization

The cross-sectional properties of the samples acquired in the meta-analysis were manipulated and converted to correspond with the methods of body size standardization employed on the specimens of the present study. More precisely, mechanical properties scaled using different methods were reverted to raw data and subsequently, re-standardized using powers of bone length while those using the same methods remained untouched. Furthermore, when biomechanical

length was not available, the type of bone length provided by the publications from which the data was extracted was used in scaling calculations for the respective specimen.

4.2.3. Data analysis
4.2.3.1. Grouping
Mobility

Populations were grouped according to the level of mobility. Since there is no quantitative measure of mobility for archaeological collections, previous studies have estimated physical activity of individuals using either temporal categories, estimated kilometers travelled annually, number of moves per year or subsistence strategy (Bridges 1989; Ruff 1999; Churchill et al. 2000; Holt 2003; Holt et al. 2017; Shackelford 2005; Stock 2002; Wescott and Cunningham 2006). Given the purpose of this research and the lack of information on specific travel distances or total area covered annually for each population, mobility groups were defined by the mode of subsistence. The first group consists of hunter-gatherers with no evidence of food production and thus, rely solely on wild resources for sustainability. The second group refers to transitional populations that likely remain highly mobile despite small-scale crop production including hunter-gatherers with evidence of plant cultivation and the introduction of agriculture. The third intermediate group comprises populations that regularly engage in intentional systematic cultivation and/or supplement parts of their diet with wild resources such as agriculturalists, intensive horticulturists and agro-pastoralists—mixed agriculture and pastoralism. The fourth group refers to sedentary populations that engage in extensive large-scale food production such as intensive agriculture with no dietary substitution with wild resources. For the samples from the current study, Euro-Canadians (EC) included intensive agriculturalists (IA) from Sainte-Marie and Pointe-aux-Trembles as well as intermediates (INT) from Notre-Dame. The Sadlermiut Inuit were hunter-gatherers (HG). Samples sizes for each subsistence group in the meta-analysis are listed in Table 3.

Table 3: Sample sizes for each subsistence strategy.

Mode of Subsistence	Sample size
Hunter-gatherer	61
Transitional	9
Intermediate	11
Intensive agriculturalist	6

Climate

The climate groups were modeled after the Köppen–Trewartha classification (KTC) which is a widely used system and offers more precision in the division of climate types than the original Köppen classification. The KTC characterises main climate groups by mean surface air temperature and further separates into subgroups according to annual precipitation levels (Belda et al. 2014; Yoo and Rohli 2016). Given that climate has remained relatively stable since the beginning of the Holocene, world climate maps of the KTC were used to determine the climate types of populations dating to the last 10,000 years (Belda et al. 2014; De Castro et al. 2007; Feng et al. 2012; Fernandez et al. 2017; Gallardo et al. 2013; Millison n.d.; Stock 2002; Yoo and Rohli 2016). However, the KTC was adapted to suit the parameters of this study. For instance, the tropical (type A) and the subtropical (type C) climates of the KTC were combined to form group 1 due to small samples sizes. Group 2 consists of arid or dry climates with little precipitation while group 3 refers to temperate oceanic and continental climates. Similar to Group 1, group 4 is composed of a combination of two KTC categories: boreal subarctic tundra (type E) and polar (type F) climates because samples are not sufficient to form separate groups. There are no samples from the KTC classification type H that refers to highland climates occurring at high elevations. Populations dating to the Tardiglacial, which includes periods of drastic climatic fluctuations from 16-10kya, were separated from statistical analysis given the ambiguity of climatic reconstructions from that period and the lack of modern analogues but included in graphs to observe their distribution relative to other climate types. For the samples from the current study, Euro-Canadians (EC) inhabited a temperate continental/oceanic (TEMP) climate and the Sadlermiut Inuit were from a polar/subarctic climate (POL). Samples sizes of each climate category in the meta-analysis are listed in Table 4.

Table 4:Sample sizes for each climate type.

Climate type	Sample size
Tropical/subtropical	16
Semi-arid/desert	9
Temperate continental/oceanic	35
Polar subarctic/tundra	6
Tardiglacial	21

4.2.3.2. Statistical analysis

The cross-sectional properties of the humerus 35%, 50% and 65%, the femur 35%, 50%, 65% and 80% as well as the tibia 35%, 50% and 65% were analysed using the statistical softwares Statistical Package for the Social Sciences (SPSS) and Paleontological Statistics (PAST). Statistical tests were not possible for the 20% and 80% sections of the humerus and tibia as well as the 20% section of the femur due to insufficient samples preventing comparison between mobility and climate groups.

In this study's original data, individuals represent the unit of analysis, but in the meta-analysis, data consists of archeological population averages for each sex. For the femur and tibia, the right limb was preferred when both sides of a skeletal element were present for one individual. For the humerus, the cross-sectional properties of left and right sides were pooled together, either for individuals or for sex-specific population averages in the meta-analysis.

First, variables were tested for normality and homogeneity of variances using the Kolmogorov-Smirnov, the Shapiro-Wilk and the Levene tests. Since the data was generally not normally distributed and many samples were small, non-parametric tests had to be performed (Norris et al. 2014). Permutational multivariate analysis of variance, or PERMANOVA, was applied to determine inter-group statistical differences in cross-sectional geometric properties as a function of grouping factors such as mobility and climate (Anderson 2014). One-way PERMANOVA tests were used for all comparative tests whether there were two or more groups. Two-way PERMANOVA was used to test the interaction between mobility and climate. Also, Kruskal-Wallis tests were done to compare the body proportions of Sadlermiut Inuit and Euro-Canadians as well as for the meta-analysis on climate. Maximum long bone length was used as the measure for bone length because data on biomechanical length was not available for Sadlermiut Inuit and samples from Sainte-Marie. For all statistical tests the threshold of significance was 0,05 and sexes were treated separately. Furthermore, studies that standardized by powers of bone length were most common and thus, that standardization method was used in the meta-analysis.

Chapter 5: Results

This chapter begins by presenting the results of statistical analyses of standardized cross-sectional geometric properties (CA, J, I_{max}, I_{min}, I_{max}/I_{min}) obtained from the humerus, femur and tibia of Sadlermiut and Euro-Canadians. Subsequently, their properties were included in the meta-analysis with data from other archaeological populations to examine variations in the skeletal morphology of the lower and upper limbs in relation to the mode of subsistence and subsequently, climate. The p-values marked in red indicate that there are significant differences in cross-sectional properties between populations overall while those marked in bold indicate that only specific groups differ significantly. The footnotes underneath result tables specify between which subsistence and climate groups statistically significant differences were observed.

5.1. Inuit and Euro-Canadians

There were no femora and humeri from Notre-Dame due to poor preservation. In that case, there are just two groups being compared (EC IA vs. Inuit H-G) and thus, no difference in the analyses comparing different climates from different subsistence strategies.

5.1.1. Bone lengths and body mass

Table 5: P-values of Kruskal-Wallis tests by sex for bone length and body mass comparing Euro-Canadians and Sadlermiut Inuit.

Variable	Maximum humerus length	Maximum femur length	Maximum tibia length	Body mass
Male	0.000[1]	0.000[1]	0.000[1]	0.001[1]
Female	0.002[1]	0.143	0.253	0.595

[1] Euro-Canadians > Inuit

Statistical tests compared the body dimensions of Sadlermiut Inuit and Euro-Canadians (Table 5). Results demonstrated that male Euro-Canadians have significantly longer maximum humerus, femur and tibia lengths as well as heavier body mass than Inuit males. In contrast, females only exhibited significant differences in the humerus which was longer in Euro-Canadian than Inuit females, but were otherwise relatively similar in lower limb lengths and body mass.

5.1.2. Lower limbs: Femur and tibia

5.1.2.1. Femur

Table 6: P-values of one-way PERMANOVA tests by sex for each femur cross section.[1]

Male femur cross sections	35%	50%	65%
CA	0.421	0.1	0.149
J	0.002^2	0.000^2	0.004^2
I_{max}	0.004^2	0.001^2	0.001^2
I_{min}	0.001^2	0.005^2	0.108
I_{max}/I_{min}	0.566	0.619	0.011^2
Female femur cross sections	35%	50%	65%
CA	0.458	0.063	0.090
J	0.002^2	0.000^2	0.000^2
I_{max}	0.007^2	0.000^2	0.000^2
I_{min}	0.001^2	0.000^2	0.000^2
I_{max}/I_{min}	0.014^3	0.462	0.350

[1] All cross-sectional properties are standardized using powers of bone length: Areas (CA) are divided by bone length[3] and then multiplied by 10^8. SMAs (J, I_{max} and I_{min}) are divided by bone length[5.33] and then multiplied by 10^{12}.
[2] Inuit>Euro-Canadians
[3] Euro-Canadians>Inuit

The cross-sectional geometry of femur cross sections in Euro-Canadian populations and Inuit were compared in all sections of the femur except for the proximal (80%) and distal (20%) slices (Table 6). Results reveal a general trend where the femora of Sadlermiut Inuit populations are more robust than Euro-Canadians. More precisely, Inuit are significantly greater in torsional rigidity (J), maximum and minimum second moments of area (I_{max} and I_{min}) than EC for all femur cross sections (Figure 9).
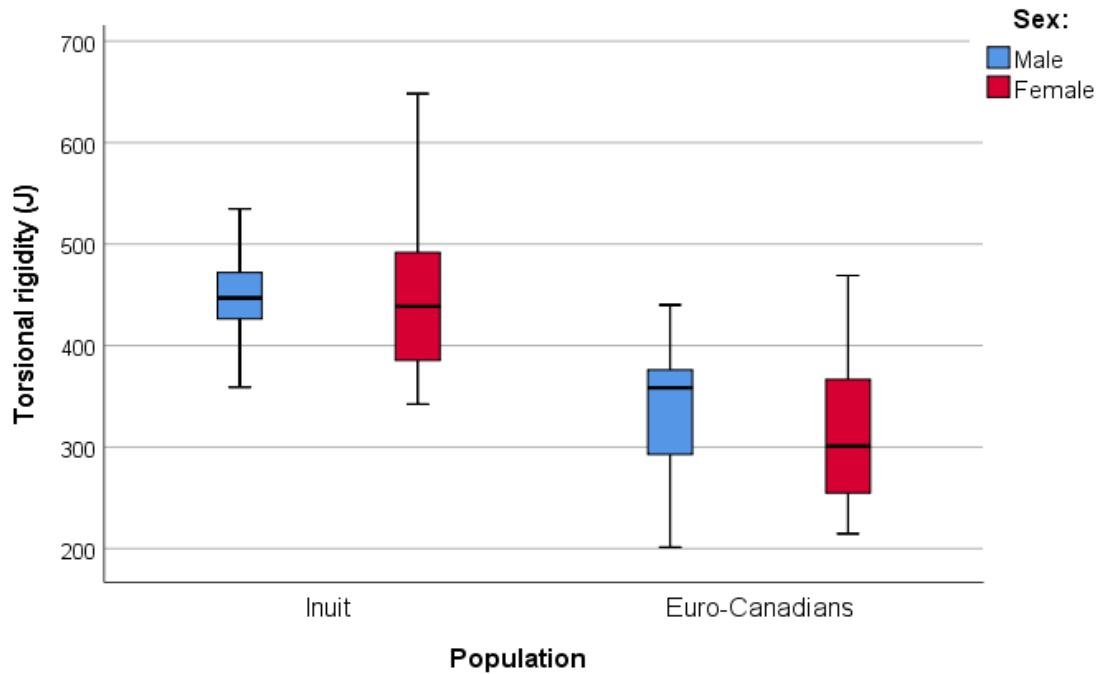
Figure 9: Torsional rigidity in mm^4 at the femur midshaft (50%) by sex in Euro-Canadians and Inuit.

Both populations are similar in cortical area (CA). The majority of femur slices do not exhibit significant differences in diaphyseal shape (I_{max}/I_{min}) between populations, except for the mid-proximal section (65%) in males and the mid-distal portion (35%) in females. At 65%, EC males have more circular femurs than Inuit (Figure 10: A), while at 35%, Inuit females have significantly rounder femur diaphyses than Euro-Canadians (Figure 10: B).
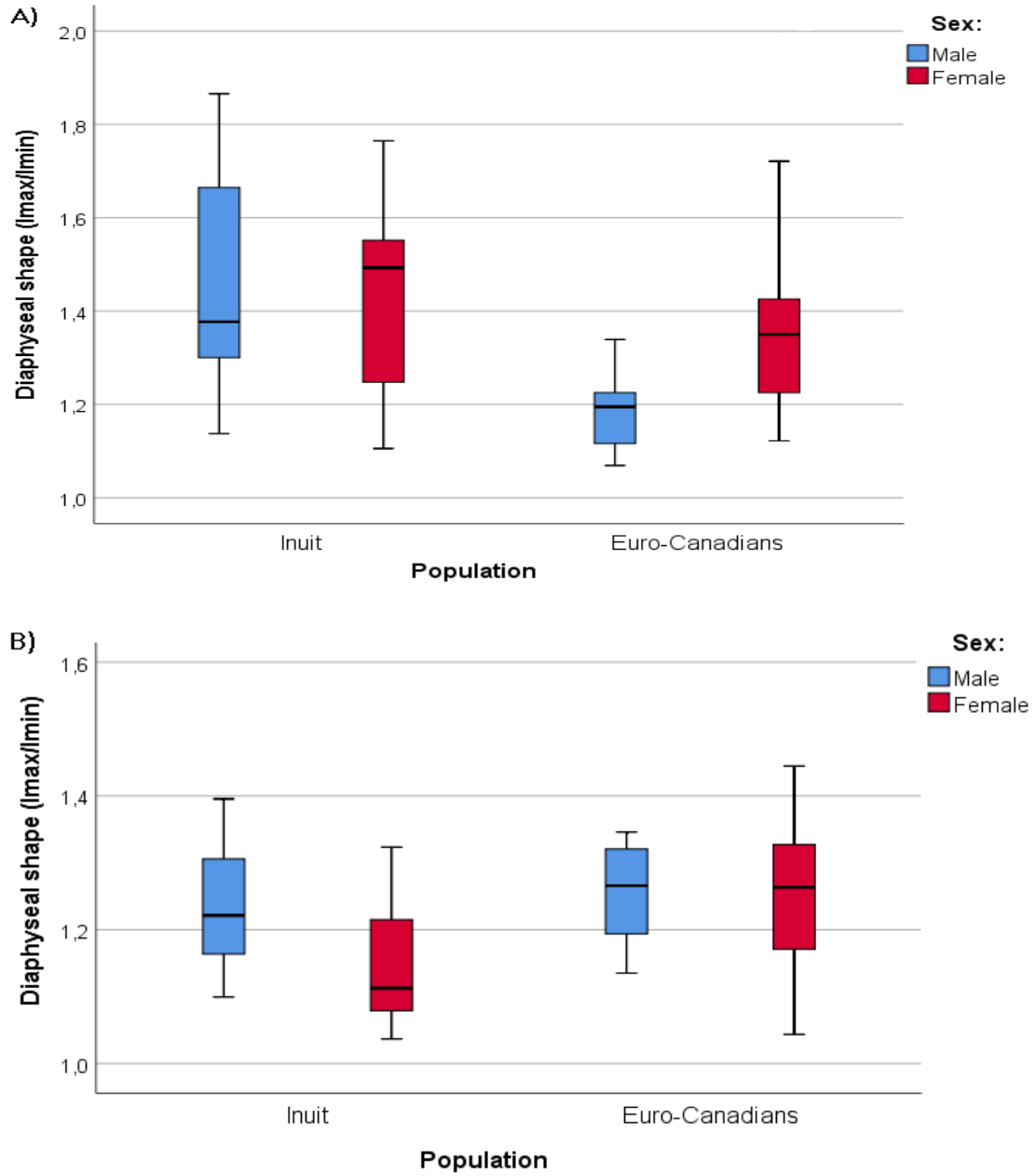
Figure 10:Diaphyseal shape (Imax/Imin) by sex in Euro-Canadians and Inuit a) at the mid-proximal femur (65%) and b) at the mid-distal femur (35%).

5.1.2.2. Tibia

Table 7: P-values of one-way PERMANOVA tests by sex for each tibia cross section using the mode of subsistence as a grouping factor.[1]

Male	35%	50%[4]	65%
CA	0.032[2]	0.014[3]	0.001[2]
J	0.001[2]	0.000[3]	0.001[2]
I_{max}	0.005[3]	0.000[3]	0.001[2]
I_{min}	0.001[2]	0.006[3]	0.001[2]
I_{max}/ I_{min}	0.422	0.323	0.860
Female	35%	50%	65%
CA	0.775	0.671	0.328
J	0.018[3]	**0.082**[3]	0.005[3]
I_{max}	**0.052**[3]	**0.099**[3]	0.003[3]
I_{min}	0.008[3]	0.137	0.022[3]
I_{max}/ I_{min}	0.261	0.887	0.528

[1] All cross-sectional properties are standardized using powers of bone length: Areas (CA) are divided by bone length[3] and then multiplied by 10^8. SMAs (J, I_{max} and I_{min}) are divided by bone length[5.33] and then multiplied by 10^{12}.
[2] HG>INT and IA
[3] HG>IA
[4] INT males N=2 (excluded)

Inuit hunter-gatherers have more robust tibia than Euro-Canadians from any other subsistence category, generally exhibiting the highest values in cross-sectional properties. Furthermore, male tibiae are more affected than females by changes in the mode of subsistence. For instance, male HG have greater cortical area (CA), torsional rigidity (J), and maximum and minimum second moments of area (I_{max} and I_{min}) than INT and/or IA Euro-Canadian groups. On the other hand, female IA are significantly lower in J, I_{max} and I_{min} than HG but are relatively similar in CA (Figure 11 and Figure 12). Subsequently, INT males are similar in bone structure to IA Euro-Canadians, however, INT females are midway between the values of HG and IA groups in torsional rigidity and second moments of area (Figure 12). There are no significant differences in diaphyseal shape between any subsistence category for all of the tibia cross sections (Table 7).
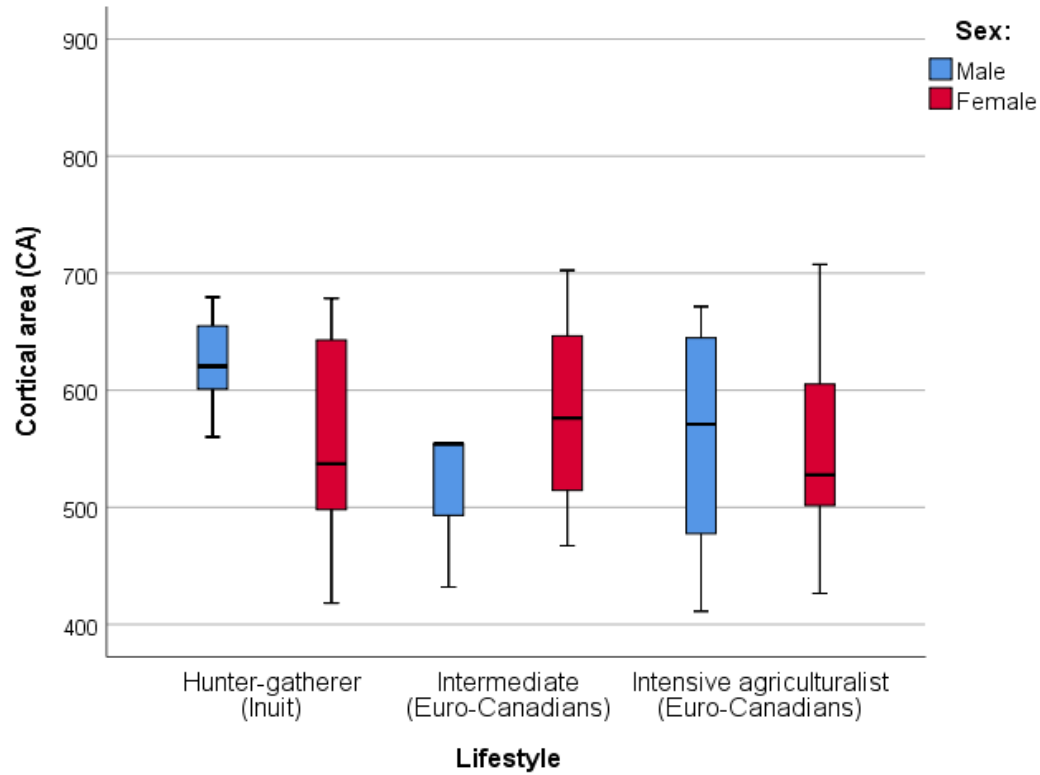
Figure 11: Cortical area in mm^2 at the mid-distal tibia (35%) by sex in relation to the mode of subsistence.
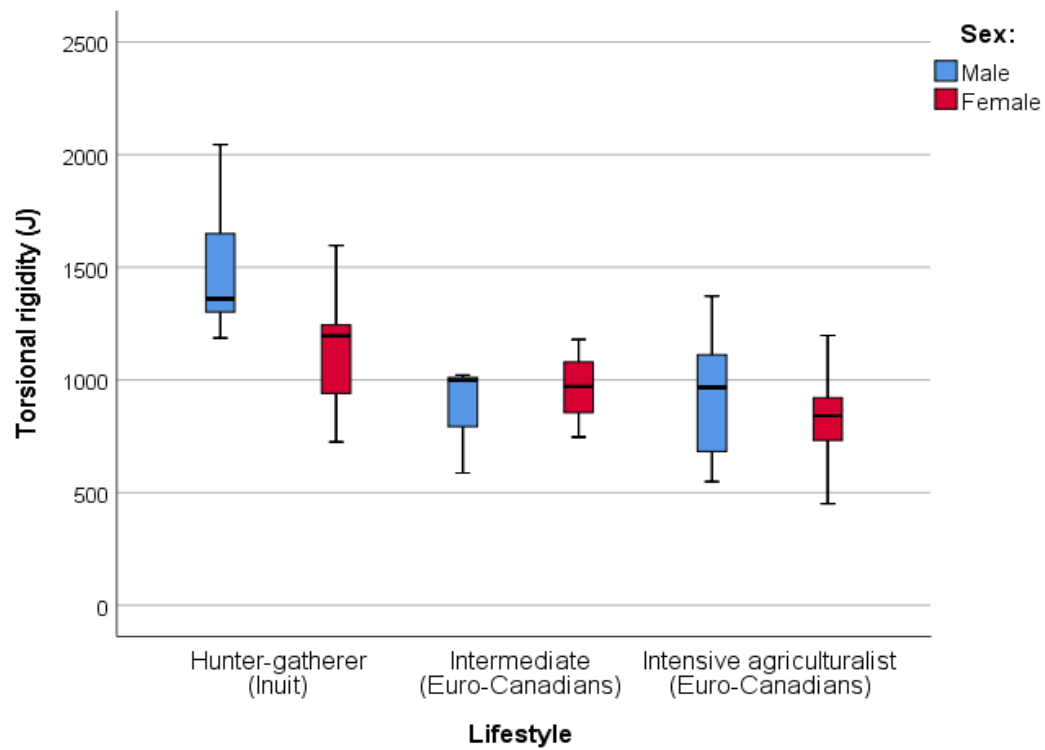
Figure 12:Torsional rigidity in mm^4 at the mid-proximal tibia (65%) by sex in relation to the mode of subsistence.

In relation to climate, cross-sectional geometry was examined by comparing Inuit of polar/subarctic tundra (POL) climates to Euro-Canadians (EC) from temperate continental/oceanic (TEMP) climates (Table 8).

Table 8: P-values of one-way PERMANOVA tests by sex for each tibia cross section using climate as a grouping factor.[1]

Male	35%	50%[3]	65%
CA	0.009[2]	-	0.000[2]
J	0.000[2]	-	0.000[2]
I_{max}	0.000[2]	-	0.000[2]
I_{min}	0.000[2]	-	0.000[2]
I_{max}/ I_{min}	0.196	-	0.667
Female	35%	50%	65%
CA	0.87	0.789	0.747
J	0.006[2]	0.029[2]	0.002[2]
I_{max}	0.016[2]	0.037[2]	0.001[2]
I_{min}	0.002[2]	0.049[2]	0.008[2]
I_{max}/ I_{min}	0.105	0.668	0.261

[1] All cross-sectional properties are standardized using powers of bone length: Areas (CA) are divided by bone length^3 and then multiplied by 10^8. SMAs (J, I_{max} and I_{min}) are divided by bone length$^{5.33}$ and then multiplied by 10^{12}.
[2] POL>TEMP
[3] At tibia 50%, males only include 2 groups therefore, the analysis for mobility and climate is the same (see Table 7).

The tibiae of Inuit from POL climates is more robust than TEMP Euro-Canadians, although, there are no significant differences in diaphyseal shape between climate groups. In fact, TEMP populations are significantly lower in torsional rigidity (J), maximum and minimum second moments of area (I_{max} and I_{min}), in addition to cortical area (CA) in males, than POL individuals (Figure 13 and Figure 14). Differences in cross-sectional geometry of the tibia are more exaggerated in males of different climate types than females.
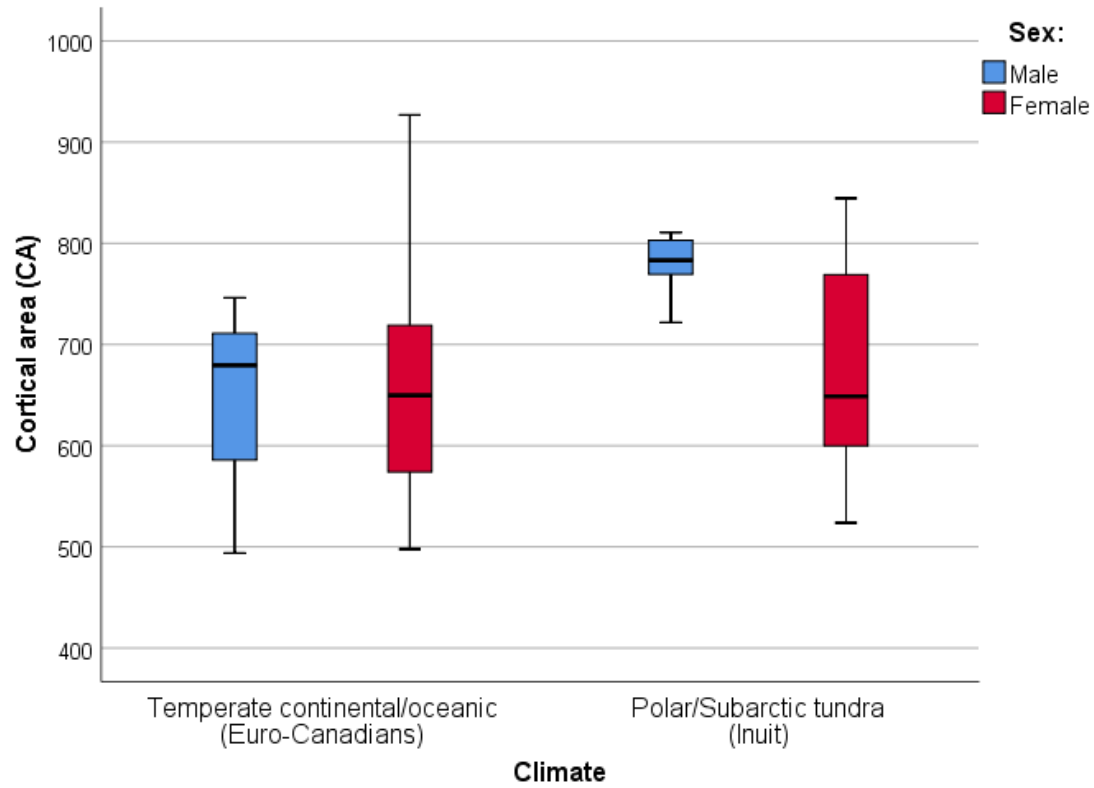
Figure 13: Cortical area in mm^2 at the mid-proximal tibia (65%) by sex in relation to climate.
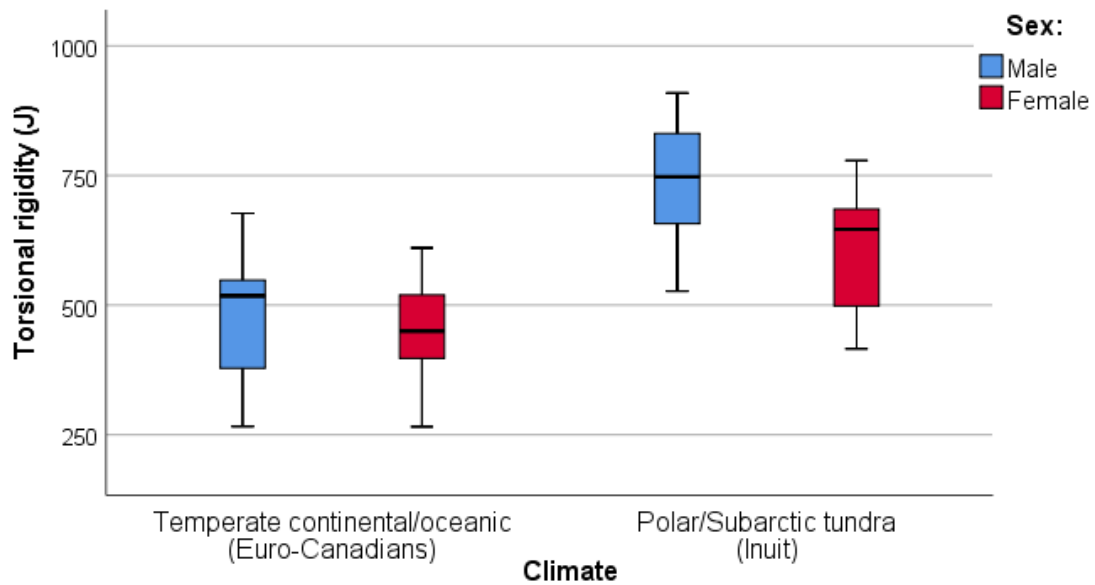
Figure 14:Torsional rigidity in mm^4 at the mid-distal tibia (35%) by sex in relation to climate.

5.1.3. Upper limbs: Humerus

Table 9:P-values of one-way PERMANOVA tests by sex for each humerus cross section.[1]

Male humerus cross sections	35%	50%	65%
CA	0.056	0.127	0.06
J	0.002[2]	0.001[2]	0.002[2]
I_{max}	0.007[2]	0.001[2]	0.006[2]
I_{min}	0.000[2]	0.002[2]	0.002[2]
I_{max}/ I_{min}	0.204	0.425	0.631
Female humerus cross sections	35%	50%	65%
CA	0.07	0.09	0.192
J	0.006[2]	0.004[2]	0.008[2]
I_{max}	0.009[2]	0.003[2]	0.007[2]
I_{min}	0.005[2]	0.018[2]	0.012[2]
I_{max}/ I_{min}	0.415	0.039[2]	0.897

[1] All cross-sectional properties are standardized using powers of bone length: Areas (CA) are divided by bone length[3] and then multiplied by 10^8. SMAs (J, I_{max} and I_{min}) are divided by bone length[5.33] and then multiplied by 10^{12}.
[2] Inuit>Euro-Canadians

The cross-sectional geometry of the humerus in Inuit was compared to the bone structure of Euro-Canadians (EC) from Sainte-Marie and Pointe-aux-Trembles (Table 9). Results show that male and female Inuit have significantly greater torsional rigidity (J), maximum and minimum second moments of area (I_{max} and I_{min}) than EC (Figure 15). These populations do not differ significantly in cortical area (CA) nor in diaphyseal shape (I_{max}/I_{min}) for all humerus cross sections except female Inuit who have significantly more oval midshaft diaphyses compared to their Euro-Canadian counterparts (Figure 16).
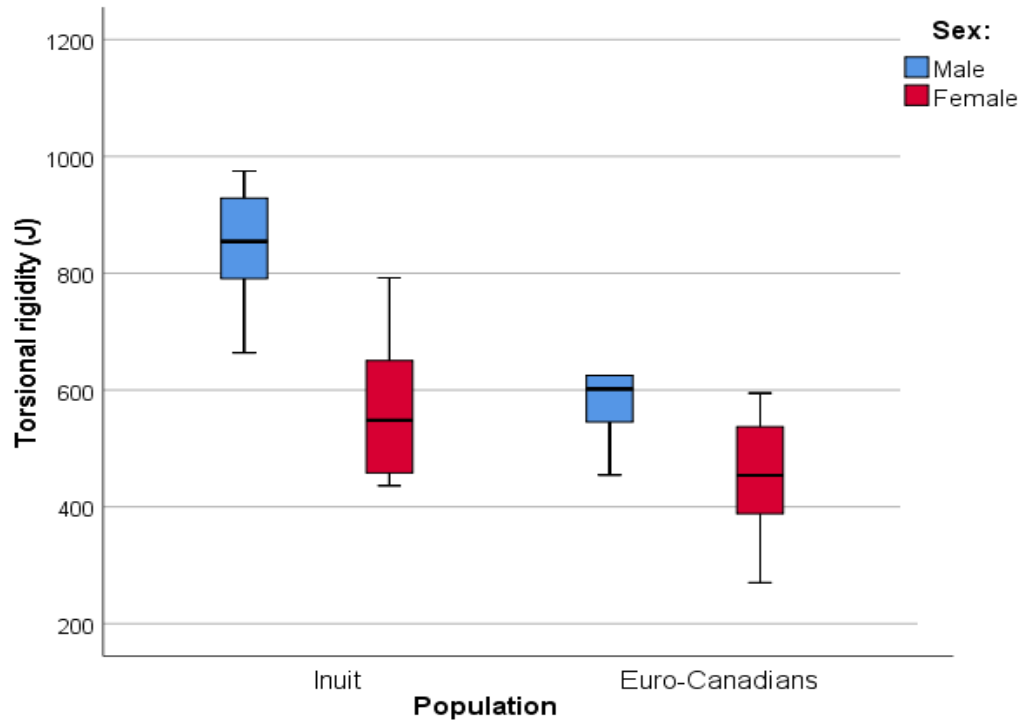
Figure 15: Torsional rigidity in mm^4 at the mid-distal humerus (35%) by sex in Euro-Canadians and Inuit.
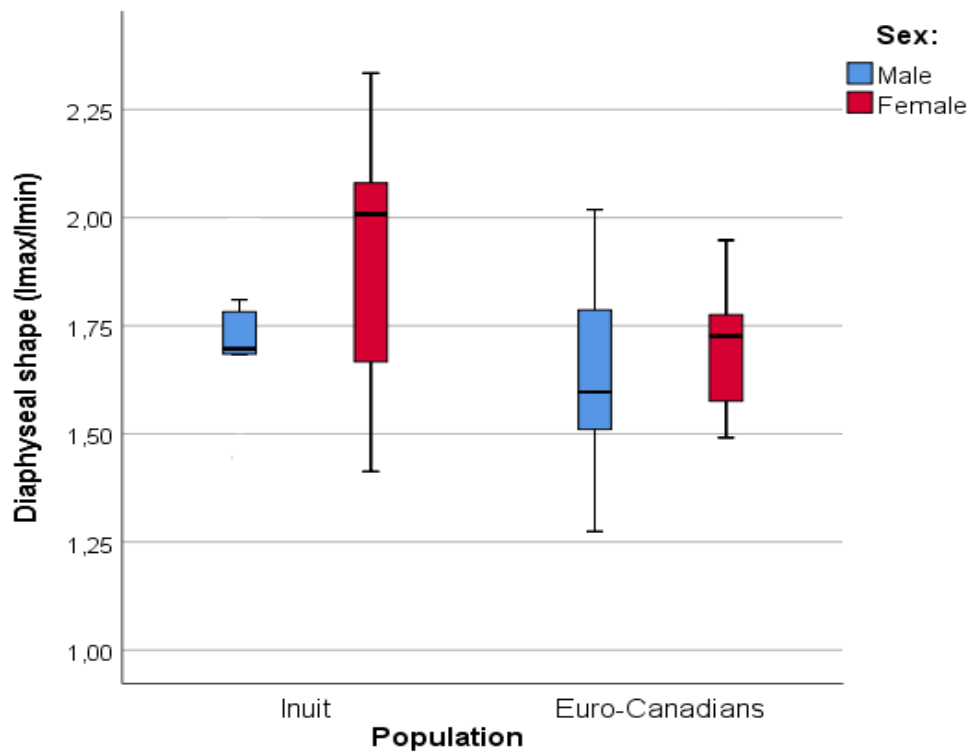
Figure 16: Diaphyseal shape (I_{max}/I_{min}) at the humerus midshaft (50%) by sex in Euro-Canadians and Inuit.

5.2. Meta-analysis: Mobility

The following section presents the results of statistical tests for the meta-analysis at the mid-distal humerus (35%), the femur and tibia midshaft (50%) as well as the femur subtrochanteric region (80%). The meta-analysis consists of this project's study samples, the Inuit and Euro-Canadians from Notre-Dame, Pointe-aux-Trembles and Sainte-Marie, along with other archaeological populations from scientific publications. Statistical tests examined variations in bone structure of each long bone cross section in relation to an individual's mode of subsistence. Subsistence divisions include hunter-gatherers (HG), transitional (TR), intermediate (INT) and intensive agriculturalists (IA) unless otherwise specified.

5.2.1. Lower limbs

5.2.1.1. Femur

Table 10: P-values of one-way PERMANOVA tests by sex for the femur midshaft (50%) and subtrochanteric region (80%) using the mode of subsistence as a grouping factor.[1]

	Male		Female	
Femur cross sections	**50%**	**80%**	**50%**	**80%**
CA	0.000[2]	0.003[2]	0.001[2]	0.018[3]
J	0.000[2]	0.102	0.001[2]	0.161
I_{max}	0.000[2]	0.279	0.001[2]	0.546
I_{min}	0.002[2]	0.622	0.007[4]	0.312
I_{max}/I_{min}	0.104	**0.074[5]**	0.049[6]	0.046[7]

[1] All cross-sectional properties are standardized using powers of bone length: Areas (CA) are divided by bone length^3 and then multiplied by 10^8. SMAs (J, I_{max} and I_{min}) are divided by bone length$^{5.33}$ and then multiplied by 10^{12}.
[2] HG>TR, INT and IA
[3] HG> TR and INT
[4] HG>TR and IA
[5] INT<HG and TR
[6] INT<HG
[7] INT<TR

Table 10 presents the results of tests examining the morphology of the femur in relation to the mode of subsistence. The subtrochanteric section (80%) does not include intensive agriculturalists due to small sample size. The majority of variations in femur cross-sectional geometry occur at the midshaft (50%). Hunter-gatherers of both sexes consistently rank highest in cortical area (CA), torsional rigidity (J), maximum and minimum second moments of area (I_{max} and I_{min}). Overall, these findings demonstrate that HG tend to have more robust femora than any other subsistence category. Noteworthy, there is significant intragroup variation in HG that may

be due to the large sample size of that group (Figure 17 and Figure 18) (Table 3). The 80% section displays no significant differences other than HG having significantly larger CA than any other subsistence group.
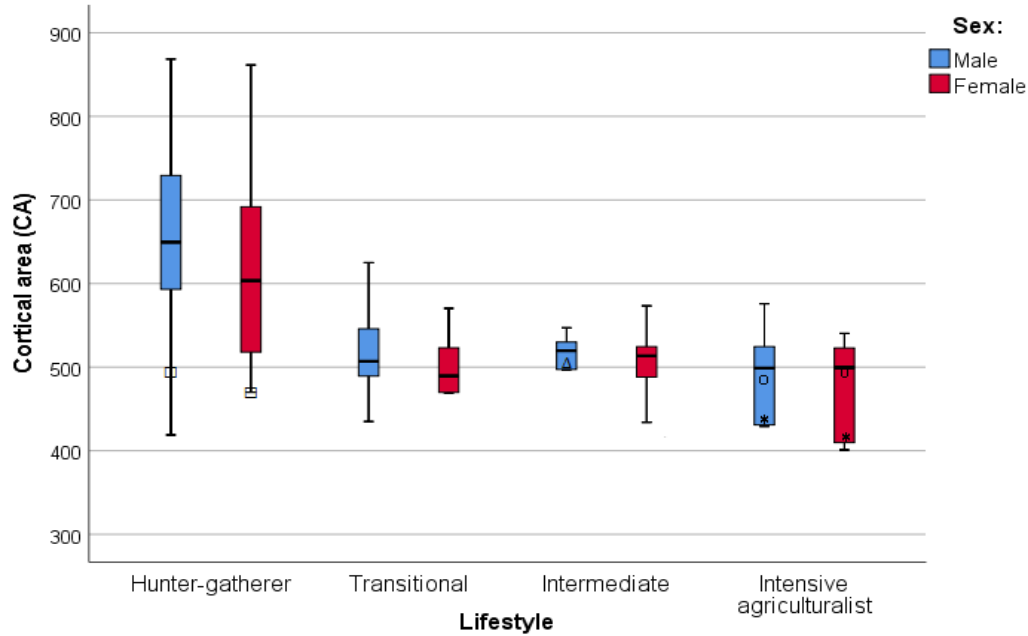
*Figure 17: Cortical area in mm² at the femur midshaft (50%) by sex in relation to the mode of subsistence. Symbols mark populations of this study: □ =Inuit, Δ=Notre-Dame (male only), ο=Pointe-aux-Trembles and *= Sainte-Marie.*
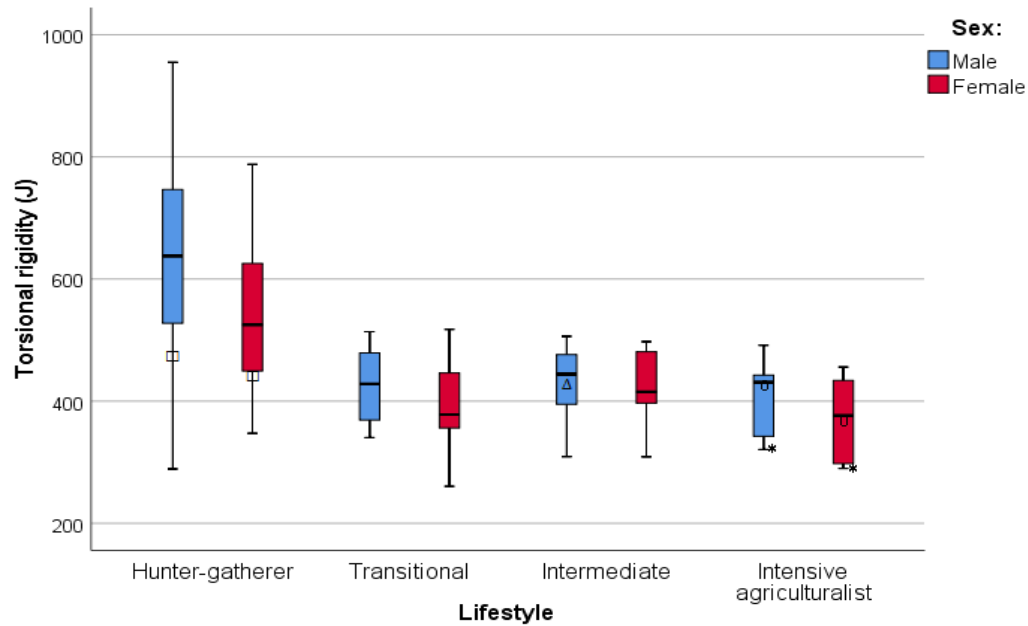
*Figure 18:Torsional rigidity in mm⁴ at the femur midshaft (50%) by sex in relation to the mode of subsistence. Symbols mark populations of this study: □ =Inuit, Δ=Notre-Dame (male only), ο=Pointe-aux-Trembles and *= Sainte-Marie.*

Average CA and J values for the Notre-Dame, Pointe-aux-Trembles and Ste-Marie Euro-Canadians and for Inuit are labelled in Figure 17 and Figure 18. Inuit hunter-gatherers and Sainte-Marie intensive agriculturalists fall below or close to the 25-75 percentile of their respective subsistence groups. In contrast, intensive agriculturalists from Pointe-aux-Trembles and intermediate individuals from Notre-Dame lie well within the average distribution of their relative subsistence groups.

Diaphyseal shape is the only variable in which significant differences were observed between transitional (TR), intermediate (INT) and intensive agriculturalist (IA) populations for all femur cross sections. At the subtrochanteric region (80%), INT males have significantly lower shape ratios (I_{max}/I_{min}), therefore rounder diaphyses than HG and TR groups. Furthermore, INT females are significantly rounder in diaphyseal shape than TR individuals (Figure 19). Diaphyseal shape does not differ significantly among males at the femur midshaft, however, female H-G have more elliptical shaped diaphyses than INT populations (Table 10).
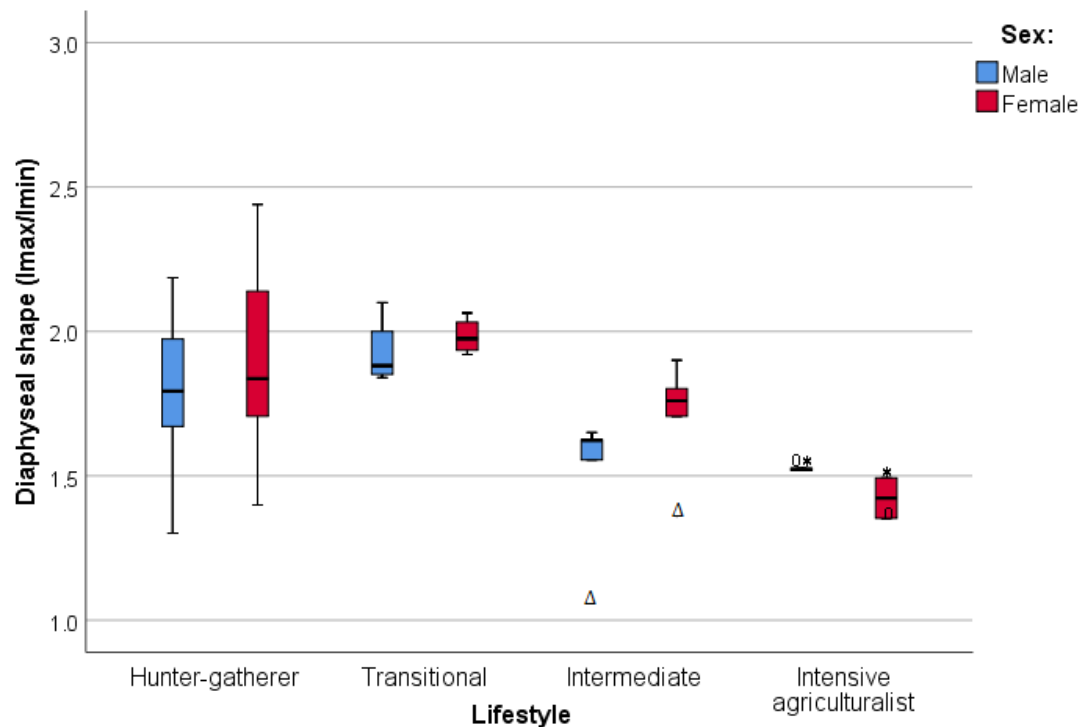
Figure 19: Diaphyseal shape (I_{max}/I_{min}) of the subtrochanteric femur (80%) by sex in relation to the mode of subsistence. Symbols mark populations of this study: No Inuit, Δ=Notre-Dame, o=Pointe-aux-Trembles and *= Sainte-Marie.

Although average values for Inuit fall below the 25-75 percentile for hunter-gatherers, intensive agriculturalists from Sainte-Marie and Pointe-aux-Trembles lie just above their group's median, and Notre-Dame has significantly lower shape indices than the remainder populations of their intermediate category (Figure 19).

5.2.1.2. Tibia

Table 11: P-values of one-way PERMANOVA tests by sex for the tibia midshaft (50%) using the mode of subsistence as a grouping factor.[1]

Tibia 50%	Male	Female
CA	0.000[2]	**0.092[3]**
J	0.001[2]	0.111
I_{max}	0.000[2]	0.034[3]
I_{min}	0.008[2]	0.060
I_{max}/I_{min}	0.208	0.324

[1] All cross-sectional properties are standardized using powers of bone length: Areas (CA) are divided by bone length^3 and then multiplied by 10^8. SMAs (J, I_{max} and I_{min}) are divided by bone length$^{5.33}$ and then multiplied by 10^{12}.
[2] HG>INT and IA
[3] HG >IA

The results of statistical tests comparing the cross-sectional geometry of the tibia midshaft (50%) in populations with different subsistence strategies are provided in Table 11. The transitional group was excluded from this analysis due to small sample size. The tibia exhibits the same general trend observed in the analysis of the femur in which hunter-gatherers have the highest values in cross-sectional properties than all other subsistence categories and thus, are more robust. Also, hunter-gatherers show large intra-group variation which may be due to their large sample size (Table 3). There is greater morphological variation among groups in males than in females. For example, INT and IA males are significantly lower in cortical area (CA), torsional rigidity (J), maximum and minimum second moments of area (I_{max} and I_{min}) compared to HG groups. Females only demonstrate significant differences in CA and I_{max} between HG who are greater than IA (Figure 20). Otherwise, subsistence groups are relatively similar in J, I_{min} in females and diaphyseal shape (I_{max}/I_{min}) for both sexes.
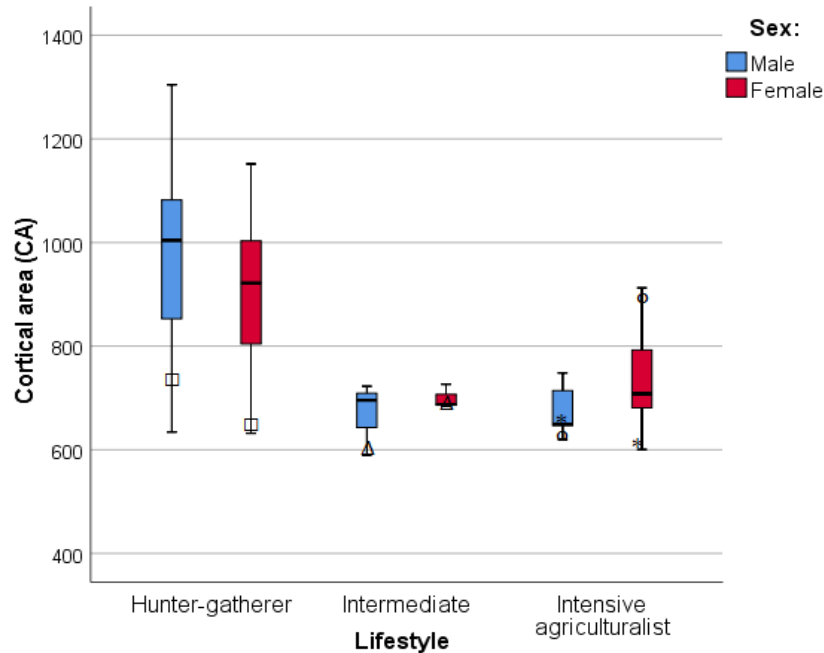
*Figure 20:Cortical area in mm^2 at the tibia midshaft (50%) by sex in relation to the mode of subsistence. Symbols mark populations from this study: □=Inuit, Δ=Notre-Dame (male only), ο=Pointe-aux-Trembles and *= Sainte-Marie.*

Female Inuit hunter-gatherers, intermediates from Notre-Dame and intensive agriculturalists from Sainte-Marie consistently rank below the 25-75 percentile of their respective subsistence groups for all variables, while female IA from Pointe-aux-Trembles lie above the median and males are also below the 25-75 percentile for their group.

5.2.2. Upper limbs: Humerus

Table 12: P-values of one-way PERMANOVA tests by sex for the mid-distal humerus (35%) using subsistence as a grouping factor.[1,2]

Humerus 35%	Male	Female
CA	0.331	0.180
J	0.764	0.326
I_x[3]	0.866	0.733
I_y[3]	0.808	0.399
I_x/I_y	0.089	0.013[4]

[1] Right and left values are averaged. Since there were large gaps in the literature for I_{max}, I_{min} and I_{max}/I_{min}, the properties I_x, I_y and I_x/I_y were analysed instead. Sample sizes for intensive agriculturalists (IA) were too small for statistical comparison.
[2] All cross-sectional properties are standardized using powers of bone length: Areas (CA) are divided by bone length^3 and then multiplied by 10^8. SMAs (J, I_x and I_y) are divided by bone length$^{5.33}$ and then multiplied by 10^{12}.
[3] Variables only compare HG to TR because of small sample size for INT.
[4] HG>TR

The cross-sectional geometry of the mid-distal humerus (35%) was examined in relation to the mode of subsistence (Table 12). There are no significant differences in any of the cross-sectional properties (CA, J, I_x, I_y and I_x/I_y) across subsistence categories for either sex, except in diaphyseal shape among females. Transitional females have more circular mid-distal humerus diaphyses than hunter-gatherers. Similar to what was observed in the lower limbs, HG have large intra-group variation which may be due to the large sample size of that group (Figure 21) (Table 3). For all variables, male Inuit hunter-gatherers and intermediate females from Notre-Dame fall below the median of their relative subsistence groups while female Inuit tend to lie at the median of HG.
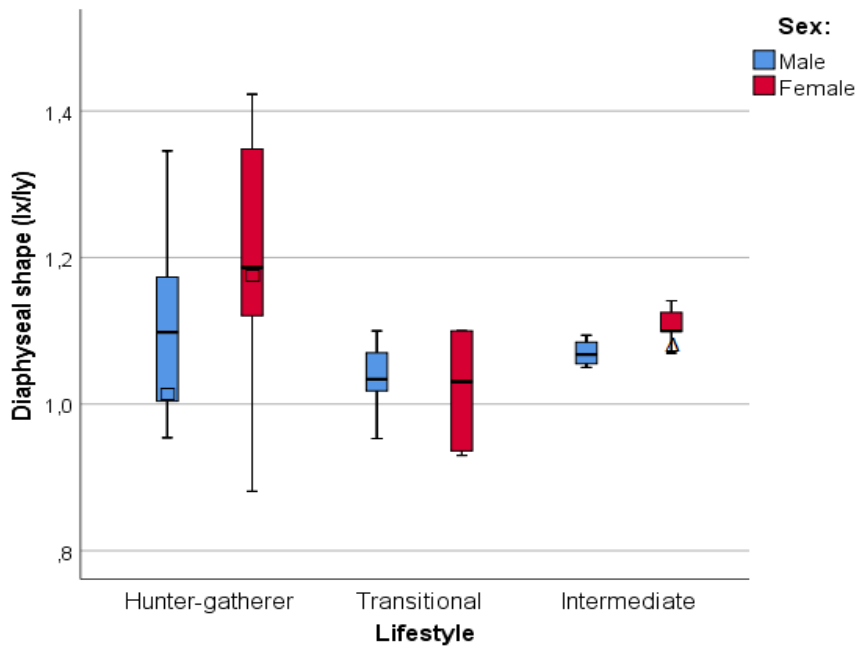
Figure 21: Diaphyseal shape (I_x/I_y) of the mid-distal humerus (35%) by sex in relation to the mode of subsistence. Symbols mark populations of this study: □=Inuit and Δ=Notre-Dame (female only).

5.2.3. Synthesis

As expected, the lower limbs demonstrate more variation in skeletal morphology in relation to the mode of subsistence than the upper limbs. The cross-sectional properties in which significant differences for all long bones are observed most frequently are torsional rigidity (J), and maximum and minimum second moment of area (I_{max} and I_{min}). Otherwise, differences in diaphyseal shape occur more commonly in females whereas males experience more variation in cortical area when comparing subsistence categories. Overall, most observations of significant differences in bone

structure occur between hunter-gatherers and intensive agriculturalists. Hunter-gatherers have the largest intragroup variation in cross-sectional properties than any other subsistence strategy which may be a bias of the large sample size of that group, but could also be due to the large spectrum of behavior that exists among hunter-gatherers. Transitional, intermediate and intensive agriculturalists typically do not differ significantly from one another which may reflect mild differences in the level of mobility and activity between these groups that do not impact bone. Alternatively, it may suggest that the divisions of the different agricultural subsistence modes in this study were not adequate to separate groups per degrees of mobility.

5.3. Meta-analysis: Climate

This section compares the bone structure of populations from the meta-analysis (Euro-Canadians and Inuit from this project and other archaeological populations) in relation to the different climate zones they inhabit. Statistical tests were performed at the mid-distal humerus (35%), the femur and tibia midshaft (50%) in addition to the femur subtrochanteric region (80%). The climate types include tropical/subtropical (TROP), semi-arid/desert (ARID), temperate continental/oceanic (TEMP) and polar/subarctic tundra (POL) unless otherwise specified. Individuals from the Tardiglacial (TG) were excluded from statistical analyses but added to the graphs to observe their distribution relative to other climate groups.

5.3.1. Bone length and body mass

Table 13: P-values of Kruskal-Wallis tests by sex for bone length and body mass according to climate.

Variable	Maximum humerus length	Maximum femur length	Maximum tibia length	Body mass
Male	0.161	0.351	0.927	0.176
Female	0.531	0.151	0.259	0.103

Statistical tests compared body proportions such as bone length and body mass in relation to climate (Table 13). There were no significant differences in bone length for any skeletal element nor body mass between different climate types.

5.3.2. Lower limbs: Femur and tibia

5.3.2.1. Femur

Table 14: P-values of one-way PERMANOVA tests by sex for the cross-sectional properties of the femur midshaft (50%) and subtrochanteric region (80%) using climate as a grouping factor.[1]

	Male		Female	
Femur cross sections	**50%**[2]	**80%**[3]	**50%**[2]	**80%**[3]
CA	0.509	0.421	0.728	**0.063**[8]
J	0.737	0.558	**0.528**[6]	0.014[6, 8]
I_{max}[4]	**0.088**[5]	0.541	**0.482**[7]	0.232
I_{min}[4]	0.288	0.733	**0.519**[7]	0.306
I_{max}/I_{min}	0.423	0.335	0.526	0.713
I_x[3]	0.827	-	0.394	-
I_y[3]	0.726	-	**0.188**[6]	-
I_x/I_y	0.674	-	0.364	-

[1] All cross-sectional properties are standardized using powers of bone length: Areas (CA) are divided by bone length[3] and then multiplied by 10^8. SMAs (J, I_{max}, I_{min}, I_x and I_y) are divided by bone length[5.33] and then multiplied by 10^{12}.
[2] Second moments of area about the M-L and A-P axis (I_x and I_y) as well as the shape index I_x/I_y were included in the analysis of the midshaft due to the small sample size for I_{max}, I_{min} and I_{max}/I_{min} in some climate categories
[3] Because of small sample sizes, the polar/subarctic tundra (POL) category was not included in these analyses.
[4] Because of small sample sizes, the semi-arid/desert (ARID) category was not included in these analyses.
[5] TROP>TEMP
[6] ARID>TROP
[7] POL>TROP
[8] TEMP>TROP

Statistical tests compared the cross-sectional geometry of the femur midshaft (50%) and subtrochanteric section (80%) in archaeological populations from different climate zones (Table 14). Cross-sectional properties differ more frequently at the midshaft than the subtrochanteric region for both sexes. Females exhibit more morphological variations in the femur than males when comparing across climate types. There are no significant differences for any variables (CA, J, I_{max}, I_{min} and I_{max}/I_{min}) in males at the 50% and 80% slice, except for TROP males who are significantly larger in maximum second moment of area (I_{max}) than TEMP groups. Females from TROP environments consistently have the lowest values for all variables, except diaphyseal shape, and thus, are significantly less robust than any other climate category (Figure 22, Figure 23 and Figure 24).
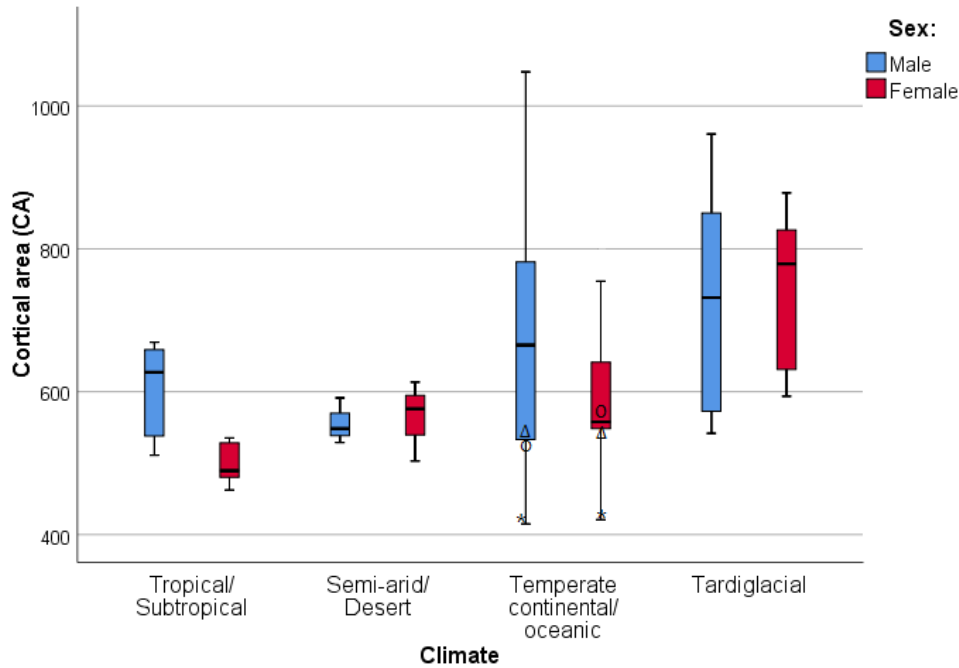
*Figure 22: Cortical area in mm² at the femur subtrochanteric region (80%) by sex in relation to climate. Symbols mark populations of this study: Δ=Notre-Dame, ο=Pointe-aux-Trembles and * = Sainte-Marie.*
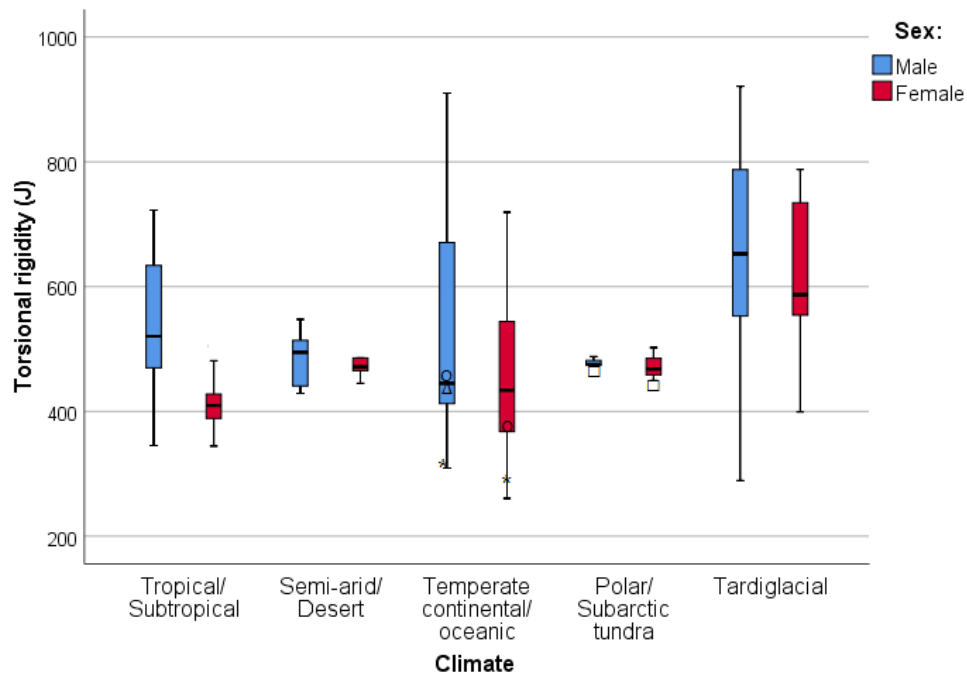
*Figure 23: Torsional rigidity in mm⁴ at the femur midshaft (50%) by sex in relation to climate. Symbols mark populations of this study: □=Inuit, Δ=Notre-Dame (male only), ο=Pointe-aux-Trembles and * = Sainte-Marie.*
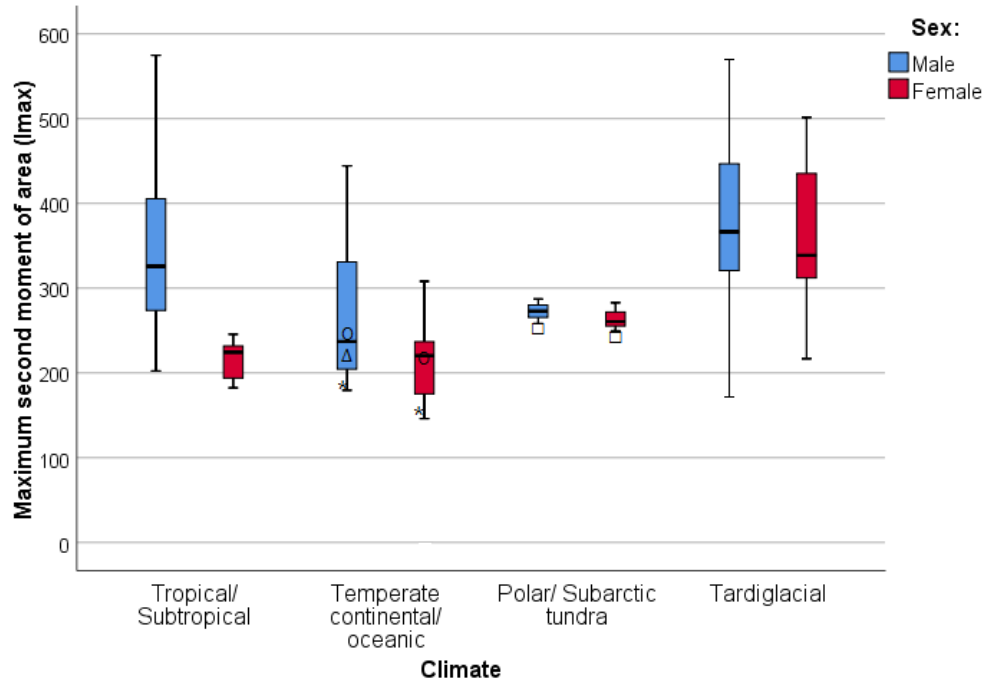
*Figure 24: Maximum second moment of area (I_{max}) in mm^4 at the femur midshaft (50%) by sex in relation to climate. Symbols mark populations of this study: □=Inuit, Δ=Notre-Dame (male only), ο=Pointe-aux-Trembles and *= Sainte-Marie.*

At the midshaft, Sainte-Marie lie at the lower extreme of the distribution while Pointe-aux-Trembles and Notre-Dame are close or within the 25-75 percentile for the TEMP group. Also, Sadlermiut Inuit are at the lower end of the POL category. The subtrochanteric region yields the same pattern for CA but, when examining other properties (J, I_{max} and I_{min}) that are not illustrated here, it is evident that Euro-Canadians from Pointe-aux-Trembles are above the 25-75 percentile for TEMP climates in both males and females.

Populations from the Tardiglacial are significantly larger for most cross-sectional properties compared to all other climate types. Although, TG individuals may simply be more robust because they are hunter-gatherers. Furthermore, TG and TEMP categories as well as TROP males consistently demonstrate significant intra-group variation in cross-sectional values, but it may be due to bias from large sample size.

5.3.2.2. Tibia

Table 15: P-values of one-way PERMANOVA tests by sex for the cross-sectional properties of the tibia midshaft (50%) using climate as a grouping factor.[1]

Tibia 50%[2]	Male	Female
CA	0.616	0.97
J	0.734	0.724
I_{max}	0.25	0.557
I_{min}	0.181	0.162
I_{max}/I_{min}	0.694	0.221

[1] All cross-sectional properties are standardized using powers of bone length: Areas (CA) are divided by bone length[3] and then multiplied by 10^8. SMAs (J, I_{max} and I_{min}) are divided by bone length[5.33] and then multiplied by 10^{12}.
[2] Includes all climate groups except for semi-arid/desert (ARID) due to small sample size.

Results from the one-way PERMANOVA tests of the tibial midshaft (Table 15) show no significant differences in any of the cross-sectional properties for either sex across all climate types. TEMP and TG males exhibit large intra-group variation (Figure 25).
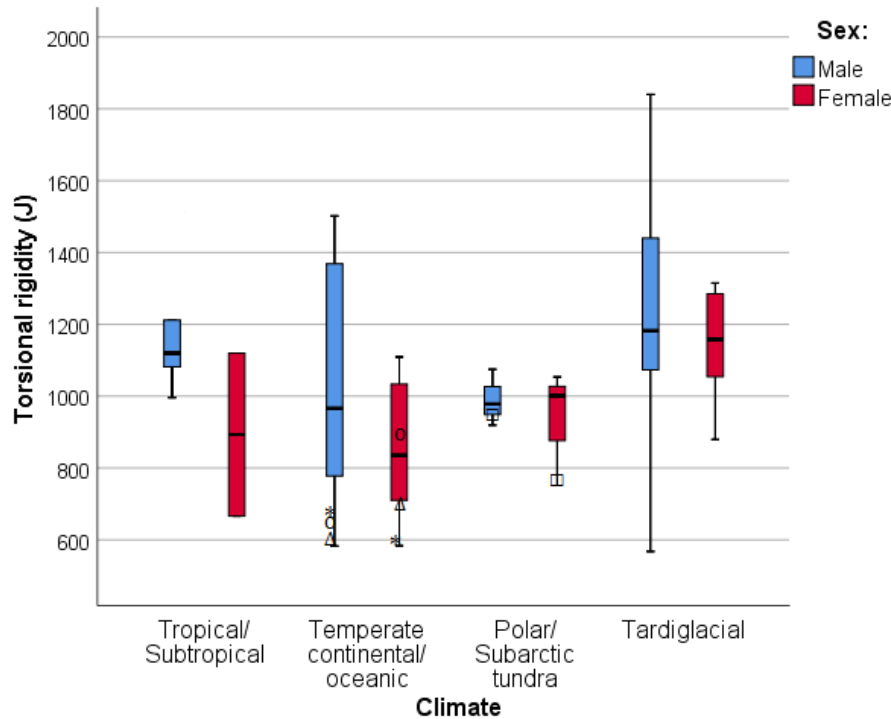
Figure 25: Torsional rigidity in mm^4 at the tibia midshaft (50%) by sex in relation to climate. Symbols mark populations of this study: □=Inuit, Δ=Notre-Dame, o=Pointe-aux-Trembles and *= Sainte-Marie.

Although tibiae midshafts do not differ significantly, the distribution of properties in Inuit and Euro-Canadians were observed compared to their respective climate groups (Figure 25). Both populations tend to have values below or at the bottom of the range for their climate type, with the

exception of females from Pointe-aux-Trembles who lie above the median. Additionally, values from the Tardiglacial (TG) are significantly larger than that of all other climate divisions, except for TROP males, indicating more robust tibiae midshafts. Lastly, TG and TEMP males exhibit large intragroup variation in cross-sectional properties.

5.3.3. Upper limbs: Humerus

Table 16: P-values of one-way PERMANOVA tests by sex for the cross-sectional properties of the mid-distal humerus (35%) using climate as a grouping factor.[1]

Humerus 35%	Male	Female
CA	0.034[2]	0.606
J	0.049[3]	**0.164[4]**
I_x	**0.154[5]**	**0.447[3]**
I_y	**0.199[5]**	0.854
I_x/I_y	0.285	**0.257[6]**

[1] All cross-sectional properties are standardized using powers of bone length: Areas (CA) are divided by bone length[3] and then multiplied by 10^8. SMAs (J, I_x and I_y) are divided by bone length[5.33] and then multiplied by 10^{12}.
[2] TEMP<TROP and POL
[3] POL>ARID and TEMP
[4] POL>TROP and TEMP
[5] POL>TEMP
[6] POL>ARID

Statistical tests were performed using the meta-analysis to examine the cross-sectional geometry in populations from various climate types (Table 16). Populations inhabiting polar/subarctic tundra (POL) environments have the highest measures in cross-sectional properties the mid-distal humerus (35%) compared to any other climate category and thus, have more robust humeri. Furthermore, temperate continental/oceanic (TEMP) males and tropical/subtropical

(TROP) females rank lowest in all measures of robusticity (
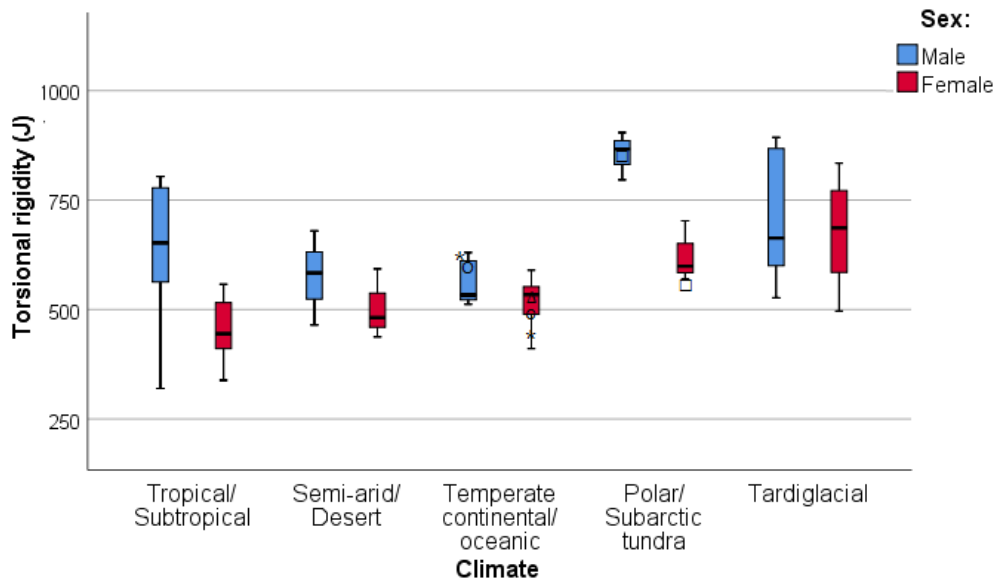
Figure 26). Climate types do not differ significantly in diaphyseal shape among males. However, POL females have humeri diaphyses that are significantly more oval in shape than females from semi-arid/desert (ARID) climates (

Figure 27).
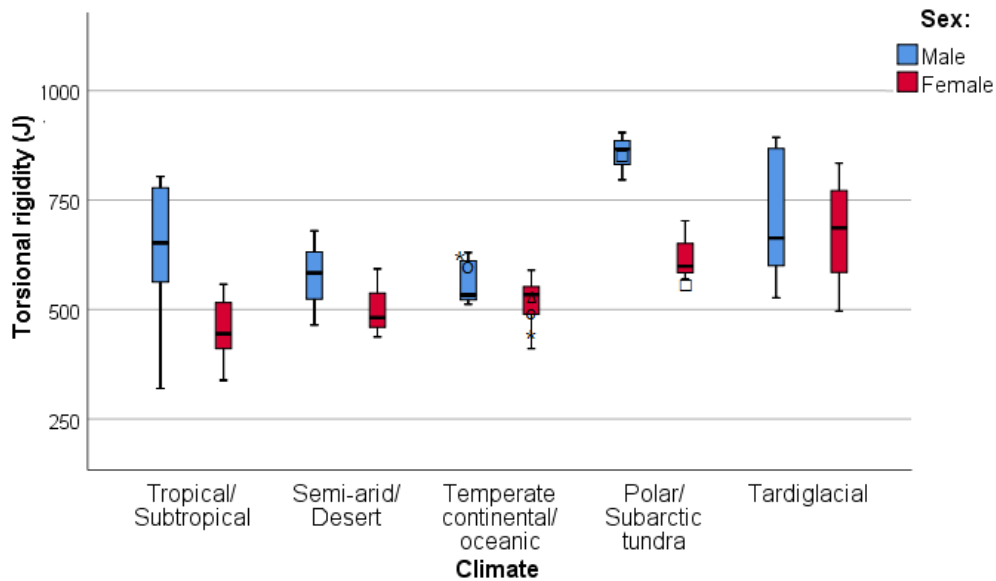
Figure 26: Torsional rigidity in mm⁴ at the mid-distal humerus (35%) by sex in relation to climate. Symbols mark populations of this study: □=Inuit, Δ=Notre-Dame (female only), o=Pointe-aux-Trembles and *= Sainte-Marie.
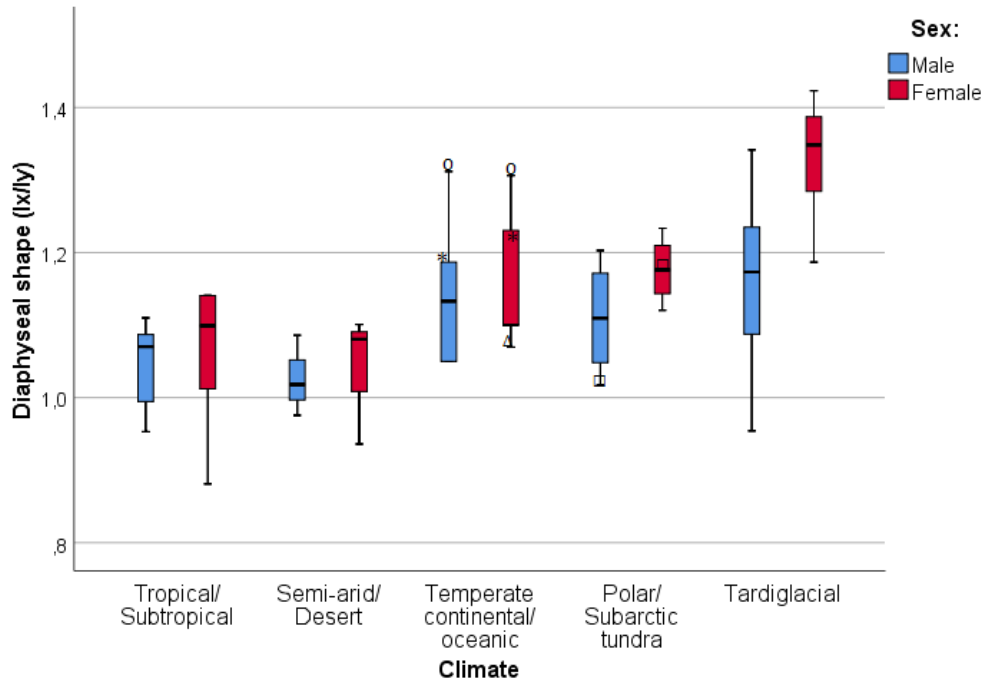
Figure 27: Diaphyseal shape (I_x/I_y) at the mid-distal humerus (35%) by sex in relation to climate. Symbols mark populations of this study: □=Inuit, Δ=Notre-Dame (female only), O=Pointe-aux-Trembles and *= Sainte-Marie.

Female Inuit and EC from Sainte-Marie and Pointe-aux-Trembles fall below the 25-75 percentile in J (Figure 26) while EC females from Notre-Dame and Inuit males are within the 25-75 percentile but below the median of their relative climate types. In contrast, EC males from Sainte-Marie and Pointe-aux-Trembles are above the median for TEMP groups. For diaphyseal shape, EC from Pointe-aux-Trembles and Sainte-Marie are at or above the median shape ratio for TEMP climates (Figure 27). Females from Notre-Dame and Inuit males are below the 25-75 percentile of I_x/I_y for their climate categories but, Inuit females are at the median of POL populations.

The distribution of Tardiglacial (TG) individuals for all cross-sectional variables differs in the humerus compared to patterns observed in the lower limbs. For instance, females from the TG exhibit the highest measures of skeletal robusticity and have significantly more oval humeri diaphyses compared to all climate categories. On the other hand, TG males have properties similar to TROP climates and tend to be smaller than POL groups, except for diaphyseal shape which

resembles that of TEMP and POL males. Additionally, TG and TROP populations have large intra-group variation in cross-sectional properties that may be attributable to their large sample sizes.

5.3.4. Synthesis

There are significant differences in the bone structure of the humerus and femur when comparing different climate types whereas none are observed for the tibia. The patterns in cross-sectional geometry between sexes are more divergent in the lower than the upper limbs. In the lower limbs, females are more affected by changes in climate than males whereas both sexes are significantly impacted in the humerus. Populations from POL climates have the most robust upper limbs while TROP males and POL/ARID females have the greatest lower limb robusticity. The lowest values tend to be observed in TROP females and TEMP males. Climate categories have similar shaped lower limb bone diaphyses, but the mid-distal humerus is more circular in TROP and ARID groups, and more oval in TEMP and POL populations.

Individuals from the Tardiglacial (TG) tend to have the highest values in cross-sectional properties of the lower limbs whereas only TG females are significantly larger in the upper limbs and TG males are similar to TROP climates. TG and TEMP populations demonstrate large intra-group variation in the femur while, at the tibia midshaft, only males have large intra-group variations. For the humeri, TG and TROP climates are the groups with the largest intragroup variation. The large samples size of TG and TEMP groups may explain their high variability (Table 4).

5.4. Climate and subsistence mode interactions

Table 17: P-values of two-way PERMANOVA tests by sex for long bone cross sections examining the interaction between the mode of subsistence and climate.[1]

Bone sections	Humerus 35%		Femur 50%		Femur 80%		Tibia 50%	
	Male	Female	Male	Female	Male	Female	Male	Female
CA	0.9153	0.959	1	0.999	0.982	1	0.964	0.226
J	0.843	0.891	0.999	0.999	0.845	0.996	0.933	0.399
I_{max}	-	-	1	1	0.97	0.448	0.999	0.991
I_{min}	-	-	0.995	0.999	0.871	0.500	0.994	0.998
I_{max}/I_{min}	-	-	0.996	0.999	0.911	0.789	0.949	0.786
I_x	0.622	0.683	-	-	-	-	-	-
I_y	0.578	0.271	-	-	-	-	-	-
I_x/I_y	0.995	1	-	-	-	-	-	-

Two-way PERMANOVA tests for the mid-distal (35%) humerus, the femur midshaft (50%) and subtrochanteric section (80%) as well as the tibia midshaft (50%) were used to examine whether mobility and climate interact to impact human post-cranial morphology (Table 17). There were no significant results for interaction tests at any of the cross-section locations. The results of the two-way PERMANOVA interaction tests suggest that the influence of mobility on bone structure is independent of that of climate and, vice versa. However, large differences in sample sizes within and between each factor may have diluted evidence of an interaction.

Chapter 6: Discussion and Conclusion

The first section of this chapter focuses on comparing the humerus, femur and tibia of the Sadlermiut Inuit and Euro-Canadians with distinct levels of mobility and inhabiting different climatic conditions. The second section uses the meta-analysis to shed light on the relationship between the postcranial morphology and mobility while the third examines morphological differences in populations from different climate types. The results for each hypothesis are provided in Table 18.

Table 18: Summary of results for each hypothesis.

Hypothesis	Results
1.1 Body proportions + Lower limb-Robusticity	• Partially supported
• Cold climate $\Rightarrow$ Sadlermiut limb length < Euro-Canadians + Sadlermiut Inuit body mass > Euro-Canadians.	• Sadlermiut body mass < Euro-Canadians.
• Hunter-gatherer $\Rightarrow$ Sadlermiut Inuit robusticity > Euro-Canadian agriculturalists.	• Supported
1.2 Lower limbs-Diaphyseal shape Hunter-gatherer Sadlermiut will have more elliptical shaped femur diaphyses than Euro-Canadian agriculturalists.	Refuted: no generalised trend in diaphyseal shape related to subsistence.
2.1 Upper limbs-Robusticity High marine mobility + short limb lengths $\Rightarrow$ Sadlermiut robusticity > Euro-Canadians.	Supported
2.2 Upper limbs-Diaphyseal shape Hunter-gatherers $\Rightarrow$ Sadlermiut Inuit will have more elliptical shaped humerus diaphyses than Euro-Canadian agriculturalists.	Refuted: no generalised trend in diaphyseal shape related to subsistence.
3.1) Meta-analysis: Mobility-Lower limbs Hunter-gatherers $\Rightarrow$ more oval long bone diaphyses + robusticity > transitional, intermediate and intensive agriculturalists.	Supported
3.2) Meta-analysis: Mobility-Lower limbs ↑ sedentism of transitional, intermediate and intensive agriculturalists = ↑ gracilization.	Refuted: no generalised trend towards gracilization in relation to the intensity of agricultural practices.
4.1) Meta-analysis: Mobility-Upper limbs Innovation of mechanized tools $\Rightarrow$ Hunter-gatherer robusticity > Intermediate populations.	Refuted: no significant differences in robusticity $\Rightarrow$ may indicate similar levels of physical activity.

4.2) Meta-analysis: Mobility-Upper limbs Hunter-gatherer habitual activities $\Rightarrow$ more oval diaphyseal shape in than any other subsistence division.	Partially supported: males exhibit no generalised trend in diaphyseal shape related to subsistence.
5.1) Meta-analysis: Climate-Lower limbs* Cold climates i.e. polar/subarctic tundra $\Rightarrow$ robusticity > all other climate categories.	Refuted: POL climates not significantly more robust than other climate types.
5.2) Meta-analysis: Climate-Upper limbs* Cold climates i.e. polar/subarctic tundra $\Rightarrow$ robusticity > all other climate categories.	Supported

*Evidence for a climatic component in the skeletal morphology of TROP populations, whether it be a factor of long-term genetic adaptation to tropical/subtropical climates and/or climate-mediated behavior: upper and lower limbs of males are highly robust whereas females are very gracile.

6.1. Comparing robusticity in Inuit and Euro-Canadians

6.1.1. Robusticity of the lower limbs: Femur and tibia

It was hypothesised that Sadlermiut Inuit had a more active lifestyle due to their hunting and gathering mode of subsistence and that this higher level of mobility would lead to larger values in cross-sectional properties indicating greater lower limb robusticity (Hypothesis 1.1). Moreover, it was predicted that the high levels of physical activity of Sadlermiut Inuit would cause stereotypical elongation along the A-P axis and result in a more oval diaphyseal shape (Hypothesis 1.2). The significantly greater values in bending and torsional rigidity (J) and second moments of area (I_{max} and I_{min}) for all femur and tibia cross sections, in addition to markedly thicker cortical area (CA) in male tibia, of Sadlermiut Inuit than Euro-Canadians with an intermediate or intensive agriculturalist mode of subsistence lend support for Hypothesis 1.1. In contrast, support for Hypothesis 1.2 is sparse since the only significant differences in diaphyseal shape of the femur and tibia are found at the mid-proximal femur (65%) where Inuit males have more elliptical shaped diaphyses than Euro-Canadians and the mid-distal femur (35%) where, conversely, Euro-Canadian females are more oval in shape than Sadlermiut females.

The differences in body proportions between these two populations may have contributed to the greater values in mechanical properties of Sadlermiut Inuit since standardization of body size was done with powers of bone length. Euro-Canadian males have significantly longer lower limb lengths and heavier body mass than Inuit males while Euro-Canadian females have longer humerus than Sadlermiut females, but are not different in lower limb bone length nor body mass.

These results partially contradict expectations of Hypothesis 1.1 for climate-mediated body shape since Sadlermiut tend to have shorter bone lengths, but smaller or similar body mass compared to Euro-Canadians. Although variations in bone length may have exaggerated differences in cross-sectional geometry between males, females still exhibit significant differences in measures of robusticity despite having similar body proportions, suggesting that these results are not simply due to differences in body shape.

Age has been shown to affect the distribution and quantity of bone through processes like endosteal and subperiosteal surface expansion (Ruff 2007; Ruff and Hayes 1982; Ruff and Hayes 1983), and thus could explain the group differences. However, the demographic distributions of Euro-Canadians and Sadlermiut Inuit resemble one another with a fairly even number of individuals distributed between the ages of 20-35 and 35-50 years old. Therefore, although the broad age ranges prevent a more thorough testing of age demographics, the significantly less robust lower limbs of Euro-Canadians are likely not a factor of the age distribution of the samples.

Metabolic or nutritional factors can impact bone growth and cause bone loss as well. Quebec history is characterized by regular bouts of disease epidemics and famine due to demographic growth and persistent conflict from the colonization of New-France that especially affected urban areas (Amorevieta-Gentil 2010; Gutierrez 2019). For this reason, the femur and tibia of Euro-Canadians may be less robust due to nutritional stress or disease induced pathologies rather than low physical activity. For instance, archaeological reports suggest that individuals from Sainte-Marie and Pointe-aux-Trembles were commonly afflicted with anemia and hypoplasia which could have resulted from malnutrition or stress (Ethnoscop 2006; 2016). These rural villages also had a diet significantly lower in protein and poorer living conditions compared to urban centers like Notre-Dame (Crépin 2018; Toupin 2016). Osteological analyses of individuals from urban Notre-Dame provided evidence of a diverse and well-balanced diet despite successive food shortages (Arkéos 2008). Consequently, the Notre-Dame group that was considered as practicing intermediate agriculture may not have been impacted by the same metabolic stress and malnutrition as the intensive agriculturalist Euro-Canadians. Therefore, individuals from Notre-Dame were less at risk of experiencing bone loss, while it may have been an issue in the more rural populations. This may explain why there were no significant differences in the tibial cross-sectional geometry of the urban Notre-Dame group compared to Sadlermiut Inuit but there were

differences with both rural Euro-Canadian villages. Although it is difficult to gage whether the samples in this study are representative of the entire Quebec population, evidence suggests that differences in bone structure between intensive agriculturalist Euro-Canadians from Sainte-Marie and Pointe-aux-Trembles, and Sadlermiut Inuit hunter-gatherers may in part be attributable to metabolic and nutritional stress leading bone loss.

Merbs (1983), examining degenerative and traumatic pathology in the skeletons of Sadlermiut Inuit, demonstrated high correlations between their daily activities and the patterns in pathology observed throughout the body. Inuit frequently engaged in arduous activities that involved transporting heavy equipment such as limestone slabs for house building and/or game meat from hunting trips over long distances on Southampton Island's difficult terrain (Merbs 1983). These findings corroborate with the results of this study indicating high lower limb robusticity, however, archaeological evidence suggests that Sadlermiut made significant use of dog sleds to bring these heavy objects with them during seasonal moves or hunting trips. This means that their robust lower limbs may not be due to high terrestrial mobility but instead, the result of consistent mechanical stress from an overall very demanding lifestyle involving strenuous subsistence related activities and intensive physical activity (Merbs 2018). For instance, they were constantly active by regularly participating in wrestling and football matches, hunting big game such as seals and walrus among others, processing game meat for consumption and clothing material, making tools, rowing, driving dog sleds on difficult terrain, carrying heavy objects for building material, and constructing houses or kayaks (Merbs 1983). Therefore, mechanical stimuli are a strong contender for explaining the skeletal variations between these two populations (Hypothesis 1.1).

On the other hand, previous studies of the Euro-Canadian samples suggest that they were more active than their subsistence mode implies. An archaeological report from Arkéos (2008) on the osteological remains of Notre-Dame cemetery showed that these individuals had generally robust skeletons with pronounced muscle attachments. This was interpreted as reflecting strenuous physical activity associated with food production, supporting descriptions from historical accounts. The population of Notre Dame was highly active due to the demands involved in establishing themselves and shaping their environment as part of being the first colonizers of New-France (Arkéos 2008). Crépin (2018), studying entheseal changes (changes at muscle insertion

sites), found that urban Notre-Dame and rural Sainte-Marie samples exhibited significant modeling at lower limb muscle insertions, that she interpreted as reflecting a physically demanding lifestyle. Bioarchaeological analyses of samples from Pointe-aux-Trembles found pathologies such as arthritis that were interpreted as signs of high physical activity (Ethnoscop 2016). The findings of these studies suggest that the level of physical activity required in an agrarian lifestyle was greater during the first waves of colonization because of the effort involved in clearing and working the land, carrying heavy equipment or materials, and using manual non-mechanised tools that necessitated repetitive and excessive force in the upper limbs and regularly engaged the lower limbs for stability (Crépin 2018). The low cross-sectional values of the EC sample relative to Sadlermiut Inuit may then be due to metabolic and nutritional stressors on the bone tissue of Euro-Canadians through reducing bone mass. The other possibility is that Euro-Canadians were more active than modern sedentary agriculturalists but not to the same degree as Sadlermiut Inuit who must survive in harsh and cold environmental conditions.

Furthermore, male tibiae were more affected than that of females by the mode of subsistence and by climate. Although Sadlermiut tend to have greater cortical area than Euro-Canadians (only statistically significant in males), the differences in patterns of skeletal morphology between the tibia of males and females may be attributable to the sharply defined sexual division of labor among Sadlermiut. Males were in charge of food procurement, gathering heavy objects and using this material for building houses or kayaks while females were responsible for child rearing, food preparation and making clothes (Merbs 1983). Characteristically male activities utilised both the lower and upper limbs whereas routinely female activities primarily involved the upper limbs, meaning that there would be differential impact of physical activity on bone structure according to sex. Consequently, the excessive loading of the lower limbs as part of male daily life imposed more stress that would have triggered the bone modeling process to resist against higher strains. Bioarchaeological analyses of rural Euro-Canadians suggest that there was sexual division of labor as well, except females were generally less active than their male counterparts who took on the bulk of agricultural work (Crépin 2018). Therefore, the lack of significant differences among groups in female lower limb morphology can be explained by the fact that, in both populations, females had more sedentary tasks and their activities mainly engaged the upper limbs. In contrast, osteological reports of Notre-Dame demonstrate that both sexes regularly engaged in intense manual labor such as tree cutting and building construction for males,

and gardening and animal husbandry for females (Arkéos 2008). This may explain why EC females with an intermediate agricultural lifestyle had cross-sectional properties that were midway between hunter-gatherers and intensive agriculturalists.

Sadlermiut exemplify how mechanical stimuli incurred by an individual's daily life activities can be a good predictor of bone structure regardless of subsistence strategy. Despite being labeled as hunter-gatherers, their active lifestyle is more a factor of the effort and intensity exerted during daily tasks or subsistence related activities rather than the mobility needed to complete these activities. Comparably, populations with modes of subsistence typically associated with low levels of mobility have been found to exhibit robust lower limbs which reflects how physically active or demanding their daily life was overall. For instance, Holt et al. (2017) demonstrated a relationship between increased lower limb robusticity in European Medieval populations, and socioeconomic and political turmoil occurring during that period that constantly imposed extreme physical demands on individuals to ensure survival. Additionally, Bridges (1989) demonstrated that intensive maize agriculturalists had more robust lower limbs than hunter-gatherers because the tasks required to intensify production created higher physical demands, thereby increasing mechanical loading on the limbs. These populations and Inuit all have high lower limb robusticity yet completely different subsistence strategies which attests to the importance of considering other activities than mobility that impose arduous physical exertion on a daily basis.

The patterns observed in the lower limbs can, in part, be interpreted as a predisposition towards shorter limbs and evidence of climate indirectly impacting Sadlermiut morphology through influencing behavior. This is corroborated by ethnographic, historic and archaeological accounts reporting Sadlermiut as being characteristically broad-bodied with short limbs and generally very strong from living in harsh environmental conditions (Merbs 1983; Merbs 2018). Davies and Stock (2014) found similar results indicating that Sadlermiut had the highest values in bending and torsional rigidity along with Yahgan, another marine mobile population from a polar climate, compared to Australian aboriginal terrestrial hunter-gatherers. Since both Sadlermiut and Yahgan exhibit high robusticity even within their own mobility category as hunter-gatherers and are both from polar climates, their bone structure may be the result of long-term genetic adaptation to cold conditions. Pearson (2000) and Stock (2002) identified a similar pattern in which

populations from colder climates had higher measures of skeletal robusticity reinforcing the notion that climate may have played a role in explaining these differences. However, when considering the findings of these studies in combination with that by Holt et al. (2017), there seems to be an interplay between difficult environmental conditions and the level of physical activity required to survive under extreme conditions whether climate, politically or socioeconomically related. Essentially, Sadlermiut Inuit have robust lower limbs as a product of their physically demanding lifestyle, which is necessary to survive in an intense high-risk environment corroborating Hypothesis 1.1.

Hypothesis 1.2 predicted more oval shaped diaphyses for populations with higher levels of mobility such as Sadlermiut Inuit, however, results hint at a more complex interpretation of diaphyseal shape that conflicts with this hypothesis. For instance, Inuit males have more oval shaped diaphyses for the mid-proximal femur than male Euro-Canadians. Contrary to predictions, Euro-Canadian females have more oval shaped diaphyses than Inuit females at the mid-distal femur. The absence of a generalised trend between mobility and diaphyseal shape suggests that these findings may reflect population differences in the type of activities differentially impacting sections of bone. This is probable given that the activities of these populations diverged according to a forager versus agriculturalist mode of subsistence as well as a temperate versus polar climate. There is also the possibility that the rough terrain of Southampton's island imposed mechanical loads on a different plane than the generally flat terrain of Quebec occupied by Euro-Canadians (Pearson et al. 2014; Ruff 1987). Alternatively, studies have shown that the proximal segments of the femur and tibia are significantly influenced by climate, partly through ecogeographical conditions mediating patterns in body laterality that would alter the distribution of bone along a certain plane (Ruff 1994; Shackelford 2005; Stock 2002). However, interpreting long-term genetic adaptation to extreme cold as the determining factor of diaphyseal shape in Sadlermiut Inuit is less plausible given that results were not significant for the tibia and differed between the sexes.

6.1.2. Robusticity of the upper limbs: Humerus

The Sadlermiut Inuit were predicted to have shorter limbs as part of their climatic predispositions to cold conditions and greater skeletal robusticity in the upper limbs than Euro-Canadians as a result of their high marine mobility (Hypothesis 2.1). Furthermore, Sadlermiut Inuit were expected to have more elliptical shaped diaphyses than Euro-Canadians due to hunting

activities that engaged the humerus stereotypically along the A-P axis and caused a thickening along that plane (Hypothesis 2.2). The significantly higher values in bending and torsional rigidity (J), maximum and minimum second moment of area (I_{max} and I_{min}) as well as generally thicker cortical area of Sadlermiut Inuit compared to Euro-Canadians for both sexes lend support for Hypothesis 2.1. Sadlermiut Inuit have significantly shorter bones than Euro-Canadians for both sexes. It is important to consider that these discrepancies in limb length could have exaggerated differences in bone structure between these two populations because cross-sectional properties were standardized for body size using powers of bone length.

Systemic factors such as age and nutrition could explain the morphological variations observed in the upper limbs. However, as observed above, the demographic profiles of Euro-Canadian and Inuit samples are similar. On the other hand, metabolic stress and poorer nutrition associated with the rural Euro-Canadian populations of Sainte-Marie and Pointe-aux-Trembles may have resulted in the loss of bone mass (Amorevieta-Gentil 2010; Crépin 2018; Ethnoscop 2006; Gutierrez 2019; Ruff 2007; Toupin 2016). Therefore, the bone structure of Euro-Canadians may not be an accurate reflection of mechanical loading patterns on the upper limbs due to the consequences of poor health possibly influencing their measures of robusticity.

The lifestyle of Sadlermiut Inuit involved intense and frequent manual labor as a consequence of a foraging mode of subsistence and living in harsh environmental conditions. The significant mechanical stresses imposed on the upper limbs during their daily activities in combination with high marine mobility suggest that mechanical factors may be responsible for high robusticity in Inuit compared to Euro-Canadians (Hypothesis 2.1) (Merbs 1983). This is corroborated by bioarchaeological analyses of Sadlermiut that demonstrated a higher incidence of pathologies related to habitual activities in the upper limbs than the lower limbs (Merbs 1983; Merbs 2018). Males regularly engaged in harpoon-throwing and kayak-paddling for food acquisition. Harpoon-throwing requires a high level of accuracy and strength specifically on the dominant limb while paddling or rowing requires pulling strength against the water to propel the watercraft and involves flexion-extension of the arm. Sadlermiut men were also responsible for hammering and flaking tools, driving dog sleds through rough terrain, constructing stone houses and watercrafts, and took pride in carrying and lifting heavy objects such as big game meat or building material as a sign of masculinity. In contrast, Inuit females were predominantly in charge

of processing animal remains, child rearing and maintaining the household. Their upper limb pathologies were most consistent with the flexion and extension of the elbow involved in the arduous scraping of animal hides that requires significant endurance when making clothing (Merbs 1983). The intensive mechanical loads associated with the habitual activities of Sadlermiut consistently imposed significant stress and strain on the upper limbs that may have triggered the modeling processes.

On the other hand, Euro-Canadians from Sainte-Marie and Pointe-aux-Trembles were shown to exhibit signs of intense mechanical loading on the upper limbs associated with their demanding agrarian lifestyle based on bioarchaeological analyses of pathologies and entheseal changes (Crépin 2018; Ethnoscop 2016). These results were interpreted as the impact of habitual activities that necessitated greater use of the upper limbs than the lower limbs. For instance, males mainly engaged in artisanal activities and were in charge of the bulk of agricultural work. Their everyday life involved hard manual labor such as clearing the land, working the soil and plowing fields with heavy percussive tools that required intense force and repetitive movements from the upper limbs. There are few historical sources on the daily activities of females other than their responsibility in maintaining the household and child rearing. Despite this gap in knowledge, the bone structure of their upper limbs suggests that their habitual activities imposed sufficient stress and strain to trigger physiological processes, thus pointing to a physically demanding lifestyle (Séguin 1974 and Pomerleau 2003a in Crépin 2018; Ethnoscop 2016; Gutierrez 2019). These findings seem to conflict with the results of the present study because they provide bioarchaeological and archaeological evidence of a lifestyle that should have resulted in high measures of upper limb robusticity among Euro-Canadians, yet they were not robust compared to Sadlermiut Inuit. However, when considered together they may reflect a level of physical activity in the upper limbs of Euro-Canadians that, although high, did not compare to that of Sadlermiut Inuit. Additionally, Inuit were predominantly right-handed and laterality was more pronounced in females whereas Euro-Canadians made regular use of both limbs (Crépin 2018; Merbs 1983). Handedness is relevant because the right limbs were preferably selected in this study which could have inflated differences in upper limb robusticity between both populations by utilising the most robust limb of the Sadlermiut.

Marine mobility was shown to have poor correlations with diaphyseal shape and typically leads to rounder cross sections because rowing or paddling involves loading the arm not stereotypically but rather on different trajectories (Stock 2002). Therefore, Sadlermiut would be expected to have more circular than oval shaped humeri from high marine mobility. This may explain why males from both populations had a rounder diaphyseal shape reflecting similar patterns in principal stress directions for the upper limbs. On the other hand, Sadlermiut females had more elliptical shaped humerus diaphyses at the midshaft than Euro-Canadian females. This may be more a factor of differences in the type of habitual activities than in the intensity of said activities. Sadlermiut females regularly participated in hide scraping when processing game for clothing or building materials which requires endurance and repetitive movements at the elbow imposing stress along the A-P axis. The patterns in diaphyseal shape do not follow predictions from Hypothesis 2.2 but lend further support to the impact of mechanical factors such as the type and intensity of physical activity on bone structure.

Alternatively, the short and robust upper limbs of Sadlermiut Inuit compared to Euro-Canadians could, in part, be interpreted as a factor of cold climate as suggested in Hypothesis 2.1 (Ruff 1994). It is common for populations from polar climates to be mobile on water given the lack of plant-based resources and abundance of aquatic resources. For this reason, there may be an interplay between the maritime lifestyle and the polar climate of Sadlermiut impacting their morphology. A study by Stock (2002) demonstrated a covariation between high marine mobility and climate that significantly impacted bending and torsional strength in males but not females, However, humerus diaphyseal shape showed little statistically significant relationships for both sexes. Also, Stock interpreted the results as an indication that climate impacted bone structure to a lesser degree than behavior suggesting, in the case of Sadlermiut Inuit, that their maritime lifestyle disproportionally impacted their morphology relative to climate (Stock 2002). Furthermore, it is difficult to ascertain whether differences in bone structure related to climate are the result of long-term genetic adaptations to extreme cold or an indirect consequence of climate mediating nutrition and subsistence related activities. An argument can be made for both when considering that the ancestors of Sadlermiut were living in a polar climate for generations and that their daily life was centered around procuring supplies to survive the harsh and cold environmental conditions (Pearson 2000; Shackelford 2005).

6.1.3 Synthesis

The intense physical activity that defines Sadlermiut daily life along with physiological adaptations to extreme environmental conditions may have contributed to their high measures of lower limb robusticity. Subsequently, the metabolic and nutritional stress experienced by rural Euro-Canadians likely impacted their bone mass and lowered mechanical properties creating further contrast with Sadlermiut morphology despite having relatively active agrarian lifestyles. On the other hand, the patterns in lower limb diaphyseal shape did not follow expectations since elliptical shaped diaphyses were also observed in certain cross sections of Euro-Canadian populations which could be interpreted as the result of activities that loaded bones in similar axes. Therefore, the patterns observed in the cross-sectional geometry of the femur and tibia can be viewed as a combination of external factors including mobility, climate, nutritional and metabolic stressors.

For the upper limbs, it is difficult to disentangle whether the greater robusticity of Sadlermiut Inuit compared to Euro-Canadians is due to their high marine mobility, their long-term genetic adaptation to cold climates, their habitually demanding lifestyle, metabolic and nutritional advantages over Euro-Canadians or a combination of these external factors. When considering patterns of the lower and upper limbs, it appears that the morphological variations between these two populations result from an interplay of genetic adaptations to cold climate and regionally specific environmental factors such as socioeconomic context and harsh climatic conditions that indirectly influence mobility through regulating behavior to ensure survival according to resource distribution and abundance.

6.2. Meta-analysis: Mobility

The following section discusses the results of the meta-analysis that included the samples from this study and other archaeological populations from previous publications in relation to mobility based on the mode of subsistence. The subsistence divisions include hunter-gatherers, transitional, intermediate and intensive agriculturalists. The first section provides a discussion of lower limb morphology consisting of the femur midshaft (50%) and subtrochanteric section (80%) as well as the tibia midshaft (50%) while the second section addresses the mid-distal humerus (35%). In spite of the inherent heterogeneity of comparing samples from a large geographical area and the small sample sizes of certain subsistence groups, the meta-analysis can not only establish

where the samples of this study are distributed relative to their respective subsistence categories but also whether overarching trends in morphological variation can be identified on the basis of subsistence strategy.

6.2.1. Lower limbs: Femur and tibia

It was predicted that hunter-gatherers are generally more mobile than agriculturalists given the high physical demands of acquiring seasonally dependent wild resources and consequently, will have greater lower limb robusticity and more oval-shaped diaphyses (Hypothesis 3.1). Subsequently, the skeletal morphology of the femur and tibia of transitional, intermediate and intensive agriculturalist populations was expected to reflect gradual gracilization since these groups represent different intensities in agricultural practices (Hypothesis 3.2). Results support Hypothesis 3.1 by demonstrating that hunter-gatherers tend to have the thickest cortical area (CA), highest bending and torsional rigidity (J), maximum and minimum second moments (I_{max} and I_{min}) as well as more elliptical shaped long bone diaphyses than any other subsistence group. It is important to note that the differences in cross-sectional properties that are statistically significant are at the femoral and tibial midshafts for males and only in the femur for females. On the other hand, the lack of significant morphological differences in the lower limbs between transitional, intermediate and intensive agriculturalists with the exception of diaphyseal shape at the femur subtrochanteric section seems to discount Hypothesis 3.2.

The introduction and development of agriculture has been associated with decreases in health, increases in zoonotic diseases, a higher incidence of parasitic infections, poorer nutrition and resultant pathologies such as anemia and hypoplasia (Larsen and Ruff 2011; Stock, O'neill, et al. 2011). For this reason, it is important to consider metabolic and nutritional factors when examining morphological differences between different modes of subsistence. Metabolic stress affects the distribution of bone and, when interacting with mechanical factors in immature individuals, can influence cross-sectional properties such as cortical area. Malnutrition, pathologies and parasites impose additional stress by blocking vitamin and mineral absorption thus resulting in the loss of bone mass (Zaleski 2013). In some cases, bone may be distributed away from the bending axis to compensate for strain, thus maximising bending rigidity with the least material possible. This results in thin cortical area and, combined with short body proportions, high measures of robusticity (Ruff 2007; 1999; Zaleski 2013).

Previous studies examining temporal trends in body proportions and skeletal robusticity have demonstrated that decreases in body mass index, stature, limb length and overall body size as well as less robust lower limbs coincide with the introduction of agriculture during the Neolithic or extreme climatic episodes such as the Last Glacial Maximum and the Little Ice Age. These historic events were shown to result in a decline in health that inadvertently led to reductions in body size and robusticity through impacting bone growth (Holt 1999; Holt et al. 2017; Ruff 2017; Shackelford 2005). Alternatively, the role of genetic predispositions in determining variations in body proportions and skeletal robusticity cannot be discounted when samples are highly ecogeographically diverse (Holt 1999; Holt et al. 2017; Ruff 2017). There may be other systemic or genetic factors at play, however, properly investigating their potential influence goes beyond the scope of this thesis. Nonetheless, environmental stressors such as climate change or subsistence transitions like the development of agriculture can have adverse effects on bone health and impact robusticity values independent of changes in physical activity.

The body proportions of the populations from this meta-analysis mirror closely the temporal trends observed by Ruff (2017) and seem to reflect the same relationship with nutritional status and health. Populations with the longest lower limbs within each subsistence type are from periods that experienced an increase in overall body size associated with environmental stability, such as the early Mesolithic, the Bronze age and modern samples from the 20th century (Ruff 2017). Despite subsistence divisions of the present study not representing a linear chronology, results demonstrate a similar relationship between bone health and nutrition (as inferred from the subsistence mode) as Ruff's temporal analyses. Hunter-gatherers have the lowest body mass and shortest lower limb lengths compared to any other subsistence category. This group not only has the largest sample size but also, includes populations that cover the entire temporal span of Ruff's project from the Late Upper Paleolithic to the 20th century. Therefore, the smaller overall body size of hunter-gatherers is likely reflective of characteristics inherent to this mode of subsistence rather than temporal tendencies. Studies have shown that hunting and gathering, despite having a highly diverse and protein rich diet, comes with the risk of food shortages and thus, malnutrition because it is dependent on the accessibility of wild seasonal resources. The chronic fluctuations in nutritional status have repercussions on bone growth, especially if experienced in early development, which lead to stunted maturation and hence, smaller body proportions (Holt 1999; Holt et al. 2017; Ruff 2017). Essentially, both the temporal analyses by Ruff (2017) and this meta-

analysis demonstrate a link between changes in environmental conditions and body proportions through directly or indirectly influencing subsistence which impacts overall health.

The differences in body proportions between subsistence categories could have acted as confounding factors when analysing mobility since cross-sectional properties are standardized by bone length. As a consequence of this length standardization, hunter-gatherers might have inflated measures of robusticity due to their shorter extremities. However, the bias associated with length-standardized properties would have solely impacted males because females did not exhibit significant differences in body mass and limb length. Since females do not have size differences, but they do show differences in robusticity, it supports the conclusion that subsistence mode is indeed influencing robusticity, even for males. Also, Cowgill (2009) demonstrated that individuals may have reduced bone strength due to very small body mass that imposed small loads on the skeleton rather than the result of nutritional or hormonal influences which stunt bone growth and decrease bone mass. Since hunter-gatherers have the lowest body mass yet the most robust lower limbs, it suggests that their body proportions had little, if any, impact on their bone structure. Furthermore, the skeletal morphology of hunter-gatherers in this meta-analysis does not fit the profile of individuals afflicted with malnutrition and metabolic stress since, despite having smaller body proportions, they have significantly thicker cortical area in the lower limbs than all other subsistence groups along with greater polar and second moments of area, and more elliptical shaped diaphyses. These features are more indicative of differences in the intensity of mechanical loading on the lower limbs suggesting that the level of mobility may explain their higher robusticity compared to more sedentary subsistence strategies (Hypothesis 3.1).

The patterns in body proportions and robustness of intensive agriculturalists lend further support for Hypothesis 3.1 which stated that hunter-gatherers will have more robust and elliptical-shaped lower limbs than agriculturalists. The intensive agriculturalist group had the highest values in body mass as well as femur and tibia length while having the lowest measures of lower limb robusticity. Their larger body proportions are to be expected according to temporal analyses by Ruff (2017) since intensive agriculturalists tend to represent more recent samples. This corresponds with the notion that health implications associated with agriculture typically involved populations at initial introduction or in transition. Moreover, intensive agriculturalists had a more structured and established food production system that helped mitigate against threats such as

famines. This was achieved through the production of surplus and participating in trade that increased the diversity of diet which was characteristically low in less intensive agricultural practices such as transitional or intermediate groups (Mummert et al. 2011; Ruff 2017). Therefore, considering that the large body proportions of intensive agriculturalists are symptomatic of good overall health and nutrition, it suggests that mechanical factors may be responsible for their gracile and circular shaped lower limbs.

The interpretation of robust and elliptical shaped lower limbs among hunter-gatherers as a consequence of mechanical factors including high mobility and intense habitual physical activity is supported by results from previous, smaller scale studies exhibiting the same general trend (Bridges, Blitz, and Solano 2000; Churchill et al. 2000; Holt et al. 2017; Holt 2003; Larsen and Ruff 2011; Marchi et al. 2006; Ruff 1999; Shackelford 2005; Stock 2002; 2006). The greater cortical thickness, and bending and torsional rigidity of hunter-gatherers at the femur and tibia midshafts compared to other subsistence categories in both sexes is indicative of high levels of terrestrial mobility. The elliptical shaped diaphyses of the femur midshaft with an elongation along the A-P axis also supports high terrestrial mobility among hunter-gatherers since it was proven as the best indicator for this kind of mobility (Ruff 1987; Shackelford 2005; Zaleski 2013). The subtrochanteric region of the femur is used an indicator of all weight-bearing activities, not just those relating to mobility, therefore the greater cortical thickness and more oval-shaped lower limbs of hunter-gatherers is suggestive of more strenuous physical activity on a daily basis and subsequently, demonstrates the influence of mechanical factors on bone structure (Ruff 1987; Holt et al. 2017; Holt 2003 and Ruff 1999 in Shackelford 2005; Zaleski 2013).

The only significant difference between intermediate, transitional and intensive agriculturalists of proximal femur shape can likewise be attributed to differences in mechanical loading. Intermediate populations have the most circular proximal femur diaphyses compared to hunter-gatherer and transitional groups which resemble one another. The same patterns occur in females at the femur midshaft suggesting that changes in strain distributions reflect differences in the type of daily activities. Foraging populations consistently engage in walking or running during subsistence-related activities such as hunting. These activities apply stress on the A-P axis which becomes extended to counteract strain and reinforce bone along that plane making it more oval in shape. In contrast, the circular shape of more sedentary intermediate populations reflects

mechanical loads coming from all directions which redistributes bone more evenly across a section causing a rounder shape.

The patterns observed in males versus females not only point towards mechanical factors but also, follow assumptions about sexual division of labor for subsistence-related tasks and habitual activities (Ruff 1987; 1999; 2007; Zaleski 2013). For instance, male tibiae appear to be more affected by changes in mechanical loading than females as demonstrated by their greater frequency of significant differences in cross-sectional geometry. In contrast, females show more variation in the diaphyseal shape of femur cross sections. In modern hunter-gatherer populations, males have higher terrestrial mobility because of hunting which demands frequent and long-distance moves (Binford 2001 in Stock 2006; Kelly 1983). In contrast, female-oriented tasks such as child rearing, clothe making or food processing are concentrated around the residential base of hunter-gatherers, and the household for sedentary populations. Consequently, females are expected to exhibit few, if any, changes in robusticity related to terrestrial mobility across subsistence divisions. Instead, they may show changes in diaphyseal shape due to differences in the type of physical activity that altered the direction of mechanical stimuli along specific axes or changes in cortical thickness from differences in the intensity of daily activities (Ruff 1999; 2007; Zaleski 2013). These patterns are exemplified by the results of this study in which males show significant differences in femur and tibia midshaft robusticity suggesting a decrease in terrestrial mobility in agriculturists while females vary significantly in diaphyseal shape at both femur cross sections indicative of changes in the type of activity. Subsequently, both sexes incurred a reduction in general activity levels between hunter-gatherers and other subsistence groups demonstrated by the decrease in cortical surface area at the proximal femur.

It is possible that the differences in bone functional adaptation between the sexes are driven by hormonal influences affecting mechanotransduction — which refers to processes whereby cells convert mechanical stimuli into biochemical signals that trigger biological responses — or heterochronic differences in the timing of cell and tissue development (Stock 2006). However, given that lower limb skeletal variations between hunter-gatherers and other subsistence groups follow expectations from ethnographic studies about sexual dimorphism (Binford 2001 in Stock 2006; Kelly 1983) and conform to findings about robusticity from previous research (Bridges, Blitz, and Solano 2000; Churchill et al. 2000; Holt et al. 2017; Holt 2003; Larsen and Ruff 2011;

Marchi et al. 2006; Ruff 1999; Shackelford 2005; Stock 2002; 2006), it appears more likely that differences are due to behavior-driven changes in mechanical loading that altered strain magnitudes and directions and consequently, determined bone functional adaptation. Overall, patterns suggest that reductions in the intensity of physical activity and in terrestrial mobility between hunter-gatherers and transitional populations resulted in decreases in robusticity of the lower limbs. This behavioral shift also occurred in intermediate and intensive agriculturalists but was accompanied by changes in the type of habitual and subsistence-related activities distinct from hunter-gatherer and transitional groups as highlighted in variations of diaphyseal shape.

6.2.2. Upper limbs: Humerus

Hunter-gatherers were predicted to have higher measures of robusticity and thus, more robust upper limbs than intermediate populations, who increasingly relied on mechanized tools in agricultural work. However, these tools that relieved some of the physical exertion involved in food production were not yet utilised by transitional groups (Hypothesis 4.1). There were no significant differences in areas or moments of area between subsistence categories for either sex that would suggest significantly lower robusticity in intermediate and intensive agriculturalists thereby contradicting Hypothesis 4.1. Although, hunter-gatherers did tend to have greater cortical area and torsional and bending rigidity than intermediate groups and resembled robusticity measures from transitional populations alluding to the patterns described in Hypothesis 4.1, none of the comparisons were significant. Diaphyseal shape was expected to differ as the result of changes in subsistence-related activities that imposed strain in different directions (Hypothesis 4.2). There is little support for Hypothesis 4.2 since only transitional females have significantly rounder mid-distal humerus diaphyses than hunter-gatherers.

There are no significant differences in humerus length among subsistence groups for either sex, however, females do tend to increase in bone length from hunter-gatherers to intermediate populations. This is opposite of that observed in the lower limbs where differences in femur and tibia length as well as body mass are most prominent in males. These sexually dimorphic trends in limb proportions and body size may highlight sex-specific physiological reactions such as hormonal changes to environmental stressors that differentially impact nutritional status and health according to sex. Nonetheless, the shorter upper limbs of female hunter-gatherers conform to expectations of overall smaller body proportions and may have affected length-standardized cross-

sectional properties (Ruff 2017). As with the lower limbs, however, since the tendency of greater robusticity in hunter-gatherers is common to both sexes and differences in body proportions are not significant, skeletal variations are most likely due to external factors such as nutrition, mechanical loading patterns or climate rather than a bias due to shorter upper limb length.

In the preceding section on the lower limbs, the potential influences of metabolic and nutritional factors were explored but proved to be small contributors of the patterns observed in bone functional adaption. Therefore, the same, low level of impact of these systemic factors can be assumed for the upper limbs. As for mechanical factors, there is significant inconsistency in the findings of previous research investigating patterns in skeletal variations of the upper limbs in connection with subsistence transitions. For instance, results have demonstrated a decrease (Churchill et al. 2000; Stock et al. 2011; Wescott 2001), an increase (Bridges 1989; Bridges, Blitz, and Solano 2000; Churchill et al. 2000; Holt et al. 2017; Marchi et al. 2006) or no change (Holt et al. 2017) in robusticity with food production. This may be due to issues related to subsistence categorization which is more problematic in understanding the impact of habitual behavior on the upper limbs than the lower limbs because manual activities are inherently more variable within modes of subsistence (Holt et al. 2017). Additionally, the cross-sectional geometry of the humerus is harder to interpret since its adaptations are multifunctional in nature and are complexified by cultural factors such as sexual division of labor and technology that particularly influence loading of the upper limbs. However, the humerus has shown through research on modern day athletes to be a good indicator of manual activities on a daily basis that involve consistent movements in stereotypical directions (Ruff 2017). Consequently, the seemingly conflicting patterns of the aforementioned studies were shown to be representative of contextually specific circumstances involved in the agricultural development of a population or geographical region and collectively demonstrated the influence of mechanical loading on upper limb cross-sectional geometry.

The tendency of hunter-gatherers in this study to have greater humeral cortical area and torsional and bending rigidity than other subsistence groups highlights a general trend of lower robusticity in agricultural groups and points towards a reduction in mechanical loading of the upper limbs (Hypothesis 4.1). These results are supported by temporal analyses from Holt et al. (2017) where upper limb robusticity decreased from the Upper Palaeolithic to recent human samples and was attributed to lower levels of manual physical activity due to technological innovations

including mechanised tools that facilitated agricultural production. The same reasoning can be applied to the patterns observed in this analysis since differences in robusticity were mainly relative to intermediate populations, which, in my sample, are populations that experienced mechanization. Given strong evidence linking upper limb morphology with manual habitual behavior, the patterns observed in this study are likely a reflection of relatively stable levels in the intensity and the type of physical activities of the upper limb regardless of the mode of subsistence.

Female hunter-gatherers have markedly more oval shaped diaphyses compared to transitional and intermediate groups. This suggests that, at the very least, the type of habitual activities changed following subsistence transitions but not the level of physical activity (Hypothesis 4.2). This was anticipated given evidence showing that various manual activities such as hide scraping or plowing differentially impact the shape of the mid-distal humerus. For instance, hide scraping repetitively imposes strain along the A-P axis whereas plowing imposes strain in a radiating pattern where bone is distributed more evenly across a section. The scraping of animal hides is a predominantly female activity and is assumed to leave considerable morphological traces since it requires hours of strenuous repetitive movement to process into usable building or clothing material. This impactful habitual activity would have decreased in popularity throughout agricultural development and thus, may partly explain the differences in the shape of the mid-distal humerus among females (Holt et al. 2017; Merbs 1983). However, interpretations of humeral diaphyseal shape are restricted by the ambiguity involved in predicting specific behaviors that are complex and vary considerably both within and across subsistence divisions. Nevertheless, these results are analogous to previous findings demonstrating increased circularity that is more continuous among females than males from the Upper Palaeolithic to contemporary populations (Holt et al. 2017). Essentially, the cross-sectional geometry of the humerus in both sexes demonstrates similar intensities in mechanical loading patterns while variations in diaphyseal shape among females indicate changes in the type of manual habitual behavior between modes of subsistence.

6.2.3. Synthesis mobility

Skeletal variations in long bone cross-sectional geometry according to the mode of subsistence can be attributed to differences in the level of mobility as well as the type and intensity of general physical activity that influenced mechanical loading which impacted bone functional

adaptation. The lower limbs exhibited significant decreases in robusticity and increased circularity in diaphyseal shape between hunter-gatherers of both sexes and other subsistence divisions, but little differences were recorded between groups representing different scales of agricultural development. In contrast, no significant morphological variations were observed in the upper limbs for either sex, except for diaphyseal shape in females, suggesting a similar intensity in mechanical loading patterns across subsistence groups. The Sadlermiut Inuit fell below the average distribution of hunter-gatherers for cross-sectional properties of the upper and lower limbs except for female humeri that lied at the median. Intermediate Euro-Canadians from Notre-Dame were well within the mean distribution in the femur but below in the tibia and the humerus. Euro-Canadian samples from Sainte-Marie fell below the average distribution of intensive agriculturalists in the femur and the tibia for females while males were within the mean range. Females from Pointe-aux-Trembles were consistently within or above the average distribution of intensive agriculturalists for the femur and tibia while their male counterparts fell below for the latter. Given that the samples of this study only partially fell within the average distribution may indicate that the populations are not fully representative of their respective subsistence groups and/or may have been affected by the variable age at death. However, this demonstrates the diversity of cultural adaptations that exists in each type of lifestyle and points towards the limitations of studying mobility based on the mode of subsistence.

Hunter-gatherers exhibited the largest intra-group variation which can either be explained by their larger sample size or by the diversity in subsistence-related behavior that is characteristic of this mode of subsistence. Understanding and predicting foraging strategies have long been restricted to generalisations based on ethnographic or archaeological evidence. This can be attributed to the variability of hunting and gathering behavior that is dependent on environmental factors such as resource availability and climate (Kelly 1983; Stock 2002). Furthermore, the lack of significant differences between transitional, intermediate and intensive agriculturalists can either demonstrate that behavior does not differ sufficiently to impact bone, be due to their small sample sizes, reflect limitations in the grouping methodology of this study or a combination of these three factors. However, the parallel between the results of this project and previous studies indicates that patterns are reflective of the influence of mechanical factors on bone structure.

6.3. Meta-analysis: Climate

The parameters for the meta-analysis investigating the relationship between postcranial morphology and climate are the same as those described for the meta-analysis on mobility (section 6.2.). The climate types consist of polar/subarctic tundra (POL), temperate continental/oceanic (TEMP), semi-arid/desert (ARID) and tropical/subtropical (TROP). Despite the limitations associated with comparing samples from a large geographical area, the meta-analysis on climate provides the diversity needed to examine the impact that various ecological conditions can have on bone structure both directly in the form of long-term genetic adaptation and indirectly through moderating behavior.

6.3.1. Lower limbs: Femur and tibia

Populations from polar/subarctic tundra (POL) zones were predicted to have the most robust lower limbs than any other climate category (Hypothesis 5.1). The cross-sectional properties of the femur and tibia midshafts in males from the POL group are not significantly larger but rather, are similar in robustness to temperate continental/oceanic (TEMP) and semi-arid/desert (ARID) types contradicting Hypothesis 5.1. On the other hand, females from POL climates are significantly larger in maximum and minimum second moment of area at the femur 50% section than tropical/subtropical (TROP) populations. These results suggest that Hypothesis 5.1 may be supported for females only. Unfortunately, the absence of data on POL individuals at the subtrochanteric region of the femur prevented further testing of Hypothesis 5.1 despite prior evidence demonstrating the strongest relationship between the morphology at this location and climate (Stock 2002; 2006).

Stock (2002) demonstrated a similar correlation between torsional strength of the femur midshaft and climate. He hypothesizes that climate may be influencing bone robusticity in females through impacting soft tissue mass which changes body weight and loading on the skeleton (Stock 2002). However, data from the meta-analysis of the present study shows no evidence of climate-related differences in soft tissue mass since measures of body size such as body mass and bone length did not differ significantly across climate types for either sex. The relationship between body proportions and climate could not be further explored due to gaps in data such as crural and brachial indices or body breadth, measures known to correlate highly with climate. Crural and brachial indices tend to be lower in colder climates and involve shortening of the distal segment

of a limb. Body breadth is useful in the calculation of surface area to mass ratio which tends to be lower in cold-adapted populations (Pearson 2000; Ruff 1994; Stock 2002; 2006).

Alternatively, climate may be determining the distribution of bone about the centroid in the form of long-term genetic adaption to extremely cold environments (Pearson 2000; Ruff 1994; Stock 2002; 2006). However, this interpretation is questionable because the femur midshaft is also a good predictor of terrestrial mobility. If the morphology of the femur midshaft was indeed shaped by climate, one would also expect to find climate-related differences in body proportions. Given that most data on body size and limb proportions were unavailable, it is difficult to disentangle whether climate or behavior was responsible for high robusticity among POL females. Therefore, skeletal variations between POL and TROP females could be the result of climate mediating behavior by imposing high physical demands on the former for surviving in harsh and cold environmental conditions. Comparably, POL males were expected to exhibit the same relationship between J and climate as observed by Stock (2002) and in the females of this study but rather, are lower in torsional and bending rigidity than TROP males. If climate-mediated behavior was a factor, POL males would have likewise been exposed to the same selective pressures as females, but they did not exhibit significant morphological differences with other climate groups, thereby rejecting Hypothesis 5.1 for males.

On the other hand, it is possible that female behavior across climate zones is inherently more variable than males through environmental influences on sexual division of labor (Stock 2006). This could have emphasised differences between POL and TROP females since POL climates are characterised by a strenuous workload that tends to be more evenly divided between sexes to better ensure survival in a hostile environment (Merbs 1983). Nonetheless, Hypothesis 5.1 is not well supported in females either because the highest measures of robusticity for the lower limbs are observed in TEMP females whereas POL samples resemble ARID populations. Moreover, samples from TROP climates were anticipated to have the least robust lower limbs based on findings from previous studies (Pearson 2000; Stock 2002; 2006). This prediction is supported by my results in females only, while TROP and TEMP males tend to have larger measures of robusticity than POL males. Males exhibit no significant differences between climate categories at any of the lower limb cross sections apart from maximum second moment of area at the femur midshaft that is significantly greater in TROP climates than TEMP males. Otherwise,

the finding that TROP females tend to have the lowest average distributions in cross-sectional properties can be interpreted as evidence of some climatic influence on bone functional adaptation in females only. Females from ARID climates have significantly greater torsional and bending rigidity as well as second moment of area along the A-P axis at the femur 50% section than TROP females. Also, the proximal femur (80%) of TEMP and ARID females is significantly larger in bending and torsional rigidity along with thicker cortical area than TROP groups. Previous studies have shown similar correlations in females between climate and J, and CA at the subtrochanteric region of the femur as well as J at the femur midshaft (Pearson 2000; Ruff 1994; Stock 2002; 2006). This suggests that climate may have played a role in determining TROP female morphology.

The findings of the present analysis corroborate the results of Stock (2002) that found no correlation between the bone structure of the tibia midshaft and climate zones. This discrepancy between the influence of climate on more proximal (femur) and distal (tibia) elements of the lower limbs observed in this study and Stock's (2002) may be the result of adaptive constraints between bone modeling and thermoregulation. A trend opposite to that of the limb-length thermoregulatory hypothesis, selective pressure exerted on the proximal end of the lower limbs is focused on optimizing thermoregulation whereas the distal end is to maximize strength against mechanical loads while balancing the energetic costs (Stock 2002; 2006). The results of this meta-analysis on climate indicate that POL individuals do not have significantly robust lower limbs compared to other climate groups, except for the femur midshaft in females, failing to support Hypothesis 5.1 for both sexes. Also, overall patterns suggest a weak relationship between lower limb bone structure and climate. However, there seems to be some climatic influence on the lower limbs since skeletal variations among females occurred in mechanical properties and sections of bone that were previously shown to correlate with climate. Also, TROP females were the least robust of any other climate division and stood in stark contrast to POL populations as anticipated. Therefore, further testing is needed to understand how climate may be responsible for these patterns and why they are not found in both sexes.

6.3.2. Upper limbs: Humerus

According to previous research by Stock (2002; 2006), Pearson (2000) and Ruff (1994), it was predicted that populations from polar/subarctic tundra (POL) climates would have the greatest

upper limb robusticity compared to all other climate divisions (Hypothesis 5.2). The results of this meta-analysis demonstrate that the highest values in cross-sectional properties of the mid-distal humerus are found in POL individuals of both sexes lending support for Hypothesis 5.2. Subsequently, males from POL climates have significantly thicker cortical, greater bending and torsional rigidity, and second moments of area along the M-L and A-P axes than temperate continental/oceanic (TEMP) populations along with greater J than semi-arid/desert groups (ARID). POL females have significantly greater torsional and bending rigidity than tropical/subtropical (TROP) and TEMP types. Also, they have significantly larger second moment of area along M-L axis compared to ARID and TEMP populations as well as markedly more oval shaped humeri than the former. The high measures of robusticity of POL groups suggest that there may be a climatic factor influencing the bone structure of their upper limbs.

Previous studies have found a similar relationship between cold climate, high upper limb robusticity and short-stocky body proportions (Pearson 2000; Ruff 1994; Shackelford 2005; Stock 2002; 2006; Stock et al. 2011). The robust humeri and significantly short limb lengths of POL groups in this analysis do conform to what is characterised as a cold-adapted physique despite inaccessibility to certain body size indices such as body breadth and trunk height that correlate more strongly with climate (Pearson 2000; Ruff 1994). Furthermore, the significantly greater torsional and bending rigidity of POL populations corresponds partly with Stock's results (2002; 2006) that demonstrated a significant covariation between J and climate in males but not females. While J had a strong relationship with climate in males, it was also highly influenced by marine mobility which tends to be associated with populations inhabiting POL climates (Stock 2002). Moreover, the thicker cortical area among POL groups may be more of an indicator of physical activity since CA was shown by Stock (2002) to correlate poorly with climate, but rather relate significantly to the level of marine mobility. Also, it is important to note that this meta-analysis as well as Pearson's (2002) study used length-standardized cross-sectional properties to investigate bone structure which is problematic since climate has proven to influence limb proportions and body size (Shackelford 2005). This may lead to inflated measures of skeletal robusticity in short limbed individuals and underestimate values in tall body types.

The robust bone structure of POL populations may be more a factor of climate-mediated behavior than solely the result of long-term genetic adaptation to cold conditions since this group

consisted entirely of hunter-gatherers. Climate has been shown to significantly influence habitual activities among foragers through affecting resource availability and abundance. For instance, in cold climates, diet primarily consists of meat-based protein through hunting and fishing, and involves intensive use of the upper limbs due to processing game meat, transportation on glaciers or snow cover and/or maritime activities using watercrafts that lead to high skeletal robusticity (Binford 1980 and Kelly 1995 in Pearson 2000). Subsequently, Stock (2002) demonstrated no significant variation in diaphyseal circularity based on the ratio of maximum and minimum second moments of area according to climate. Consequently, the elliptical shaped humerus diaphyses in POL females compared to ARID populations is likely the result of strenuous habitual activities in the upper limbs such as hide scraping (Ruff 2017). Additionally, long-term genetic adaptation to cold climates is not well supported when considering results in the lower limbs where POL groups were not significantly more robust than individuals from other climate zones because the same covariation with climate is expected throughout the body (Stock 2002). Therefore, the discrepancy in robusticity between the upper and lower limbs of POL populations may be more of a reflection of different mechanical loading patterns and intensities in the lower and upper limbs.

Despite ambiguity in identifying the underlying cause(s) of robusticity in the upper limbs of POL climates, morphological tendencies in TROP groups hint at a climatic component. For instance, as with the lower limbs, TROP males have high measures of upper limb robusticity, second only to POL types for the upper limbs, and significantly thicker cortical area than TEMP males. Comparably, Pearson (2000) recorded high humeral robusticity in populations from TROP climates such as Zulu and Australian Aborigines that was interpreted as the result of a combination of climatic adaptation and high levels of physical activity. In contrast, TROP females of the present meta-analysis tend to be the least robust compared to other climate categories similar to results observed in the lower limbs. This consistency in patterns of bone functional adaptation in the upper and lower limbs of TROP populations suggests that there may be a climatic component influencing skeletal morphology. Whether this is long-term genetic adaptation or climate-mediated behavior to hot and humid environmental conditions is difficult to determine. They do have lower body mass and are on the higher end of the spectrum for humerus length which seems to conform to predictions about body proportions among tropical climates. However, behavior cannot be discounted as a factor since males are typically active in TROP climates, therefore differences in the division of labour may explain this sexual dimorphism in robusticity (Pearson 2000).

The results of the present meta-analysis on the upper limbs lend support for hypothesis 5.2 given that POL types have the largest cross-sectional values not only among groups divided by climate zones but also among hunter-gatherers. This suggests that there is a climatic aspect to their high skeletal robusticity beyond the level of physical activity but there is no indication as to its degree of influence in determining POL bone functional adaptation. Moreover, TROP populations exhibit similar trends in the upper and lower limbs for each sex which may indicate body predispositions related to climate. On the other hand, morphological tendencies in POL and TROP groups can be partly explained by the type and intensity of their habitual activities and division of labor. Therefore, these patterns highlight the known interplay between behavior and climate. However, statistical tests found no significant interactions between these two factors on impacting the bone structure of the upper nor lower limbs. Nonetheless, further testing is needed once information on crural and brachial indices as well as body breadth and trunk height is available to better understand the climatic component. Future research should be conducted on the ulna and radius because climate was shown to have a greater influence on the distal elements of the upper limbs contrary to the proximal end in the lower limbs as a consequence of needing to create an optimal balance between mechanical reinforcement, tissue economy and thermoregulation (Stock 2006).

6.3.3. Synthesis

The results of statistical tests examining the relationship between bone functional adaptation and climate failed to support Hypothesis 5.1 but demonstrated support for Hypothesis 5.2. The lower limbs exhibited only a weak relationship with climate among females in which the morphology of individuals from TROP climates was significantly less robust than POL groups. POL females did not have the highest measures of robusticity, and no statistically significant climate-related variation was observed in their male counterparts who tended to be less robust than TROP and TEMP types. Interestingly, females varied more frequently in the lower limbs according to climate than males and experienced morphological differences in sections of bone (femur 50% and 80%) and variables (CA and J) that were previously shown to correlate with climate (Stock 2002).

In contrast, skeletal variations in the cross-sectional properties of the upper limbs demonstrated a relationship with climate through either long-term genetic adaptation to

environmental conditions or climate-mediated behavior. More precisely, humeri of populations inhabiting extremely cold conditions had higher measures of robusticity than all other climate divisions for both sexes. Since the mid-distal humerus correlates highly with marine mobility, the robust upper limbs of POL individuals may be more a factor of their environmental conditions determining habitual and subsistence-related activities. This interpretation is further supported when considering the discrepancy observed in the robustness of their upper versus lower limbs because long-term genetic adaptation to cold climates would have likely resulted in more uniform bone structure throughout the body. On the other hand, the consistency of morphological patterns in the long bones of TROP populations, where males were highly robust and females were the least, suggests a climatic component that combined with the differential adaptation according sex points towards climate-mediated differences in behavior to hot/humid conditions.

The cross-sectional properties of the lower limbs in Sadlermiut Inuit were consistently below the average distributions of POL populations for both sexes. The same can be said for females in the upper limbs whereas male humeral properties were within the average range of POL groups. The lower limbs of Euro-Canadians from Sainte-Marie were consistently below the average distribution of TEMP climates while males from Pointe-aux-Trembles were also below, except for the femur midshaft, and females were within the average range. In contrast, the upper limbs of Euro-Canadian males from Pointe-aux-Trembles and Sainte-Marie had measures that were consistently above the median while their female counterparts tended to be below the average distribution for TEMP groups. The lower limbs of males from Notre-Dame tended to be within the average distribution of TEMP populations, but females were below yet had upper limbs at the median of said climate division. The variability in patterns of upper compared to lower limb morphology between the sexes is reminiscent of an overall trend observed in the meta-analysis that suggests there may be differential adaptations to climate according to sex, possibly due to differences in sexual division of labor mediated through climate or particular cultural factors.

Populations from TEMP climates demonstrated the largest intra-group variability in the lower limbs by having both the highest and lowest values for cross-sectional properties along with Tardiglacial (TG) populations. This could be due to large sample size or may reflect the large portion of hunter-gatherers that were classified under the TEMP category. The high variation could be attributed to the diversity in the level of physical activity that is inherent to a foraging mode of

subsistence (discussed in section 6.2; Stock 2006) rather than to the influence of climate. However, TEMP individuals were not as variable in the upper limbs and did not have the largest properties despite having the largest sample sizes apart from the TG group. This suggests mobility may indeed be responsible for their diverse and robust lower limbs and not climate since their upper limbs did not exhibit the same pattern. Subsequently, the TG division consisted of individuals that inhabited highly unstable and fluctuating environmental conditions since this period encompasses climatic events such as the Bølling–Allerød interstadial and the Younger Dryas (Shackelford 2005). The populations forming a sort of catch-all category experienced climatic conditions with no modern-day analog and were all hunter-gatherers. Therefore, considering they have upper limb morphology lower than POL groups, but similar to that of TROP climates further supports the interpretation that their robust lower limbs are a factor of their high mobility as foragers.

6.4. Conclusion

The results of biomechanical analyses demonstrated that Sadlermiut Inuit have significantly more robust upper and lower limbs than Euro-Canadians. Skeletal variations between these populations can be interpreted as a combination of behavioral and climatic factors. For instance, morphological differences attributed to the levels of physical activity of Sadlermiut Inuit may have been compounded by the tendency towards poor health in rural Euro-Canadians from Pointe-aux-Trembles and Sainte-Marie which could have lowered their measures of robusticity in comparison. Moreover, the habitual activities of Inuit are more strenuous than the active agrarian lifestyle of Euro-Canadians because their foraging lifestyle was intensified by the demands of surviving in a cold and harsh environment. The patterns in diaphyseal shape of the humerus, femur and tibia further attest to the limitations of oversimplified hypotheses by demonstrating that certain cross sections are more oval in Inuit whereas others in Euro-Canadians. These seemingly conflicting results can be attributed to differences in the type and intensity of physical activities in each population based on bioarchaeological and ethnohistorical data, rather than simply a factor of being more or less active. Essentially, morphological differences between Sadlermiut Inuit and Euro-Canadians point towards a more complex interaction between the cold-adapted body form of Sadlermiut Inuit, health/nutrition and mechanical loading patterns on the skeleton.

The present study demonstrates the difficulty in determining the degree of influence of physical activity versus climate on long bone cross-sectional geometry. However, it shows that the

lower limbs are good indicators of mechanical loading on the skeleton and weak indicators of climate, especially in males, whereas the upper limbs relate more highly to climate and vary more frequently in females. Still, the relationship between climate, behavior and postcranial robusticity remains equivocal and highlights that skeletal variations may indeed result from interactions between these factors. Further research that includes more information on body proportions such as body breadth, trunk height, stature, crural and brachial indices would provide the necessary data to allow for a more extensive analysis on populations that are so ecogeographically diverse and may answer some of the questions that arose over the course of this project. Previous research has shown how different body-size standardization methods can alter biomechanical measures (Friedl et al. 2016; Ruff 2000). Subsequently, Friedl et al. (2016) demonstrated how discrepancies in evolutionary trends could be attributed to differences in the composition of samples and whether they consist of a small or large geographical area, or represent changes within a single lineage. Therefore, it would be beneficial to run a meta-analysis with cross-sectional properties standardized by body mass to compare with the results of this study. Overall, this study highlighted the potential that biomechanical research has to offer in deepening our understanding of bone modeling and showed that cross-sectional geometry is a useful analytical method to explore behavior in past human populations as well as the interplay between mobility and climate in determining bone functional adaptation.

Bibliography

Amorevieta-Gentil, Marilyn. 2010. "Les niveaux et les facteurs déterminants de la mortalité infantile en Nouvelle-France et au début du Régime Anglais (1621–1779)." Ph.D., Ann Arbor, United States. https://search.proquest.com/docview/765287191/abstract/DA48E1612D5B495EPQ/1.

Anderson, Marti J. 2014. "Permutational Multivariate Analysis of Variance (PERMANOVA)." *Wiley Statsref: Statistics Reference Online*, 1–15.

Auerbach, B. M. 2014. "Morphologies from the Edge: Perspectives on Biological Variation among the Late Holocene Inhabitants of the Northwestern North American Arctic." *Cambridge Studies in Biological and Evolutrionary Anthropology* 1 (68): 235–265.

Belda, Michal, Eva Holtanová, Tomáš Halenka, and Jaroslava Kalvová. 2014. "Climate Classification Revisited: From Köppen to Trewartha." *Climate Research* 59 (1): 1–13.

Bertram, J.E.A., and S.M. Swartz. 1991. "The 'Law of Bone Transformation': A Case of Crying Wolff?" *Biological Reviews* 66 (3): 245–273.

Bridges, Patricia S. 1989. "Changes in Activities with the Shift to Agriculture in the Southeastern United States." *Current Anthropology* 30 (3): 385–394.

Bridges, P.S. 1985. "Changes in long bone structure with the transition to agriculture: implications for prehistoric activities (biomechanics, Southeastern United States)." Ph.D., Ann Arbor, United States. http://search.proquest.com/docview/303380593/abstract/2DB48C6B2D244747PQ/1.

Bridges, P.S., J.H. Blitz, and M.C. Solano. 2000. "Changes in Long Bone Diaphyseal Strength with Horticultural Intensification in West-Central Illinois." *American Journal of Physical Anthropology* 112 (2): 217–38.

Collins, Henry B. 1956. "Vanished Mystery Men of Hudson Bay." *National Geographic* 110 (5): 669–87.

Churchill, S.E. 1994. "Human upper body evolution in the Eurasian later Pleistocene." Ph.D., Ann Arbor, United States.

Churchill, S.E., V. Formicola, T.W. Holliday, B. Holt, and B.A. Schumann. 2000. "The Upper Palaeolithic Population of Europe in an Evolutionary Perspective." *Hunters of the Golden Age-the Midupper Palaeolithic of Eurasia* 30 (20,000).

Coltrain, J.B. 2009. "Sealing, Whaling and Caribou Revisited: Additional Insights from the Skeletal Isotope Chemistry of Eastern Arctic Foragers." *Journal of Archaeological Science* 36 (3): 764–75. https://doi.org/10.1016/j.jas.2008.10.022.

Cowgill, L.W. 2014. "Femoral Diaphyseal Shape and Mobility: An Ontogenetic Perspective." In *Reconstructing Mobility*, 193–208. Springer, Boston, MA. https://doi.org/10.1007/978-1-4899-7460-0_11.

Crépin, Magali. 2018. "Étude de «marqueurs d'activités» Au Sein de Deux Populations Historiques de La Vallée Du Saint Laurent: Analyses Des Observations Macroscopiques et Essais d'interprétations En Lien Avec Des Milieux Contrastés (Urbain versus Rural)."

Davies, T.G., and J.T. Stock. 2014. "Human Variation in the Periosteal Geometry of the Lower Limb: Signatures of Behaviour among Human Holocene Populations." In *Reconstructing Mobility*, 67–90. Springer, Boston, MA. https://doi.org/10.1007/978-1-4899-7460-0_5.

De Carvalho, O.A. 2015. "Propriétés géométriques des sections transversales diaphysaires sur les humérus, fémurs et tibias des individus humains provenants des sites archéologiques des premiers cimetières de Sainte-Marie, CcEs 1 (Québec) et de Sadlermiut Inuit (Nunavut), Canada". Postdoc diss., Université de Montréal.

De Castro, M., C. Gallardo, K. Jylha, and H. Tuomenvirta. 2007. "The Use of a Climate-Type Classification for Assessing Climate Change Effects in Europe from an Ensemble of Nine Regional Climate Models." *Climatic Change* 81 (1): 329–341.

Doube, Michael, Micha\l M. K\losowski, Ignacio Arganda-Carreras, Fabrice P. Cordelières, Robert P. Dougherty, Jonathan S. Jackson, Benjamin Schmid, John R. Hutchinson, and Sandra J. Shefelbine. 2010. "BoneJ: Free and Extensible Bone Image Analysis in ImageJ." *Bone* 47 (6): 1076–1079.

Feng, Song, Chang-Hoi Ho, Qi Hu, Robert J. Oglesby, Su-Jong Jeong, and Baek-Min Kim. 2012. "Evaluating Observed and Projected Future Climate Changes for the Arctic Using the Köppen-Trewartha Climate Classification." *Climate Dynamics* 38 (7–8): 1359–1373.

Fernandez, Julio P. R., Sergio H. Franchito, V. Brahmananda Rao, and Marta Llopart. 2017. "Changes in Koppen–Trewartha Climate Classification over South America from RegCM4 Projections." *Atmospheric Science Letters* 18 (11): 427–34. https://doi.org/10.1002/asl.785.

Friedl, Lukáš, Stanislava Eisová, and Trenton W Holliday. 2016. "Re-Evaluation of Pleistocene and Holocene Long Bone Robusticity Trends with Regards to Age-at-Death Estimates and Size Standardization Procedures." *YJHEV Journal of Human Evolution* 97: 109–22.

Gallardo, Clemente, Victoria Gil, Edit Hagel, César Tejeda, and Manuel de Castro. 2013. "Assessment of Climate Change in Europe from an Ensemble of Regional Climate Models by the Use of Köppen–Trewartha Classification." *International Journal of Climatology* 33 (9): 2157–2166.

Guetter, P.J., and J.E. Kutzbach. 1990. "A Modified Köppen Classification Applied to Model Simulations of Glacial and Interglacial Climates | SpringerLink." *Climate Change* 16 (2): 193–215.

Gutierrez, Eléa. 2019. "Évolution Des Pratiques Du Sevrage à Montréal (XVIIe–XIXe Siècles): Analyse Isotopique Des Concentrations En Azote 15 Par Micro-Échantillonnage de La Dentine."

Holt, B., E. Whittey, M. Niskanen, V. Sládek, M. Berner, and C.B. Ruff. 2017. "Temporal and Geographic Variation in Robusticity." In *Skeletal Variation and Adaptation in Europeans*, edited by C.B. Ruff, 91–132. Hoboken, NJ, USA: John Wiley & Sons, Inc. https://doi.org/10.1002/9781118628430.ch5.

Holt, B.M. 2003. "Mobility in Upper Paleolithic and Mesolithic Europe: Evidence from the Lower Limb." *AJPA American Journal of Physical Anthropology* 122 (3): 200–215.

Holt, Brigitte Muller. 1999. "Biomechanical evidence of decreased mobility in Upper Paleolithic and Mesolithic Europe." Ph.D., Ann Arbor, United States.

Kelly, Robert L. 1983. "Hunter-Gatherer Mobility Strategies." *Journal of Anthropological Research* 39 (3): 277–306.

Knobbe, S. 2010. "Reconstructing activity patterns in prehistoric Jomon people using long bone cross-sectional geometry." M.A., Ann Arbor, United States.

Larsen, Clark Spencer, Simon W. Hillson, Başak Boz, Marin A. Pilloud, Joshua W. Sadvari, Sabrina C. Agarwal, Bonnie Glencross, et al. 2015. "Bioarchaeology of Neolithic Çatalhöyük: Lives and Lifestyles of an Early Farming Society in Transition." *Journal of World Prehistory* 28 (1): 27–68. https://doi.org/10.1007/s10963-015-9084-6.

Larsen, Clark Spencer, and Christopher Ruff. 2011. "'An External Agency of Considerable Importance': The Stresses of Agriculture in the Foraging-to-Farming Transition in Eastern North America." *Human Bioarchaeology of the Transition to Agriculture*, 293–315.

Larsen, C.S., and C.B. Ruff. 2011. "'An External Agency of Considerable Importance': The Stresses of Agriculture in the Foraging-to-Farming Transition in Eastern North America." In *Human Bioarchaeology of the Transition to Agriculture*, edited by R. Pinhasi and J.T. Stock, 293–315. Chichester, UK: John Wiley & Sons, Ltd. https://doi.org/10.1002/9780470670170.ch12.

Lieberman, D., and A.W. Crompton. 1998. "Responses of Bone to Stress: Constraints on Symmorphosis."

Macintosh, A. A., R. Pinhasi, and J. T. Stock. 2014. "Lower Limb Skeletal Biomechanics Track Long-Term Decline in Mobility across ~6150 Years of Agriculture in Central Europe." *Journal of Archaeological Science* 52 (December): 376–90. https://doi.org/10.1016/j.jas.2014.09.001.

Macintosh, Alison A, Thomas G Davies, Timothy M Ryan, Colin N Shaw, and Jay T Stock. 2013. "Periosteal versus True Cross-Sectional Geometry: A Comparison along Humeral, Femoral, and Tibial Diaphyses." *AJPA American Journal of Physical Anthropology* 150 (3): 442–52.

Marchi, Damiano, Vitale S. Sparacello, Brigitte M. Holt, and Vincenzo Formicola. 2006. "Biomechanical Approach to the Reconstruction of Activity Patterns in Neolithic Western Liguria, Italy." *American Journal of Physical Anthropology* 131 (4): 447–55. https://doi.org/10.1002/ajpa.20449.

Martin, R.B., D.B. Burr, N.A. Sharkey, and D.P. Fyhrie. 1998. *Skeletal Tissue Mechanics*. Vol. 190. Springer.

Merbs, C. F. 1974. "The Effects of Cranial and Caudal Shift in the Vertebral Columns of Northern Populations." *Arctic Anthropology* 11: 12–19.

———.1983. *Patterns of Activity-Induced Pathology in a Canadian Inuit Population*. Ottawa: National Museums of Canada.

———.2018. "The Discovery and Rapid Demise of the Sadlermiut." In *Hunter-Gatherer Adaptation and Resilience: A Bioarchaeological Perspective*, edited by Christopher M. Stojanowski and Daniel H. Temple, 302–27. Cambridge Studies in Biological and Evolutionary Anthropology. Cambridge: Cambridge University Press. https://doi.org/10.1017/9781316941256.013.

Millison, Andrew. n.d. "Appendix D: Koppen-Trewartha Climate Classification Descriptions." In *Permaculture Design: Tools for Climate Resilience*. Oregon State University. Accessed February 27, 2020. https://open.oregonstate.education/permaculturedesign/back-matter/koppen-trewartha-climate-classification-descriptions/.

Mongle, Carrie S, Ian J Wallace, and Frederick E Grine. 2015a. "Cross-Sectional Structural Variation Relative to Midshaft along Hominine Diaphyses. I. The Forelimb." *AJPA American Journal of Physical Anthropology* 158 (3): 386–97.

———. 2015b. "Cross-Sectional Structural Variation Relative to Midshaft along Hominine Diaphyses. II. The Hind Limb." *AJPA American Journal of Physical Anthropology* 158 (3): 398–407.

Mummert, A., E. Esche, J. Robinson, and G.J. Armelagos. 2011. "Stature and Robusticity during the Agricultural Transition: Evidence from the Bioarchaeological Record." *Economics & Human Biology* 9 (3): 284–301.

Norris, Gareth, Faiza Qureshi, Dennis Howitt, and Duncan Cramer. 2014. *Introduction to Statistics with SPSS for Social Science*. Routledge.

Ogilvie, M.D. 2000. "A biological reconstruction of mobility patterns at the foraging to farming transition in the American *Southwest." Ph.D., Ann Arbor, United States.

Ogilvie, M.D., and C.E. Hilton. 2011. "Cross-Sectional Geometry in the Humeri of Foragers and Farmers from the Prehispanic American Southwest: Exploring Patterns in the Sexual Division of Labor." *American Journal of Physical Anthropology* 144 (1): 11–21. https://doi.org/10.1002/ajpa.21362.

Pearson, O.M. 2000. "Activity, Climate, and Postcranial Robusticity: Implications for Modern Human Origins and Scenarios of Adaptive Change." *Current Anthropology* 41 (4): 569–607. https://doi.org/10.1086/317382.

Pearson, O.M., and D.E. Lieberman. 2004. "The Aging of Wolff's 'Law': Ontogeny and Responses to Mechanical Loading in Cortical Bone." *American Journal of Physical Anthropology* 125 (39): 63–99. https://doi.org/10.1002/ajpa.20155.

Pearson, O.M., T.R. Petersen, V.S. Sparacello, S.R. Daneshvari, and F.E. Grine. 2014. "Activity, 'Body Shape,' and Cross-Sectional Geometry of the Femur and Tibia." In *Reconstructing Mobility*, 133–51. Springer, Boston, MA. https://doi.org/10.1007/978-1-4899-7460-0_8.

Ruff, C.B. 1999. "Skeletal Structure and Behavioral Patterns of Prehistoric Great Basin Populations." *Prehistoric Lifeways in the Great Basin Wetlands: Bioarchaeological Reconstruction and Interpretation*, 290–320.

———. 2000. "Body Size, Body Shape, and Long Bone Strength in Modern Humans." *Journal of Human Evolution* 38 (2): 269–90. https://doi.org/10.1006/jhev.1999.0322.

———. 2007. "Biomechanical Analyses of Archaeological Human Skeletons." In *Biological Anthropology of the Human Skeleton*, 183–206. Wiley-Blackwell. https://doi.org/10.1002/9780470245842.ch6.

Ruff, C.B., and W.C. Hayes. 1983a. "Cross-Sectional Geometry of Pecos Pueblo Femora and Tibiae—A Biomechanical Investigation: I. Method and General Patterns of Variation." *American Journal of Physical Anthropology* 60 (3): 359–381.

———. 1983b. "Cross-Sectional Geometry of Pecos Pueblo Femora and Tibiae—A Biomechanical Investigation: II. Sex, Age, and Side Differences." *American Journal of Physical Anthropology* 60 (3): 383–400. https://doi.org/10.1002/ajpa.1330600309.

Ruff, C.B., B. Holt, and E. Trinkaus. 2006. "Who's Afraid of the Big Bad Wolff?: 'Wolff's Law' and Bone Functional Adaptation." *American Journal of Physical Anthropology* 129 (4): 484–98. https://doi.org/10.1002/ajpa.20371.

Ruff, Christopher. 1987. "Sexual Dimorphism in Human Lower Limb Bone Structure: Relationship to Subsistence Strategy and Sexual Division of Labor." *Journal of Human Evolution* 16 (5): 391–416. https://doi.org/10.1016/0047-2484(87)90069-8.

Ruff, Christopher B. 1993. "Climatic Adaptation and Hominid Evolution: The Thermoregulatory Imperative." *Evolutionary Anthropology: Issues, News, and Reviews* 2 (2): 53–60. https://doi.org/10.1002/evan.1360020207.

Ruff, Christopher B. 1994. "Morphological Adaptation to Climate in Modern and Fossil Hominids." *AJPA American Journal of Physical Anthropology* 37 (S19): 65–107.

Ruff, Christopher B. 2017. *Skeletal Variation and Adaptation in Europeans: Upper Paleolithic to the Twentieth Century*. John Wiley & Sons.

Ruff, Christopher B., and Wilson C. Hayes. 1982. "Subperiosteal Expansion and Cortical Remodeling of the Human Femur and Tibia with Aging." *Science* 217 (4563): 945–948.

Ruff, Christopher B., Clark Spencer Larsen, and Wilson C. Hayes. 1984. "Structural Changes in the Femur with the Transition to Agriculture on the Georgia Coast." *American Journal of Physical Anthropology* 64 (2): 125–36.

Ruff, Christopher B., William W. Scott, and Allie Y.-C. Liu. 1991. "Articular and Diaphyseal Remodeling of the Proximal Femur with Changes in Body Mass in Adults." *American Journal of Physical Anthropology* 86 (3): 397–413.

Ruff, Christopher B., Erik Trinkaus, and Trenton W. Holliday. 1997. "Body Mass and Encephalization in Pleistocene Homo." *Nature* 387 (6629): 173–76. https://doi.org/10.1038/387173a0.

Ruff, Christopher B., Alan Walker, and Erik Trinkaus. 1994. "Postcranial Robusticity in Homo. III: Ontogeny." *American Journal of Physical Anthropology* 93 (1): 35–54.

Shackelford, L.L. 2005. "Regional variation in the postcranial robusticity of Late Upper Paleolithic humans." Ph.D., Ann Arbor, United States.

———. 2014. "Variation in Mobility and Anatomical Responses in the Late Pleistocene." In *Reconstructing Mobility*, 153–71. Springer, Boston, MA.

Shaw, Colin N., and Jay T. Stock. 2009. "Intensity, Repetitiveness, and Directionality of Habitual Adolescent Mobility Patterns Influence the Tibial Diaphysis Morphology of Athletes." *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists* 140 (1): 149–159.

Stock, J., and S. Pfeiffer. 2001. "Linking Structural Variability in Long Bone Diaphyses to Habitual Behaviors: Foragers from the Southern African Later Stone Age and the Andaman Islands." *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists* 115 (4): 337–348.

Stock, J.T., Matthew C. O'neill, Christopher B. Ruff, Melissa Zabecki, Laura Shackelford, and Jerome C. Rose. 2011. "Body Size, Skeletal Biomechanics, Mobility and Habitual Activity from the Late Palaeolithic to the Mid-Dynastic Nile Valley." In *Human Bioarchaeology of the Transition to Agriculture*, edited by Ron Pinhasi and Jay T. Stock, 347–67. Chichester, UK: John Wiley & Sons, Ltd. https://doi.org/10.1002/9780470670170.ch14.

Stock, J.T. 2002. "Climatic and Behavioural Influences on Postcranial Robusticity among Holocene Foragers." University of Toronto.

———. 2006. "Hunter-Gatherer Postcranial Robusticity Relative to Patterns of Mobility, Climatic Adaptation, and Selection for Tissue Economy." *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists* 131 (2): 194–204.

Stock, J.T., V.I. Bazaliiskii, O.I. Goriunova, N.A. Savel'ev, and A.W. Weber. 2011. "Skeletal Morphology, Climatic Adaptation, and Habitual Behavior among Mid-Holocene Cis-Baikal Populations." *Prehistoric Hunter-Gatherers of the Baikal Region, Siberia: Bioarchaeological Studies of Past Life Ways. Philadelphia: University of Pennsylvania Press. p*, 193–216.

Stock, J.T., M.C. O'neill, C.B. Ruff, M. Zabecki, L.L. Shackelford, and J.C. Rose. 2011. "Body Size, Skeletal Biomechanics, Mobility and Habitual Activity from the Late Palaeolithic to the Mid-Dynastic Nile Valley." In *Human Bioarchaeology of the Transition to Agriculture*, 347–67. Wiley-Blackwell.

Stock, J.T., and C.N. Shaw. 2007. "Which Measures of Diaphyseal Robusticity Are Robust? A Comparison of External Methods of Quantifying the Strength of Long Bone Diaphyses to Cross-Sectional Geometric Properties." *American Journal of Physical Anthropology* 134 (3): 412–423.

Symchych, Natalie. 2016. "An Ecogeographic Study of Body Proportion Development in the Sadlermiut Inuit of Southampton Island, Nunavut." Thesis.

Toupin, Rémi. 2016. "Évolution Des Pratiques Alimentaires En Cours de Vie: Une Étude Isotopique Multi-Matérielle de La Population Du Cimetière Saint-Matthew (Québec, 1771-1860)."

Weiss, E. 2003. "Effects of Rowing on Humeral Strength." *American Journal of Physical Anthropology* 121 (4): 293–302. https://doi.org/10.1002/ajpa.10240.

———. 2009. "Sex Differences in Humeral Bilateral Asymmetry in Two Hunter-Gatherer Populations: California Amerinds and British Columbian Amerinds." *American Journal of Physical Anthropology* 140 (1): 19–24. https://doi.org/10.1002/ajpa.21025.

Wescott, D.J. 2001. "Structural variation in the humerus and femur in the American Great Plains and adjacent regions: Differences in subsistence strategy and physical terrain." Ph.D., Ann Arbor, United States.

Wescott, D.J., and D.L. Cunningham. 2006. "Temporal Changes in Arikara Humeral and Femoral Cross-Sectional Geometry Associated with Horticultural Intensification." *Journal of Archaeological Science* 33 (7): 1022–36. https://doi.org/10.1016/j.jas.2005.11.007.

Woo, Sy-L., Steve C. Kuei, David Amiel, M. A. Gomez, W. C. Hayes, F. C. White, and W. H. Akeson. 1981. "The Effect of Prolonged Physical Training on the Properties of Long Bone: A Study of Wolff's Law." *The Journal of Bone and Joint Surgery. American Volume* 63 (5): 780–787.

Yoo, J., and R.V. Rohli. 2016. "Global Distribution of Köppen-Geiger Climate Types during the Last Glacial Maximum, Mid-Holocene, and Present | Elsevier Enhanced Reader." *Palaeogeography, Palaeoclimatology, Palaeoecology* 446: 326–37.

Zaleski, S.M. 2013. "Analysis of Humeral and Femoral Cross-Sectional Properties at Morton Shell Mound (16IB3)." M.A., United States -- Mississippi: Mississippi State University.

Appendix 1: Sadlermiut and Euro-Canadian cross-sectional geometry

Table 19: Mean of mechanical properties for each long bone cross section in Sadlermiut males[1]

Cross sections	CA	J	I_{max}	I_{min}	I_{max}/I_{min}
Humerus 20%	-	-	-	-	-
Humerus 35%	729.76	866.63	484.32	382.31	1.28
Humerus 50%	724.65	1089.51	682.24	407.27	1.68
Humerus 65%	727.15	1225.90	697.34	528.56	1.32
Humerus 80%	-	-	-	-	-
Cross sections	CA	J	I_{max}	I_{min}	I_{max}/I_{min}
Femur 20%	-	-	-	-	-
Femur 35%	425.31	470.79	262.64	208.15	1.26
Femur 50%	498.71	475.57	258.18	217.39	1.20
Femur 65%	520.86	514.88	303.10	211.78	1.46
Femur 80%	-	-	-	-	-
Cross sections	CA	J	I_{max}	I_{min}	I_{max}/I_{min}
Tibia 20%	-	-	-	-	-
Tibia 35%	639.32	764.44	484.83	279.62	1.73
Tibia 50%	734.80	978.17	670.39	307.78	2.19
Tibia 65%	802.37	1528.60	1059.29	469.31	2.28
Tibia 80%	-	-	-	-	-

[1]Cross-sectional properties are standardized by powers of bone length.

Table 20:Mean of mechanical properties for each long bone cross section in Sadlermiut females[1].

Cross sections	CA	J	I_{max}	I_{min}	I_{max}/I_{min}
Humerus 20%	-	-	-	-	-
Humerus 35%	583.13	599.01	328.27	270.74	1.22
Humerus 50%	608.85	755.92	500.88	255.04	1.96
Humerus 65%	597.16	828.61	483.56	345.05	1.4
Humerus 80%	-	-	-	-	-
Cross sections	CA	J	I_{max}	I_{min}	I_{max}/I_{min}
Femur 20%	-	-	-	-	-
Femur 35%	417.89	452.18	241.31	210.87	1.15
Femur 50%	474.76	449.39	249.78	199.61	1.25
Femur 65%	505.76	502.50	296.75	205.75	1.45
Femur 80%	-	-	-	-	-
Cross sections	CA	J	I_{max}	I_{min}	I_{max}/I_{min}
Tibia 20%	-	-	-	-	-
Tibia 35%	557.65	600.71	373.52	227.19	1.69
Tibia 50%	631.78	751.17	509.04	242.13	2.15
Tibia 65%	678.67	1136.64	797.45	339.19	2.39
Tibia 80%	-	-	-	-	-

[1]Cross-sectional properties are standardized by powers of bone length.

Table 21: Mean of mechanical properties for each long bone cross section in Euro-Canadian males from Pointe-aux-Trembles[1].

Cross sections	CA	J	I_{max}	I_{min}	I_{max}/I_{min}
Humerus 20%	654.34	682.09	431.78	250.31	1.72
Humerus 35%	610.21	610.91	357.98	252.92	1.39
Humerus 50%	616.05	700.30	432.87	267.42	1.63
Humerus 65%	594.65	801.70	464.71	336.99	1.38
Humerus 80%	494.81	896.26	480.61	415.65	1.16
Cross sections	CA	J	I_{max}	I_{min}	I_{max}/I_{min}
Femur 20%	376.95	628.61	380.35	248.26	1.52
Femur 35%	427.12	459.71	260.00	199.70	1.30
Femur 50%	487.83	437.89	240.58	197.31	1.22
Femur 65%	536.39	492.47	278.62	213.85	1.30
Femur 80%	536.73	802.39	483.99	318.40	1.53
Cross sections	CA	J	I_{max}	I_{min}	I_{max}/I_{min}
Tibia 20%	438.65	565.79	326.78	239.01	1.36
Tibia 35%	550.27	484.26	315.37	168.88	1.89
Tibia 50%	619.91	645.58	434.20	211.38	2.15
Tibia 65%	609.19	957.94	657.06	300.88	2.22
Tibia 80%	649.04	1960.33	1388.11	572.22	2.43

[1]Cross-sectional properties are standardized by powers of bone length.

Table 22:Mean of mechanical properties for each long bone cross section in Euro-Canadian females from Pointe-aux-Trembles[1].

Cross sections	CA	J	I_{max}	I_{min}	I_{max}/I_{min}
Humerus 20%	596.83	531.76	327.59	204.17	1.63
Humerus 35%	539.24	489.20	279.57	209.63	1.35
Humerus 50%	548.90	605.07	396.52	208.54	1.90
Humerus 65%	562.98	656.94	395.37	261.57	1.51
Humerus 80%	503.25	743.04	417.12	325.92	1.28
Cross sections	CA	J	I_{max}	I_{min}	I_{max}/I_{min}
Femur 20%	483.23	728.64	439.05	289.59	1.49
Femur 35%	450.70	398.00	220.48	177.52	1.26
Femur 50%	499.64	384.13	223.20	160.94	1.47
Femur 65%	530.61	409.85	234.43	175.42	1.31
Femur 80%	577.95	826.70	470.46	356.24	1.35
Cross sections	CA	J	I_{max}	I_{min}	I_{max}/I_{min}
Tibia 20%	620.03	743.00	453.72	289.29	1.57
Tibia 35%	728.19	552.94	342.09	210.85	1.62
Tibia 50%	912.42	908.88	620.01	288.86	2.13
Tibia 65%	936.32	1176.28	791.57	384.71	2.06
Tibia 80%	1041.63	2209.55	1396.38	813.17	1.72

[1]Cross-sectional properties are standardized by powers of bone length.

Table 23: Mean of mechanical properties for each long bone cross section in Euro-Canadian males from Sainte-Marie[1].

Cross sections	CA	J	I_{max}	I_{min}	I_{max}/I_{min}
Humerus 20%	725.84	759.05	524.31	234.74	2.23
Humerus 35%	673.75	630.29	360.81	269.47	1.33
Humerus 50%	693.89	759.61	471.68	287.93	1.67
Humerus 65%	660.09	833.75	478.07	355.67	1.34
Humerus 80%	555.08	919.70	496.06	423.64	1.17
Cross sections	**CA**	**J**	**I_{max}**	**I_{min}**	**I_{max}/I_{min}**
Femur 20%	373.20	540.42	314.84	225.57	1.40
Femur 35%	395.42	334.51	187.30	147.21	1.32
Femur 50%	430.92	320.66	179.47	141.20	1.31
Femur 65%	463.40	365.81	203.44	162.37	1.27
Femur 80%	414.93	468.25	282.48	185.77	1.52
Cross sections	**CA**	**J**	**I_{max}**	**I_{min}**	**I_{max}/I_{min}**
Tibia 20%	479.70	635.73	357.77	277.97	1.30
Tibia 35%	556.83	488.46	316.60	171.86	1.86
Tibia 50%	649.24	667.79	445.52	222.27	2.01
Tibia 65%	660.81	942.48	653.96	288.53	2.27
Tibia 80%	722.86	1746.69	1193.51	553.17	2.15

[1]Cross-sectional properties are standardized by powers of bone length.

Table 24: Mean of mechanical properties for each long bone cross section in Euro-Canadian females from Sainte-Marie[1].

Cross sections	CA	J	I_{max}	I_{min}	I_{max}/I_{min}
Humerus 20%	555.47	497.75	313.42	184.33	1.72
Humerus 35%	482.61	410.65	229.94	180.70	1.28
Humerus 50%	517.80	496.76	306.89	189.87	1.62
Humerus 65%	493.12	523.50	303.32	220.18	1.38
Humerus 80%	463.26	587.35	318.11	269.24	1.18
Cross sections	**CA**	**J**	**I_{max}**	**I_{min}**	**I_{max}/I_{min}**
Femur 20%	334.39	469.75	292.98	176.77	1.68
Femur 35%	369.23	311.45	172.31	139.14	1.24
Femur 50%	409.68	297.71	166.38	131.33	1.28
Femur 65%	438.70	335.06	191.11	143.96	1.35
Femur 80%	420.89	457.47	272.83	184.64	1.49
Cross sections	**CA**	**J**	**I_{max}**	**I_{min}**	**I_{max}/I_{min}**
Tibia 20%	426.92	490.21	285.49	204.72	1.40
Tibia 35%	528.72	447.49	292.03	155.46	1.90
Tibia 50%	600.67	583.60	390.13	193.48	2.06
Tibia 65%	608.41	794.24	551.43	242.81	2.29
Tibia 80%	631.19	1374.96	926.45	448.51	2.09

[1]Cross-sectional properties are standardized by powers of bone length.

Table 25:Mean of mechanical properties for each long bone cross section in Euro-Canadian males from Notre-Dame[1].

Cross sections	CA	J	I_{max}	I_{min}	I_{max}/I_{min}
Humerus 20%	818.48	797.88	489.23	308.66	1.59
Humerus 35%	-	-	-	-	-
Humerus 50%	779.84	852.18	493.18	358.99	1.40
Humerus 65%	748.10	992.92	564.41	428.51	1.32
Humerus 80%	712.90	1195.47	649.77	545.70	1.19
Cross sections	CA	J	I_{max}	I_{min}	I_{max}/I_{min}
Femur 20%	**468.37**	**574.52**	**345.61**	**228.91**	**1.51**
Femur 35%	-	-	-	-	-
Femur 50%	505.24	431.76	225.46	206.30	1.09
Femur 65%	489.22	434.17	236.50	197.67	1.20
Femur 80%	548.55	724.73	372.75	351.98	1.06
Cross sections	**CA**	**J**	I_{max}	I_{min}	I_{max}/I_{min}
Tibia 20%	455.84	546.26	312.45	233.81	1.33
Tibia 35%	513.51	450.08	292.31	157.77	1.83
Tibia 50%	590.14	582.93	393.36	189.57	2.04
Tibia 65%	657.32	869.51	595.32	274.19	2.17
Tibia 80%	854.64	2105.74	1454.42	651.32	2.23

[1]Cross-sectional properties are standardized by powers of bone length.

Table 26:Mean of mechanical properties for each long bone cross section in Euro-Canadian females from Notre-Dame[1].

Cross sections	CA	J	I_{max}	I_{min}	I_{max}/I_{min}
Humerus 20%	-	-	-	-	-
Humerus 35%	693.13	552.31	306.32	245.98	1.25
Humerus 50%	674.57	581.67	342.78	239.89	1.49
Humerus 65%	614.11	528.91	295.90	233.00	1.27
Humerus 80%	609.54	677.23	356.94	320.30	1.11
Cross sections	**CA**	**J**	I_{max}	I_{min}	I_{max}/I_{min}
Femur 20%	451.60	598.82	379.25	219.56	1.71
Femur 35%	448.19	404.09	225.88	178.21	1.27
Femur 50%	-	-	-	-	-
Femur 65%	-	-	-	-	-
Femur 80%	548.29	663.86	375.13	288.72	1.34
Cross sections	**CA**	**J**	I_{max}	I_{min}	I_{max}/I_{min}
Tibia 20%	468.84	485.33	264.96	220.37	1.21
Tibia 35%	580.50	489.92	316.64	173.28	1.85
Tibia 50%	687.65	672.70	451.44	221.27	2.02
Tibia 65%	740.96	967.08	671.94	295.14	2.27
Tibia 80%	796.04	1624.69	1106.37	518.32	2.13

[1]Cross-sectional properties are standardized by powers of bone length.

Appendix 2: Populations included in the meta-analyses on mobility and climate

Table 27:Characteristics of each population in the meta-analysis.

Population	Climate	Lifestyle	Period	Reference
Georgia Bight (Atlantic coastal Georgia)	Tropical/Subtropical	Hunter-gatherer	Early Prehistoric Guale 2400 B.P.-950 B.P. (400 B.C.-A.D. 1000)	Larsen et al. 2007; Larsen and Ruff 2011; Ruff and Larsen 2001
Georgia Bight (Atlantic coastal Georgia)	Tropical/Subtropical	Transitional	Late Prehistoric Guale 950-500 B.P.(A.D. 1000–1450)	Larsen et al. 2007; Larsen and Ruff 2011; Ruff and Larsen 2001
Georgia Bight (St-Catherine's Island)	Tropical/Subtropical	Intermediate	Early Mission Guale 350-270 B.P. (AD 1600–1680)	Larsen et al. 2007; Larsen and Ruff 2011; Ruff and Larsen 2001
Georgia Bight (Florida: Amelia Island)	Tropical/Subtropical	Intermediate	Late Mission Guale 270-250 B.P. (AD 1680–1700)	Larsen et al. 2007; Larsen and Ruff 2011; Ruff and Larsen 2001
Georgia Bight (Florida: Amelia Island)	Tropical/Subtropical	Intermediate	Early Mission Yamasee 350-270 B.P. (A.D. 1600-1680)	Larsen et al. 2007; Larsen and Ruff 2011; Ruff and Larsen 2001
Andamanese Islanders Southeast Asia	Tropical/Subtropical	Hunter-gatherer	1858: Period after first European Settlements	Stock 2002; Personal communication
Late Archaic Great Lakes region Ontario	Temperate continental/oceanic	Hunter-gatherer	2920-2875 B.P. terminal archaic (Glacial Kame)	Stock 2002
Yahgan, Tierra del Fuego	Polar/Subarctic tundra	Hunter-gatherer	proto-historic 1860-1900	Stock 2002; Personal communication
Morton Shell Mound Weeks Island on the Louisiana coast	Tropical/Subtropical	Transitional	Occupied 700-1200 AD (cemetery between 1000 and 1100 BP)	Zaleski 2013
Gold Mine Louisiana (Richland Parish)	Tropical/Subtropical	Hunter-gatherer	1175-1065 BP (AD775-885, calibrated)	Zaleski 2013
Plash Island in Baldwin County, Alabama	Tropical/Subtropical	Hunter-gatherer	AD 325 to 642 in Middle Woodland	Zaleski 2013
Aleuts	Polar/Subarctic tundra	Hunter-gatherer	range from late prehistoric to historic	Wescott 2001 in Knobbe 2010

California Amerindians	Tropical/Subtropical	Hunter-gatherer	2180 - 250 BP and prior to European contact	Weiss 2009 in Knobbe 2010
Jomon	Tropical/Subtropical	Transitional	Late to Final Jomon period 3200 to 2800 cal BP	Knobbe 2010
Great Salt Lake east of Lake in Utah	Semi-arid/Desert	Transitional	all but one range in age between A.D. 600 and 1150; one burial had a mean determination of A.D. 1381	Ruff 1999
Malheur Lake in southwestern Oregon	Semi-arid/Desert	Hunter-gatherer	Sample around 3000 B.C. to the protohistoric period, but most burials date after A.D. 1000	Ruff 1999
Stillwater Marsh in the western American Great Basin (west-central Nevada)	Semi-arid/Desert	Hunter-gatherer	ca. 2300 to 300 B.P., in the Underdown phase (1250-650 B.P.)	Ruff 1999
Point Hope Alaska	Polar/Subarctic tundra	Hunter-gatherer	Ipiutak culture 1619±210 years B.P. or Tigara culture o 300-400 years B.P.	Wallace et al. 2014
Gough's Cave 1 (England)	Temperate continental/oceanic	Hunter-gatherer	Cheddarian/Creswellian: 9100 ± 200	Holt 1999; Shackleford 2005
Chancelade 1 (France)	Tardiglacial	Hunter-gatherer	Magdalenian 3 and 4: Tardiglacial	Holt 1999; Shackleford 2005
La Madelaine (France)	Tardiglacial	Hunter-gatherer	Tardiglacial	Holt 1999; Shackleford 2005
Veyrier (France)	Tardiglacial	Hunter-gatherer	Upper Magdalenian/ Azilian: Late Tardiglacial, c . 10000?	Holt 1999; Shackleford 2005
Rochereil (France)	Tardiglacial	Hunter-gatherer	Azilian: Late Tardiglacial or Holocene	Holt 1999; Shackleford 2005
St. Germaine-La-Rivière 4 (France)	Tardiglacial	Hunter-gatherer	Magdalenian 3 and Upper Magdalenian: 14500, 15300 ± 410	Holt 1999; Shackleford 2005
Bruniquel 24 (France)	Tardiglacial	Hunter-gatherer	Upper Magdalenian: Tardiglacial	Holt 1999; Shackleford 2005
Cap Blanc 1 (France)	Tardiglacial	Hunter-gatherer	Magdalenian 3: Tardiglacial	Holt 1999; Shackleford 2005
Farincourt 1 (France)	Tardiglacial	Hunter-gatherer	Late Tardiglacial or Holocene	Holt 1999; Shackleford 2005
Obercassel 1 (Germany)	Tardiglacial	Hunter-gatherer	Magdalenian: Tardiglacial	Holt 1999; Shackleford 2005

Obercassel 2 (Germany)	Tardiglacial	Hunter-gatherer	Magdalenian: Tardiglacial	Holt 1999; Shackleford 2005
Arene Candide	Tardiglacial	Hunter-gatherer	Final Epigravettian: 11800-10900	Holt 1999; Shackleford 2005
Riparo Continenza 1 (Italy)	Tardiglacial	Hunter-gatherer	Late Epigravettian: 10230 ± 110	Holt 1999; Shackleford 2005
Riparo Tagliente 1 (Italy)	Tardiglacial	Hunter-gatherer	Final Epigravettian: 13430 ± 180, 12040 ± 70	Holt 1999; Shackleford 2005
Romanelli 1 (Italy)	Tardiglacial	Hunter-gatherer	11800 ± 600	Holt 1999; Shackleford 2005
Romito 3 (Italy)	Tardiglacial	Hunter-gatherer	11200 ± 200, 10960 ± 350	Holt 1999; Shackleford 2005
Romito 4 (Italy)	Tardiglacial	Hunter-gatherer	11200 ± 200, 10960 ± 350	Holt 1999; Shackleford 2005
San Teodoro 4 (Italy)	Tardiglacial	Hunter-gatherer	Final Epigravettian: Allerod (Late Tardiglacial)	Holt 1999; Shackleford 2005
Grotte-des-Enfants 3 (Italy)	Tardiglacial	Hunter-gatherer	Late Epigravettian: 12200 ± 400	Holt 1999; Shackleford 2005
Minatogawa (Japan)	Tardiglacial	Hunter-gatherer	18000	Shackleford 2005
Tam Hang (Northern Laos)	Tardiglacial	Hunter-gatherer	15740 ± 80	Shackleford 2005
El-Wad (Israel)	Tropical/Subtropical	Hunter-gatherer	Early Holocene	Shackleford 2005
Kebara (Israel)	Tropical/Subtropical	Hunter-gatherer	Early Holocene	Shackleford 2005
Ohalo 2 (Israel)	Tardiglacial	Hunter-gatherer	19000	Shackleford 2005
Bell Beaker Culture	Temperate continental/oceanic	Intermediate	Late Eneolithic: 4619 B.P.-4019 B.P.(2600–2000 BC)	Sladek et al. 2006a/b
Corded Ware Culture	Temperate continental/oceanic	Intermediate	Late Eneolithic: 4919 B.P.- 4319 B.P.(2900–2300 BC)	Sladek et al. 2006a/b
Unetice Culture	Temperate continental/oceanic	Intensive agriculturalist	Early Bronze Age: 4220-3840 B.P. (2200–1820 BC)	Sladek et al. 2006a/b
Unterwolbling Culture	Temperate continental/oceanic	Intensive agriculturalist	Early Bronze Age: 4040-3790 B.P. (2020–1770 BC)	Sladek et al. 2006a/b
Wieselburger Culture	Temperate continental/oceanic	Intensive agriculturalist	Early Bronze Age: 4020-3720 B.P. (2000–1700 BC)	Sladek et al. 2006a/b
Tyrolean Iceman (Otzi)	Temperate continental/oceanic	Hunter-gatherer	5200 B.P.	Ruff et al. 2006

Arikara Extended Coalescent	Temperate continental/oceanic	Transitional	Extended Coalescent period: A.D. 1500 to 1650	Wescott and Cunningham 2006
Arikara Post-Contact Coalescent	Temperate continental/oceanic	Transitional	Post-Contact Coalescent period: A.D. 1650 to 1780	Wescott and Cunningham 2006
Arikara Disorganised Coalescent	Temperate continental/oceanic	Intermediate	Disorganised Coalescent period: A.D. 1780 to 1845	Wescott and Cunningham 2006
Sainte-Marie	Temperate continental/oceanic	Intensive agriculturalist	19th century	The present study
Sadlermiut	Polar/Subarctic tundra	Hunter-gatherer	13-19th century	The present study
Notre-Dame	Temperate continental/oceanic	Intermediate	17-18th century	The present study
Pointe-aux-Trembles	Temperate continental/oceanic	Intensive agriculturalist	18th-mid 19th century	The present study
Lower Illinois Valley	Temperate continental/oceanic	Transitional	Middle Woodland (50 BC–AD 200)	Bridges et al. 2000
Lower Illinois Valley	Temperate continental/oceanic	Intermediate	Early Late Woodland (AD 600–800)	Bridges et al. 2000
Lower Illinois Valley	Temperate continental/oceanic	Intermediate	Later Late Woodland (AD 800–1050)	Bridges et al. 2000
Lower Illinois Valley	Temperate continental/oceanic	Intensive agriculturalist	Mississippian (AD 1050–1250)	Bridges et al. 2000
Pickwick basin	Tropical/Subtropical	Transitional	Archaic 8020-3020 B.P. (6000-1000 B.C.)	Bridges 1985/1989 in Larsen and Ruff 2011
Pickwick basin	Tropical/Subtropical	Intermediate	Mississippian (A.D. 1200-1500)	Bridges 1985/1989 in Larsen and Ruff 2011
Southwest Texas (Pecos region)	Semi-arid/Desert	Hunter-gatherer	Blue Hills phase of the Late Archaic (ca, 2300-1300 B,P,)	Ogilvie 2000
Southeastern Arizona (Pecos region)	Semi-arid/Desert	Transitional	late Archaic period 3000 BP-1800 BP(1200 B,C,-A,D, 150)	Ogilvie 2000
Central New Mexico (Pecos region)	Semi-arid/Desert	Intermediate	Pueblo IV period (A,D, 1300-1500)	Ogilvie 2000
Cis-Baikal Siberia	Polar/Subarctic tundra	Hunter-gatherer	Pre-hiatus of 8000-7000 cal.B.P.: Early Neolithic Kitoi culture	Lieverse et al. 2011
Cis-Baikal Siberia	Polar/Subarctic tundra	Hunter-gatherer	Post-hiatus 6000- 4000 cal. B.P.: Late Neolithic Isakovo-Serovo and Bronze Age Glazkovo culture	Lieverse et al. 2011

Bloksbjerg 251-15006 (Denmark)	Temperate continental/oceanic	Hunter-gatherer	Mesolithic:	Holt 1999
Holmegaard-Jutland (Denmark)	Temperate continental/oceanic	Hunter-gatherer	Ertebolle: 6280 ± 130, 6020 ± 100	Holt 1999
Melby (Denmark)	Temperate continental/oceanic	Hunter-gatherer	Mesolithic (Ertebolle): 3880 ± 110 B.C.	Holt 1999
Korsor-Nor Glasvaerk (Denmark)	Temperate continental/oceanic	Hunter-gatherer	Mesolithic: 6180 ± 95	Holt 1999
Sejrø (Denmark)	Temperate continental/oceanic	Hunter-gatherer	Mesolithic: 5220 ± 70, 5410 ± 90	Holt 1999
Koelbjerg (Denmark)	Temperate continental/oceanic	Hunter-gatherer	Boreal: c. 9000	Holt 1999
Dragsholm (Denmark)	Temperate continental/oceanic	Hunter-gatherer	Mesolithic: 5160 ± 100	Holt 1999
Culoz (France)	Temperate continental/oceanic	Hunter-gatherer	Tardenoisien: c. 9150-7950, 8640 ± 381	Holt 1999
Hoedic (France)	Temperate continental/oceanic	Hunter-gatherer	Tardenoisien: 6575 ± 351	Holt 1999
Gramat 1 (France): Cuzoul de Gramat	Temperate continental/oceanic	Hunter-gatherer	Tardenoisien: 7800 ± 50, 6640 ± 55	Holt 1999
Teviec (France)	Temperate continental/oceanic	Hunter-gatherer	Tardenoisien: 6600 B.P.	Holt 1999
Bottendorf (Germany)	Temperate continental/oceanic	Hunter-gatherer	Mesolithic:	Holt 1999
Unseburg (Germany)	Temperate continental/oceanic	Hunter-gatherer	Mesolithic	Holt 1999
Grotta della Molara 2 (Italy)	Tropical/Subtropical	Hunter-gatherer	Mesolithic: 8600 ± 100	Holt 1999
Mondeval de Sora (Italy)	Temperate continental/oceanic	Hunter-gatherer	Mesolithic (Castenovian): 7330 ± 59	Holt 1999
Grotta dell'Uzzo 2 (Italy)	Tropical/Subtropical	Hunter-gatherer	Mesolithic: 8570± 80, 10370± 100	Holt 1999
Vatte di Zambana (Italy)	Temperate continental/oceanic	Hunter-gatherer	Mesolithic (Final Sauveterrian): 7740± 150, 8000± 110	Holt 1999
Loschbour (Luxembourg)	Temperate continental/oceanic	Hunter-gatherer	Mesolithic: 7205 ± 50	Holt 1999
Muge Cabeco da Arruda 3 (Portugal)	Tropical/Subtropical	Hunter-gatherer	Mesolithic: 6360 ± 80, 6990± 110	Holt 1999

Moita de Sebastiao (Portugal)	Tropical/Subtropical	Hunter-gatherer	Mesolithic: 6810 ± 70, 7240 ±70	Holt 1999
Birsmatten (Switzerland)	Temperate continental/oceanic	Hunter-gatherer	Mesolithic: 6290	Holt 1999