Shape in the Proximal Femoral Metaphyseal Region During Growth: Age or Activity Related Change?

by

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Abstract

The metaphyseal regions of long bones have been largely overlooked by biological anthropologists, despite these regions being highly biologically active during growth and development. Further, while the levels of plasticity and constraint in response to biomechanical loading in the epiphyses and diaphysis of long bones have received attention, levels in the developing metaphyseal region are less well understood. In response to this gap in understanding, this project seeks to describe shape variation in the proximal femoral metaphyseal region during ontogeny and develop possible plasticity through the relationship of shape and activity by applying approaches from 3D Geometric Morphometrics and Cross-Sectional Geometry to scans of archaeologically derived highly active forager populations. The results of the study will summarize ontogenetic shape change in the metaphyseal region and suggest that this region exhibits limited plasticity in response to biomechanical loading. However, it is also suggested that further research should be conducted concerning the metaphyseal surface, and that culturally mediated factors impacting habitual activity should be firmly integrated via a biocultural approach to provide a more nuanced view of the relationship of shape to age and activity.

Keywords

ontogeny; developmental plasticity; subadults; metaphysis; geometric morphometrics; cross-sectional geometry; biocultural approach

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Introduction

The development and growth of different skeletal elements, and different regions of these elements, is of particular interest within physical anthropology. However, the metaphyseal regions of long bones, which lie between the epiphysis and diaphysis (shaft) of a long bone, have received little attention, despite their important role in growth. There has been limited study of ontogenetic change in metaphyses and virtually no quantitative description for that of the proximal femur. Little is known about the process by which this region develops its adult morphology or how it may be influenced by behaviour.

This project discusses the relationship of shape to chronological age and activity level using data derived from Geometric Morphometrics (GM), Cross-Sectional Geometry (CSG) which was then analysed using various statistical analyses. Archaeologically derived 3D surface scans from forager populations are used to generate data for this project because their highly active lifestyles result in responses to biomechanical loading that are more visible when compared to responses in sedentary populations (Doershuk et al., 2019). Using these samples, this project aimed to: 1) quantitatively describe change in shape across growth; and 2) identify if the metaphyseal region demonstrates plasticity, endeavoring to fill the gap in understanding about a biologically significant region of long bones. These goals generated the following questions: what change in shape occurs in the metaphyseal region of the proximal femur throughout ontogeny? And secondly, does the shape of the metaphyseal region demonstrate plasticity in response to changes in biomechanical loading during growth?

I begin with a literature review focused on current knowledge surrounding the proximal femur, surveying current knowledge on long bone plasticity and constraint, and describing the theory and general use of GM and CSG. I also review the biocultural approach to bioarchaeology, identifying how archaeologically derived contextual information can enrich the study of biological phenomena. In a second section, I discuss the methodology and analytical approaches used to derive and analyse shape, age, and activity variables. I address my results in relation to my questions and discuss how these findings relate to current literature. Lastly, I detail the limitations of my project and suggest avenues for future research.

Literature Review

The Proximal Femur

The femur (Figure 1) is a bone of particular interest for research of all kinds due to its interaction with the pelvis to form the hip joint, that joint's role in the generation and transmission of forces associated with routine activities (Büchler et al., 2018). Additionally, the significance of the hip joint for the evolution of bipedalism has led to a wealth of interest in the femur and its development (Büchler et al., 2018). While stumbling, the human hip joint can experience a peak force of up to eight times body weight. During normal walking or standing, forces are two to three times body weight (Büchler et al., 2018, pp. 11-13). This suggests that the femur experiences a great deal of loading during daily life. If the development of the metaphyseal region is impacted significantly by biomechanical loading, the proximal femur would be an especially relevant location to identify this effect. As such, plasticity in this region is a variable that this project aims to assess.

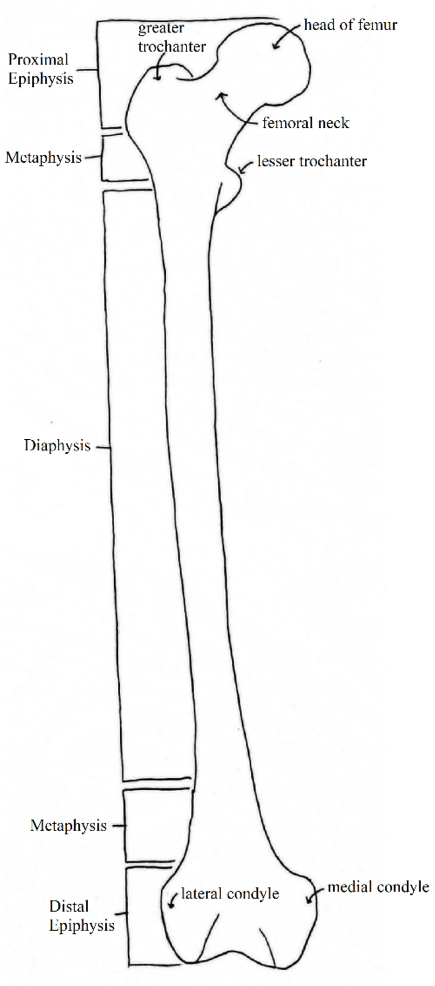

Figure 1: Anatomy of the mature femur. In a growing femur, the metaphyseal region lies under the epiphyses of the greater trochanter and the head of the femur. Anterior view. Adapted from Martini, Tallitsch & Nath (2018, Figure 7.13).

While some studies have provided a quantitative description of the ontogeny of the distal femoral metaphyseal surface and have discussed its relevance to the biomechanics of the knee joint, as discussed below, the proximal metaphyseal region, though not completely unstudied, has received far less focus. The proximal femur has two epiphyses, the capital epiphysis (sometimes referred to as the proximal femoral epiphysis) and the traction epiphysis of the greater trochanter. These develop as separate centers and enlarge by appositional cartilage cell proliferation and subsequent ossification (Weinstein & Dolan, 2018, p. 331). The three main regions of growth of the proximal femur are the physeal plate, the greater trochanter, and the femoral neck isthmus (Figure 1; Weinstein & Dolan, 2018, p.331. Each of these three regions contains a growth plate (d'Heurle et al., 2018, p. 100). Balance between the growth rates of these centers is necessary for normal femoral development and functioning of its associated joint (Weinstein & Dolan, 2018, pp. 331-332). As a result, this process is highly genetically and hormonally regulated. Weinstein and Dolan (2018, p. 332) note that, as with all bones, the growth of the proximal femur is also affected by muscle pull and weight-bearing force transmission, as well as by normal joint nutrition, circulation, and muscle tone.

The metaphyseal region of the proximal femur has a major role in the development of the bicondylar angle, the angle of the femoral neck, and as a result, has ramifications for locomotion. Tardieu and Trinkaus (1994, p. 192) suggested that the emergence of the bicondylar angle in early hominids, and its persistence through the Hominidae, is likely the result of developmental plasticity, where differential forces acting on the epiphyseal cartilage result in differential mediolateral metaphyseal growth. Multiple studies which mention the proximal femoral metaphyseal region, including Tardieu and Trinkaus (1994), focus on the measurement of the bicondylar angle and its relationship with age. They provide little to no description of actual shape change in the metaphyseal region through ontogeny. Nonetheless, Kandzierski, Matuszewski & Wójcik (2012, p. 2518) have demonstrated that the capital growth plate of a healthy proximal femur changes shape throughout growth from a pleated to a more spherical shape. Given that the growth plate changes shape through ontogeny, the underlying metaphyseal surface may show a similar change. This may be the case because the metaphyseal region which transfers the force from the weight-bearing joint epiphysis to the diaphysis and anchors the growth plate. However, there appears to be no quantitative description of shape change during growth for the proximal femoral metaphyseal region in humans. This study therefore has the potential to fill a significant gap in current knowledge about this biologically significant region.

Surveying the literature, research on the distal metaphyseal region appears to outweigh investigation of the proximal region, as significant focus has been placed on the role of the knee joint in locomotion. For example, Stamos and Weaver's (2020) interspecies comparison of the distal femur during growth sought to delineate features associated with differing locomotor styles by examining the topography of the metaphyseal surface. The authors argued that the topography of the metaphyseal surface is subject to the general principle that growth plates, and the metaphyseal surfaces below them, tend to be oriented perpendicularly to the principal stress to which they are most commonly subjected (Stamos & Weaver, 2020, p. 463). The angle of principle stress varies based on the location of the bone and the specific movements done with that appendage. Regardless of the angle, orienting metaphyseal surface topography perpendicular to this stress acts to reduce the shear component of stress, protecting the growth plate from injury and therefore allowing for regularly patterned growth of bone. Stamos and Weaver (2020, p. 472) found consistent patterning in traits associated with changes in locomotor mode that occur throughout growth in different primate species, suggesting that the topography of the metaphyseal surface of the distal femur is developmentally plastic. Their findings are unsurprising given that weight-bearing behaviours in humans follow a well-established sequence (from sitting with support to walking alone), each corresponding to different patterns and magnitudes of skeletal loading (Swan et al., 2020). Further, it is known that after learning to walk the direction of loading continues to change over time as the individual develops a fully mature striding bipedal gait. Given that immature bone found in subadults is especially sensitive to changes in mechanical stress, it is expected that shifts in loading can be identified in the morphology of weight-bearing bones like the femur.

Plasticity and Constraint

This project was focused around two themes: ontogeny; and plasticity vs. constraint. My focus is on growth and its effect on bone shape, and specifically on how the proximal metaphyseal region of the femur changes throughout development. This encompasses ontogeny, the period of time in which ontogenesis, or the development of an individual from fertilization to adulthood, occurs. When discussing shape change across ontogeny, research tends to focus on varying levels of plasticity and developmental constraint between regions of a bone. Plasticity refers to "...an organism's ability to change its phenotype in response to environmental changes" (Stark, 2018, p. 16). In the context of this project, plasticity refers to how bone alters its size, shape, and properties through modeling and remodeling processes in response to its environment. Conversely, developmental constraint refers to a bone's inability to respond to its environment due to physical, mechanical, or structural limitations.

Bone's response to loading (functional adaptation) is complicated. Traditionally, this was understood via Wolff's law (1986), which stated that bone is laid down where it is needed and resorbed (removed) where it is not. Through this, the shape of bone comes to be related to the mechanical stress it regularly endures (Chen et al., 2010). As an extension of this, in 1996 Harold Frost proposed his 'mechanostat' hypothesis (Frost, 2003). This theory suggested that if a bone is subjected to a certain threshold of non-traumatic strain (i.e., not enough to cause a full fracture), bone mass will be increased via bone remodeling processes (Frost, 2003). Similarly, if a bone is continuously loaded below this threshold, bone is resorbed, and bone mass is decreased. In the years since, we have come to understand functional adaptation at the cellular level. It is understood that bone deposition, performed by osteoblasts, and bone resorption, performed by osteoclasts, occurs in response to signals sent out by osteocytes (osteo – bone, cyte – mature cell). Osteocytes are subject to hydrostatic pressure because of fluid flow created by the application of mechanical load on bone (Chen et al., 2010). These cells signal the other bone cells to either lay down or remove bone following the rules outlined above. Admittedly how bone responds to loading is not quite so straightforward, with different bones requiring different thresholds of strain to generate a response, and some variation being likely between the degree of responsiveness in male and female skeletons (Laurent et al., 2014). Additionally, remodeling does not always occur in response to mechanical strain. For example, hormones may produce systemic change. Nonetheless, the notion that bone is responsive to mechanical loading, and that variation in that loading produces variation in the skeleton (i.e., changes in phenotype that signal plasticity), holds true.

It is known that different regions of long bones exhibit varying degrees of plasticity and constraint. Diaphyses tend to be more biologically plastic during growth, responding significantly to biomechanical loading, while epiphyses are less plastic and more developmentally constrained (Nadell & Shaw, 2016). However, there is some variation within these regions. For example, research by Nadell & Shaw (2016) suggests that the distal sections of diaphyses are more tightly constrained by safety factors, which refer to the ways in which bone accounts for loading scenarios that are higher than the expected peak stress, compared to bony tissue at the mid shaft and proximal diaphysis. This suggests that the mid and proximal diaphysis display greater plasticity to habitual loading. Complicating the notion that epiphyses are necessarily constrained, Meyers' (2017) GM based examination of adult proximal humeral and femoral epiphyses concluded that there was a relationship between activity and shape in her samples, suggesting that epiphyses may be somewhat plastic in their remodeling response to habitual activity. That said, Meyers (2017) notes that this relationship is exceedingly complex since shape is influenced by several factors and the interactions of these factors, which include genetics, health, and population adaptation.

The role of the metaphyseal region likely impacts how plastic it can be in response to behaviour in subadults as bone growth is tightly genetically and hormonally regulated. During growth in length (endochondral ossification), this region contains a cartilaginous growth plate. On the epiphyseal side of the growth plate, chondrocytes divide and enlarge, increasing the length of the element. On the diaphyseal side, chondrocytes degenerate and are replaced by bone via osteoblast action (ossification). At maturity, the rate of epiphyseal cartilage division and enlargement slows, and ossification on the diaphyseal side speeds up. Eventually, between the ages of 14 to 19 for modern human populations, femoral epiphyseal closure occurs and bone growth in length stops (Buikstra & Ubelaker, 1994). When examining subadult bones before fusion, the most proximal part of the bone is the metaphyseal surface, the region of ossification. As outlined above, the levels of plasticity and constraint in developing metaphyseal regions are less well understood than those in the epiphyseal and diaphyseal regions. However, some studies seem to conclude that the metaphyseal surface is developmentally plastic during growth and is significantly impacted by levels and patterns of biomechanical loading (Stamos & Weaver, 2020).

Geometric Morphometrics and Cross-Sectional Geometry

Expanding upon traditional morphometrics (which examine linear dimensions in bivariate space), 3D Geometric Morphometrics (GM) allows examination of shape using 3D landmarks and permits the removal of the confounding influence of size variation. Physical anthropologists have used GM to examine a broad range of skeletal elements, samples, and processes, exploring a wide variety of shape-related questions. Shape is defined as "... all the geometric features of an object except for its size, position and orientation" (Klingenburg, 2013, p. 16). Differences in shape may signify variation in "processes of growth and morphogenesis, different functional roles played by the same parts, different responses to the same selective pressures, or differences in the selective pressures themselves" (Zelditch, Swiderski & Sheets, 2012, p.1). Study of variation in shape, therefore, holds potential to shed light on many processes and can aid in answering many biologically derived questions.

For most applications, GM involves digitizing Cartesian coordinate-based landmarks on a group of specimens in order to capture the morphology of the object. Landmarks are chosen based on homology (points on one individual correspond to the same point on all other specimens); adequate coverage of the form; repeatability; and consistency of relative position (landmarks do not switch positions relative to one another; Zelditch et al., 2012, pp. 24 - 32). Landmarks can be defined as one of three types:

1. Locally defined points tied to the discrete juxtaposition of tissues (e.g., a foramen);
2. Locally defined points which refer to geometric constructs (e.g., maximum point of curvature of the orbit);
3. Points which are geometrically defined in relation to the whole structure, which generally are extreme points (e.g., the most distal point of the humerus; Klingenburg, 2012A, pp. 8 -10).

If a shape has complex curves, or if identifying well-defined landmarks would prove difficult due to specimens varying widely in morphology, semi-landmarks (sliding landmarks) may be employed (Slice, 2007, p. 271). Rather than tied to a specific locus, the positions of these landmarks are arbitrary. They simply sample the curve between two fixed landmarks, sliding along that curve to best capture its shape. Applying semi-landmarks has the potential to vastly increase the shape data that can be derived from difficult-to-landmark regions. Initially, a lack of software limited the use of semi-landmarks (Slice, 2007). However, this issue has since been resolved as there are now a variety of available software for their generation and use (Slice, 2007). Once landmarks and semi-landmarks are generated, their coordinates are subjected to a preprocessing step called Generalized Procrustes Analysis (GPA), which standardizes the landmark coordinates to remove size, orientation, and positional data. This step yields Procrustes coordinates which contain only shape information (Slice, 2007). This process brings all the landmark configurations into a common coordinate system in which differences in landmark coordinate values are reflections of difference in shape. Variation in landmark values can in turn be quantified using multivariate statistical analyses to explore questions about shape variation and biological processes (Slice, 2007).

GM is useful for describing shape variation within a sample, but its use is extended when correlations of shape with other factors like age and loading history are considered (Slice, 2007). As a result, GM is often used in concert with Cross-Sectional Geometry (CSG; Slice, 2007). CSG examines the distribution of bone in a cross-section of a skeletal element, generally a cross-section of the diaphysis. It works within the premise that the skeleton responds to changes in mechanical stress by adding or removing bone through modeling and remodeling processes (Swan et al., 2020). Studies applying CSG use biomechanical principles originally derived in the engineering field to explore robusticity, which refers to the “strengthening or structural buttressing” of skeletal elements in response to their environments (Ruff et al., 1993, pp. 21-22). Bone strength is increased by distributing bone tissue further from the neutral or bending axis, which increases its resistance to loading, such that a bone with further distributed tissue is stronger (more robust). Immature bone is particularly sensitive and responsive to change and, as such, much interest has been focused on describing the relationship between loading and age/development (Swan et al., 2020). Additionally, Meyers (2017, p. 15) notes that "since bone formation and remodeling respond to mechanical loading, the size and shape of the diaphysis can be used to examine habitual activity within populations." Examining cross-sectional properties has often been used to discuss behaviour in archaeological contexts (Auerbach, 2008; Cowgill; 2014, Macintosh & Stock, 2019 and Stock & Pfeiffer, 2001).

A Biocultural Approach to Bioarchaeology

The main theoretical perspective informing this research is a biocultural approach, which necessitates integrating knowledge from both archaeology and biological anthropology. While this project is focused on the biological reality of growing up, there is social/cultural nuance to this process. It can and is impacted by the individual's physical and social environments. Along these lines, the biocultural approach sees the skeleton as a collection of biological, ecological, and behavioral (cultural) facts and "explicitly emphasizes the dynamic interaction between humans and their larger social, cultural, and physical environments" (Zuckerman & Armelagos, 2011, p. 20). Therefore, the cultural context of the remains under study is important as factors like activity and diet may have significant impact on the human skeleton.

The skeletons of subadults carry "a wealth of information on their physical and social life, from their birth, growth and development, diet and age at death, to the social and economic factors that exposed them to trauma and disease at different stages of their brief lives" (Lewis, 2018, p. 119). However, historically there has been limited bioarchaeological study of children compared to adults (Beauchesne & Agarwal, 2018). It was thought that juvenile, and especially infant remains, tended to be more poorly preserved and less recoverable than adult remains (Beauchesne & Agarwal, 2018 , p.1). This has been shown to be overstated, with excavation techniques and curation practices responsible for some of the absence of infant and child remains on sites and in collections (Lewis, 2018, p. 120). With increased interest in children as active and identifiable individuals, analysing plasticity in the form of growth--as this project attempts to do--has become central to bioculturally based research focused on the remains of subadults (Beauchesne & Agarwal, 2018, p. 5).

How a biocultural approach is operationalized varies and, as was the case in this project, the integration of variables like subsistence strategy and environmental factors may prove difficult if not considered from the beginning of a study. However, at the very least one must keep in mind that this project does not detail shape variation in the entire human population but applies to four specific populations who had variable lifestyles and contexts, which may impact the phenomena being explored. As there is not a universal 'childhood' or way of growing up, the children from these four groups would have had different experiences, and there is likely variation within the groups as well. While population-based grouping variables are not directly included in the study, as skeletal tissue is influenced by multiple biocultural influences over the life course, contextual archaeological and bioarchaeological information is central to understanding the physical and cultural environments in which growth took place.

Samples and Methods

The Samples

Four different hunter-gather groups are examined in this project, an Alaskan Point Hope population; a population from Indian Knoll in Kentucky; a Sadlermiut population from Native

Point on Southampton Island at the entrance to Hudson's Bay; and a sample which is an amalgamation of four Later Stone Age southern African collections. While the samples used in this research vary both temporally and spatially, all are forager groups under the broader classification of "hunter-gatherer" groups. Hunter-gathers have been defined several ways. They have been defined economically, as groups who do not rely on domesticated plants and animals, and socially, as *band* societies of small, flexible groups with egalitarian socio-political relations, or as a combination of both the economic and social characteristics (Kelly, 2013, p.1-2). In all cases, groups engaged in this form of subsistence strategy would have been highly active. However, anthropology has moved beyond the search for the "essential core of the foraging lifeway" and instead, acknowledges the considerable variation between individual groups (Kelly, 2013, p. 2). For the purposes of this study, variation in lifeways is likely to impact the loading of the femur and as a result, impact its shape and cross-sectional properties.

In an attempt to garner a biocultural understanding of growth, this study was informed by the known archaeological and bioarchaeological information about these populations. Below I provide a short description/summary of each population. I focus on the activities associated with the lifeways of each group, highlighting differences in habitual activity that result from their foraging patterns and differences that may arise from biological adaptation to differing climates. I also discuss information about the excavations of the collections and their current housing. Prior biological anthropological studies of the juvenile remains in these collections and their results are also addressed. However, while the archaeology of childhood continues to gain greater recognition (Lewis, 2018), archaeological information directly linked to subadult and childhood activity in these populations is limited. As such, I discuss general activity, with an understanding that subadult activity likely varied from that of adults. To conclude this section, I discuss the ethical dimensions that need to be considered when studying collections like these.

Point Hope

The Point Hope sample originates from the northwest coast of Alaska and is particularly well studied. The sample is an amalgamation of four different cultural periods with the main ones being the Ipiutak (100BC - 500 AD) and Tigara (1300 - 1800 AD) periods (Auerbach, 2008, pp.138, 594-595; Meyers, 2017). According to Collins (1984) via Hilton, Auerbach, and Cowgill (2014), the site is one of the oldest continuously occupied sites in North America, though it is suggested that "... the occupations likely do not represent any linear ancestor-descendant temporal sequences" (p. 3). The Point Hope material was excavated in the first half of the 19th century (1939-1941) by Helge Larsen (Danish National Museum) and Froeligh Rainey (University of Pennsylvania) (Meyers, 2017). These excavations uncovered around 10,000 artifacts and approximately 500 skeletons, which are currently housed at the American Museum of Natural History, in New York NY (Holliday & Hilton, 2010; Meyers, 2017). This population is referred to as "PH" in specimen names.

The Point Hope collection has often been included in discussions of cold stress adaptation (the average January high temperatures in the area today are around -15.7°C; Holliday & Hilton, 2010). Unsurprisingly, the bioarchaeological remains of both the Ipiutak and Tigara peoples suggest that they possessed cold-adapted body proportions, tending to be shorter and heavier than those individuals adapted to warmer-climes (Holliday & Hilton, 2010). In her study exploring variation in morphology associated with substance shifts within the juvenile members of the Point Hope sample, Cowgill (2014) proposed that, given similarities in body proportion between the two populations, they likely display a convergence on cold-adapted morphology, following Bergmann's and Allen's rules (p. 226). Bergmann's and Allen's rules are explanations for the relationship of climate to adult body proportion and size (James, 2018). Bergmann's rule states that, in a species with a large range of geographic dispersal, those in colder regions will have larger body-sizes while those in warmer regions will have smaller ones. Allen's rule concerns morphology and suggests that, in colder climates, arms, legs, and other appendages (like ears) will be shorter. Both rules relate to the body's ability to dissipate or conserve heat. Essentially, the further from the equator a population is, the more likely it is they will have a larger body size (be more robust) and be shorter. This helps to conserve heat, maintaining thermal homeostasis. On the other hand, the closer to the equator a population is, the smaller in body-size (more gracile) and taller individuals are likely to be. Adherence to these principals is demonstrated in *Homo sapiens,* but also in numerous other warm-blooded species (James, 2018). Following these rules, arctic populations, like the Point Hope sample and the Sadlermiut, will have different body proportions and morphology than those in non-arctic climates.

While they generally share cold-climate adaptive features, the Point Hope populations show variation in their patterns of resource exploitation. The Ipiutak individuals were involved in both terrestrial and marine hunting, with archaeological deposits containing high frequencies of caribou skeletal remains and caribou-derived artifacts, suggesting seasonal reliance on inland caribou (Cowgill, 2014, p. 213). Subsistence for the Tigara periods was mainly focused on marine exploitation, with a high frequency of large harpoons, flotation devices and walrus, seal and whale bone being present in the archaeological record (Cowgill, 2014, p. 213; Dabbs, 2011). Compared to the Tigara, the bones of the Ipiutak population suggest they endured more chronic stresses, which may be related to overland travel, while the Tigara likely experienced short-term acute stresses due to resource shortages and trauma risk associated with hunting bowhead whale as a primary resource (Dabbs, 2011, p.100). Both populations, due to their at least partial reliance on marine resources, engaged in marine transportation that would have resulted in heavy loading patterns on the upper limbs (Meyers, 2017). While the biomechanical stresses the populations endured would be different due to variation in subsistence strategy, Cowgill (2014, p. 227) did not find any significant differences in the morphology of juvenile individuals of the different periods. She relays that, for both juveniles and adults, differences in subsistence strategy are not discernible in the cross-sectional geometric properties of the two populations.

Indian Knoll

The Indian Knoll sample originates from central western Kentucky within the Green River Archaic period (Meyers, 2017). Its habitation has been dated to roughly between 6415 - 4143 years BP (Auerbach, 2008). The site was excavated in the early to mid-19th century by Clarence B. Moore and William S. Webb and is currently housed at the University of Kentucky, Lexington, as a part of the W.S Webb Museum (Auerbach, 2008). According to Hermann (2002, p. 21), as was convention in 1915-16, most of the burials excavated by Moore during the first season of excavations (n = 298) were not completely removed. Rather, only 66 crania and a small number of pathological specimens were curated in these initial excavations, unsurprising given the focus on examining racial differences in the skull at the time (Hermann, 2002, p. 21). Nonetheless, this excavation was the first extensive collection of human remains in the region and the resulting collection, and its expansion through later excavation seasons, has been included in many bioarchaeological studies (Hermann, 2020, p. 20). The Indian Knoll skeletal series contains over 1,100 individuals, making it one of the largest samples drawn from a population of people who lived by hunting and gathering excavated from a single North American site (Hermann, 2002, p. 37). This population is referred to as "IK" in specimen names.

The site of Indian Knoll (15OH2) is a large shell mound that contains a wealth of archaeological information (Hermann, 2002, p. 37). According to the contents of the mound, the population relied on a broad range of resources, with fresh-water mussels being a significant resource across time periods, despite changing technologies (Meyers, 2017). Archaeological remains from the site and surrounding region suggest that bows, arrows, and spears were likely used frequently in the pursuit of other essential resources like deer and wild turkey (Meyers, 2017, p. 29). In his thesis outlining robusticity in Holocene hunter-gatherer groups across North America, Auerbach (2008) found that broad-spectrum foragers, like the Indian Knoll population, had stronger femora than those populations relying on marine or fresh-water resources, indicating high levels of terrestrial mobility. Comparing the robusticity of juveniles from the Point Hope and Indian Knoll populations, Cowgill (2010, p. 23) found that the Indian Knoll population exhibited less upper-body robusticity, possibly stemming from their limited reliance on aquatic resources and resulting limited use of watercraft (Meyers, 2017, p. 30). Nonetheless, as with all the samples in this project, the Indian Knoll population were highly active, especially when compared to the levels of activity seen in modern living populations.

Sadlermiut

The site of Native Point is located on southeastern Southampton Island in Hudson's Bay (Merbs, 2018). The site was initially excavated between 1954 and 1959 by Drs. Henry B. Collins, Willian Laughlin, and Charles Merbs (Meyers, 2017, p.33). During the first season, Collins found approximately 90 semi-subterranean homes (Holland, 2007, p.38). The

Sadlermiut collection is currently curated by the Canadian Museum of History in Ottawa, with decisions about continued study being made by the Inuit Heritage Trust. This group is referred to as “NP” in specimen names.

Unlike the other populations in this project, there are some historical accounts of the Sadlermiut. Comparing these accounts and archaeological remains to other populations in the area, researchers have suggested that the Sadlermiut were likely of Thule ancestry, but that their isolation on Southampton Island, as well as on Walrus and Coats Islands, led to the development of technology and culture distinct from the mainland Inuit populations (Holland, 2007, pp. 35-36). However, mtDNA analysis identified the Sadlermiut as having both Dorset and Thule haplogroups, genetic markers of population affinity, suggesting that the two founding populations interacted for a period of time (Hayes et al., 2005). That other Inuit peoples referred to the Sadlermiut as Tunit (the old people) supports an older and different ancestry for the Sadlermiut compared to mainland Inuit (Holland, 2006, p.37). During the winter of 1902-03, the Sadlermiut population at Native Point suffered the devastating effects of an epidemic brought by a community member who visited a whaling station in nearby Cape Low (Holland, 2007, p. 40). Only five individuals, a mother and four children, survived, the last of whom died in 1948 (Holland, 2007, p. 40). The current collection is thought to represent an occupation period from the early 1400s to 1903 (Holland, 2007, p.41).

Kayak rests and kayak lances, as well as zooarchaeological remains of seal, caribou and walrus, have all been linked to the Native Point site (Holland, 2007, p. 38). Hunting of bowhead whales from both kayak and ice is well established by historical accounts (Holland, 2007). In terms of the impact of activity and climate on morphology, the Sadlermiut were cold-adapted and would have dealt with high levels of upper arm habitual loading due to both marine transportation/hunting and hide processing (Meyers, 2017, p. 34). In her master's thesis examining shape in the humerus and femur of archaeological populations with a variation of subsistence strategies, Meyers identified that the Point Hope and Sadlermiut populations likely demonstrate similarities in morphology tied to long-term cold climate adaptation (2007, p. 108). Both populations are marine hunters living in arctic environments, meaning that they may display distinct patterning from the LSA and Indian Knoll groups who are largely terrestrial hunters in non-arctic climes. While neither climate-related adaptation nor marine vs. terrestrial subsistence patterns are a direct part of the current study, it is relevant to keep them in mind as possible sources of variation.

Later Stone Age (LSA) South Africa

Later Stone Age sites in southern Africa are most dense in the Cape coast region, likely due to the regions high resource variability and agreeable climate, as well increased preservation rates in cave environments (Cameron & Stock, 2018, pp. 112 - 113). This region includes multiple biomes, particularly forest, savannah, and fynbos (Stock & Pfeiffer, 2004). Archaeological evidence drawn from the southern African coast has helped to identify subsistence as relying on small game browsers, as well as marine resources, primarily in the form of shellfish and seals (Osipov et al., 2016). However, there is no evidence to suggest that Later Stone Age foragers used boats (Osipov et al., 2016, p. 136).

Big game hunting in forest biomes likely involved spears, which is supported by the relative symmetry of the upper limb bones in samples derived from these regions (Stock & Pfeiffer, 2004, p. 1009). Bows would likely have been preferred in the hunting of smaller game (Stock & Pfeiffer, 2004). Rock art from the region and period depict a multitude of hunting methods and the use of weighted digging sticks, likely for tubers and bulbs (Stock & Pfeiffer, 2004, p. 1000). Archaeological evidence has been used to argue that populations likely moved between inland and coastal regions on a seasonal basis, though there is considerable variation in the relative importance of marine resources between different regions and time periods (Stock & Pfeiffer, 2004, p. 1001). In any case, the groups making up this sample would have been highly mobile terrestrial foragers who had shifting home bases and diverse diets (Pfeiffer & Harrington, 2018, p. 39). This mobility is reflected in this population's high levels of limb robusticity (Osipov et al., 2016). In terms of the direct impact of climate on body size, Later Stone Age hunter-gatherers display quite different body types than cold-adapted populations. Generally they have a small body size, and are noticeably gracile and lean (Osipov et al., 2016, p. 136).

Skeletal material for this population is drawn from the collections currently named Florisbad (specimens NMB), McGregor (specimens MMK), Albany (specimens ALB), and University of Cape Town (specimens UCT). Within these collections, material is derived from multiple sites (see Stock & Pfeiffer, 2004, p. 1003). The broad time span for the individuals included in this study is 9120-200 years BP, uncalibrated (Kurki & Harrington, 2017).

Ethical Dimensions

The study of skeletal remains, in particular those which are tied to descendent indigenous communities, raises ethical concerns, especially given anthropology's current efforts to engage with Indigenous reconciliation and resurgence. This is especially the case when discussing collections like those used in this project. When working with these collections, one should be cognisant of, and explicit about, the circumstances of their excavation and those that make them available for continued study.

Of relevance to the creation of bioarchaeological collections, Trigger (1984, p. 356) observed that "the nature of archaeological research is shaped to a significant degree by the roles that particular nation states play, economically, politically, and culturally, as interdependent parts of the modern world-system." Trigger argues that social contexts generate distinctive archaeologies, where the questions asked, and methods used, are impacted by these social contexts. Excavations of populations in the archaeological record, and much of the bioarchaeological study of the resulting collections, including my own, has been undertaken by those belonging to a colonising population who have no ties to the past they attempt to understand or the individuals they study (Trigger, 1984, p. 360).

North American archaeology at the turn of the twentieth century was underpinned by the assumption that Indigenous cultures had experienced limited change over time and that any change could be attributed to cultural diffusion (Trigger, 1984, p. 361). This suggested that Indigenous groups were incapable of innovation and were not responsible for the ideas which led to archaeological features like burial mounds, pottery, and agriculture (Trigger, 1984, p. 361). Most archaeologists during this period underestimated the abilities of Indigenous peoples in the past and instead assigned 'complex' ideas as coming from outside influences. It was not until the 1960's that these beliefs and the resulting explanations for archaeological sites lost credibility (Trigger, 1984, 361). This period, from roughly 1910 to 1960, is referred to as the "culture history" period and encompasses the excavations of the North American samples in this project (IK, PH & NP). In this period, colonial archaeologists highlighted what they saw as static cultures with limited ability to develop on their own, requiring new technologies and ideas to come from external sources via migration (Trigger, 1984, p. 363). This served to justify colonial control over or removal of Indigenous peoples, and by extension, the excavation and curation of large collections of indigenous remains. Archaeology in southern Africa is similarly complicated by colonial, national, and imperialist ideologies and interests (Trigger, 1984). In the context of generating the collections from which this project draws, the excavation and curation of ancestral remains was likely done by individuals who had no relation to descendent communities, and these groups likely had no say in what was done with the remains of their ancestors. Further, how the archaeological material and remains associated with these sites were interpreted served to support a particular narrative that generally had the effect of denigrating Indigenous individuals of the past and present.

While biological anthropology has taken strides to recognize its dark and often racist past (de la Cova, 2019; Watkins, 2018; Zukerman & Armelagos, 2011), research today is, as always, embedded in its own context. Despite our best efforts, the questions we ask, the approaches we take, and the conclusions we reach will always be impacted by the socio-political context of the discipline in which they are made and the points of view of those who make them. The hope is that, with increased awareness of this and reflection on the obvious biases in the history of the discipline, we will be able to get closer to a 'true' idea of the past, and ensure we conduct research in an ethical way. Related to this, Mant, de la Cova, and Brickley (2021, p.1) argue that "complicating, problematizing, and questioning what we think we know about past lives demonstrates our respect to the individuals whose remains we have the privilege of studying." In the same vein, grappling with how remains come to be in collections and why they are accessible is key. That I am able to work with these collections is a privilege and one cannot ignore the history that led to their creation and the potentially problematic nature of their continued use. A poignant example of researchers acknowledging, and problematizing, the circumstances in which collections have been amassed is the discussion surrounding the key American anatomical collections on which biological anthropology's main methods have been built (de la Cova, 2019; Mant, de la Cova, and Brickley, 2021; Watkins, 2018). These collections are largely comprised of marginalized individuals, with a high frequency of African American individuals present in the Robert. J. Terry collection for example (de la Cova, 2019).

With respect to collections of remains belonging to Indigenous groups it is especially vital that the historic silence surrounding the origins and colonial contexts of their amassment do not continue. Trouillot (1995) proposes that power has profound impacts on the production of history. For Trouillot, silences come about in the manufacturing of history because of processes of power (p. 27). As such, for Trouillot, silences are not simple absences but are rather active processes (p. 27). In some cases, the information required to produce an alternative narrative that does not contain these silences is available in the same materials from which the initial 'histories' were derived (Trouillot, 1995, p. 27). In others, silencing in the production of sources, archives, and narrative requires an author to "make the silences speak for themselves" (Trouillot, 1995, p. 27). This impacts the 'histories' bioarchaeologists generate for past populations, but also the history we relay for our discipline and the collections on which we work. Put simply, sometimes we have the information on the context surrounding the amassment of collections, and sometimes the pertinent information is in the remains of the individuals themselves. We must ensure that we build a narrative that includes these facts, regardless of how uncomfortable that may feel for the researchers working with these remains.

Additionally, unlike in other sciences, or even within other anthropological disciplines, the individuals who bioarchaeologists analyse do not 'consent' to being used in studies or to being a part of a collection. In cases where repatriation efforts have not occurred, a descendant community does not consent to their use either. In attempts to deal with this issue, bioarchaeology as a discipline has moved towards including and consulting descendant groups, their worldviews, and wishes with respect to ancestral remains into its research (Nash & Colwell, 2020). Support for repatriation and reconciliation efforts continues to grow, especially in North America. This movement concerns the future of the remains contained in collections like those used in this study as it necessitates their continued curation and use in scientific study being under the discretion of descendant communities.

The Indian Knoll and Point Hope populations, originating from locations within the United States and currently housed in that country, may fall within the bounds of the Native American Graves Protection and Repatriation Act (NAGPRA). This is a piece of American federal legislation which details laws surrounding "ancestral human remains and sacred, funerary, and communally owned objects" (Nash & Colwell, 2020, p.225). While it can be seen as an improvement from the lack of legislation that came before it, NAGPRA is far from perfect. It only requires institutions that receive federal funding to inventory their collections, and only requires formal repatriation if ancestors or artifacts are claimed by a federally recognized tribe or lineal descendants (Nash & Colwell, 2020, p. 226). Liebmann (2008) critiqued this, arguing that the notion of a federally recognized tribe is a result of colonial bureaucracy and that lineal descendance is difficult to identify with any degree of certainty. In 2010 a new regulation established a hierarchy of rights to unaffiliated remains which requires federal museums to return remains to the tribes which claim them, unless the museum can demonstrate that it has a right of possession (Nash & Colwell, 2020, p. 229). Despite its implementation, the majority of indigenous remains that were in collections before NAGRPA (pre-1990) remain there today (Nash & Colwell, 2020, p. 232). This is both an effect of the requirements for inclusion under NAGPRA and failure of federally funded institutions to fully comply with the law (Nash &

Colwell, 2020, p. 232). There is limited information regarding repatriation processes for the Point Hope and Indian Knoll collections but both institutions housing these collections indicate their compliance with NAGPRA on their websites.

While NAGPRA is flawed, there is, to my knowledge, no equivalent law in Canada or South Africa, where the other two collections used in this study are located. Seemingly, in countries where repatriation is not formalized in law, it is the responsibility of individual institutions, researchers, and descendant communities to ensure that repatriation efforts are supported. As addressed above, decisions regarding the continued study of the Sadlermiut collection are made by the Inuit heritage trust as repatriation has occurred in this instance. This collection has additional ethical dimensions surrounding it given that, due to the recency of some of the burials, there is a clear connection between these individuals and groups living today. To my knowledge, no repatriation of the LSA samples has occurred.

In summary, there is need for continued acknowledgement of the problematic past of bioarchaeology and biological anthropology as disciplines, especially regarding the amassment of collections of ancestral remains. In many cases, there still exists an uneven power balance between researchers and these remains. Acknowledging the work there is to do and grappling with the contexts in which the individuals I work with in this project were collected is my way of beginning to ensure my engagement with skeletal remains is as ethically informed as possible. Bearing these challenges in mind now and in the future, I turn now to the substance of my study, during the course of which I came to recognize the importance of grappling with our discipline's history.

<u>Model Creation and Age Estimation</u>

This project used a subsection (n = 40) of a larger set of 3D surface scans generated from the four collections by Dr. Helen Kurki (University of Victoria) and Dr. Lesley Harrington (University of Alberta). Digital surface scans were captured using a Konica Virtuoso structured light scanner, and fused into 3D models in GeoMagic Design X. Each scan was accompanied by estimated age derived using the QMUL dental method by Dr. Harrington (see Alqahtani, Hector, & Liversidge, 2010 for discussion of this method). According to these estimations, individuals were placed in the following groups, allowing for discussion of shape variation by ontogenetic locomotory group: 1) Toddling (ages 1.5 - 4.5); 2) Mature Walking (ages 4.6 to 12.9); and 3) Stabilized Gait (13+ years) (Table 1). Following Swan et al. (2020, p. 4), I identified the group of 1.5 to 4.5-year-old individuals as likely to engage in an immature form of bipedalism (toddling) . There is likely large variation in the "style" used in this age group as gait would rapidly improve with experience during this time (Swan et al., 2020, p. 4). The middle group (4.6 – 12.9 years) are likely to have a matured bipedal gait that still improves overtime, but at a much more gradual rate (Cowgill et al., 2010; Swan et al., 2020, p. 4). Stamos and Weaver (2020, p. 471) identify the stabilization of the human bipedal gait as occurring between the ages of 13 – 15, providing the justification for the beginning of the oldest group.

There is significant variation in when the different stages of locomotor development begin and end in living populations, given that many factors, like diet and sleeping position, influence their timing (Swan et al., 2020). This timing is likely to vary among archaeological populations as well, a factor that could not be controlled for. No individuals were included under the age of 1.5 due to difficulty identifying homologous landmarks on the fairly indeterminate morphology of these younger individuals. Individuals were included up until fusion of the epiphysis and diaphysis, after which the metaphyseal surface is not visible. For the proximal femur this occurs between 14 to 19 years of age, with variation in timing noted between sexes and populations (Buikstra & Ubelaker, 1994).

Table 1: Breakdown of sample by Age Group and Population**.** (n=40). One individual from Sadlermiut Age Group 2 was used as the Atlas specimen* and is not included in the statistical analyses to follow (NP075). Mean ages for groups are: 1) 2.6; 2) 9.2; and 3) 15.5. Age range of the sample is 1.5 yrs. to 18.5 yrs.

Age Group	Sadlermiut	Point Hope	Indian Knoll	LSA	Total
1	5	0	0	3	8
2	7	4	5	5	21
3	2	4	2	3	11
Total	15	8	7	11	40

* This term refers to the specimen used to project the semi-landmarks onto the other individuals in the sample. See section below for a description of how this was performed.

Shape Data – Landmark Placement and Geometric Morphometrics

As described above, this study used both fixed landmarks and sliding semi-landmarks. Five fixed landmarks were placed on each of the 40 specimens in the sample using Meshlab (Figure 2).

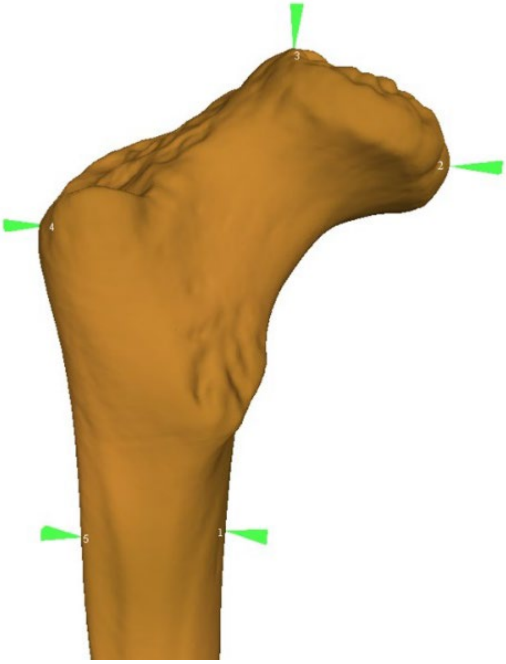

Figure 2: Fixed Landmark Placement. NP075 Atlas Specimen.

All fixed landmarks used in this study belong to the third category of landmarks, meaning they are geometrically defined, rather than biologically or both, and represent extreme points in various directions (Klingenberg, 2012A). Because the region has few homologous biological points, defining the landmarks geometrically ensured they would be present and locatable on specimens which vary widely in their morphology. The definitions for each fixed landmark are presented in Table 2. The area captured contains a fair segment of the proximal shaft due to the definitions of landmarks 1 and 5. Landmarks were preferentially placed on left-sided bones, but when only a right-sided bone was available for an individual, models were mirrored in GeoMagic Design X.

Table 2: Definition of fixed landmarks**.** All fixed landmarks are Type III (geometrically defined). Reporting landmark (LM) number, definition, and the number of semi-landmarks between the fixed LM and the next fixed LM.

Fixed Landmark	**Definition**	**Semi-landmark #**
LM 1	Most medial point at 75% total bone length	15
LM 2	Most medial point at proximal end	6
LM 3	Most superior point	11
LM 4	Most lateral point at proximal end	5
LM 5	Most lateral point at 75% total bone length	n/a

To capture more of the shape of the metaphyseal region, this project also employed sliding semi-landmarks, which are used to capture complex curves (Zelditch, Swiderski & Sheets, 2012, p. 23). A total of 37 sliding semi-landmarks were generated for each individual. The number of semi-landmarks to be generated between each fixed landmark was determined on the basis of capturing the entire curve but limiting the data which needed to be processed (Table 2).

The fixed landmarks were manually digitized onto each specimen using MeshLab. A template (atlas) was created and used to project the semi-landmarks onto all the other specimens in R. The atlas used was an individual from the Sadlermiut population with an estimated age of 12.5 years (NP075). This individual was chosen due to Stark (2018, p. 67) identifying that the semi-landmarking process is computationally easier when scaling down with age rather than up. Atlas creation (createAtlas & placePatch) and semi-landmark sliding (slider3d) was performed using the Morpho package in R (see Bardua et al., 2019, p. 6; Schlager, Jeggeris & Ian, 2020). This process resulted in 42 landmarks for each of the 39 individuals in the project. Together the landmarks for each individual are called a landmark configuration, which captures the shape of the proximal metaphyseal region. These landmark configurations were subjected to a GPA and the resulting coordinates were used to quantify shape variation within the sample using Principal Components Analysis (PCA), as discussed below. The sample size of this project is more than three times larger than the number of fixed landmarks used, meeting the suggestions put forth by Klingenberg (2012A) to maintain statistical significance. Guidelines surrounding sample size to semi-landmark ratio are still debated (Bardua et al., 2019).

Loading History – Cross-Sectional Geometry

The polar second moment of area (J) at 50% total diaphyseal length was used as a measure of activity in this project (F50J). J is a representation of the torsional strength of the diaphysis where a higher J indicates a bone that is better able to resist torsional stress (Stock & Pfeiffer, 2001, p. 342). J is calculated by summing perpendicular second moments of area, "the maximum and minimum distances of bone distribution from the central axis" (Meyers, 2017, p. 16). Fifty percent was chosen following Nadell & Shaw's (2016, p. 418) finding that the mid and proximal shaft may display a more plastic response to habitual loading when compared to the distal section that is likely more tightly constrained by safety factors. F50J was calculated using Ascii-section (see Davies, Shaw, & Stock, 2012 for discussion of this software; values in Appendix A).

In most studies, cross-sectional properties are standardized to remove the effect of body mass and body size, aiming reduce differences in robusticity that stem from variation in body proportion (Meyers, 2017; Osipov et al. 2016). There are a variety of methods for standardizing cross-sectional properties. However, as the lower limbs bear weight during locomotion (i.e., most activity), methods of standardization that employ an estimate of body mass are generally considered to be the most appropriate (Stock & Pfeiffer, 2001, p. 342). When standardizing J in particular, research suggests that those methods that standardize using the product of body mass and bone length^2 are the most appropriate (Cowgill 2010; Ruff, 2000). For this project, body mass was calculated using equations outlined in Ruff (2007), which are specifically for predicting body mass in immature remains. Following Cowgill (2010) and Osipov et al. (2016), a linear regression was performed of log(J) on log(body mass*femoral length^2) to produce standardized residuals that could be used as a body mass standardized J, which functioned as a measure of activity (Appendix A).

Statistical Analysis

Three sets of statistical tests were applied to address the research questions; a PCA, a set of ANOVAs and sets of correlation tests. A PCA used the landmark data to quantify shape variation, identifying the axes of greatest variation within the sample. PCA is a method of dimension reduction which transforms sets of variables into new variables called Principal Components (PCs). These PCs describe the axes of greatest variation within the sample (Klingenberg, 2012b). The number of PCs derived in a PCA relates to the number of variables in the initial dataset, and the first PCs represent a greater proportion of variation than those further down. In the case of this project, PC1 represents the largest pattern of variation while PC 38 represents the least. The relative "importance" of a PC to overall shape variation can be determined by examining either the proportion of variance explained or the eigenvalues. Individual PCs can be analysed to discern how shape varies between the positive and negative ends of the axis and they may be used to create visualizations of shape variation within a sample. This is done using PC coefficients, which indicate the weighting of the different variables that make up a PC score, identifying which landmark/semi-landmark regions contribute most to the calculation of where individuals fall along the axis of variation (Klingenburg, 2012b). When determining shape change represented by each PC, I tended to avoid focusing on shape change occurring the in shaft. While this area was captured by the analysis, it is not the area of interest. Each individual receives a PC score on each PC, detailing where they fall along these axes (Appendix B). These PC scores are used as new variables in further statistical analyses.

In determining which PCs to run in the proceeding ANOVAs, I aimed to analyse those PCs accounting for 90% of total variance, resulting in the top 6 being included in the ANOVA tests. ANOVAs were not run for all PCs due to the amount of time available, as well as an attempt to avoid running too many tests and driving up the possibility of a false positive significance result (type I error). ANOVAs were used to assess ontogenetic locomotor group difference in PC score for the first six PCs (accounting for a summed 92.5% of total shape variation). Developmentally induced changes in mechanical loading are known to impact cross-sectional properties at the diaphysis of femora (Gosman et al., 2013). Attempting to identify similarly patterned change in the metaphysis hints at how locomotor regime and age is related to shape during ontogeny and may aid in understanding the grouping of individuals along the PC axes. All data were normally distributed apart from the PC5 scores for the fully bipedal group (ages 4.6 – 12.9 yrs.; Appendix C). Differences in group mean on PC2, 3 and 4 score were assessed using a one-way ANOVA. PC 1 had a p-value of 0.54 in the Barlett's test, so to be more conservative, a Welch's test was applied to adjust for possible non-homogeneity of variance. PC6 failed to reject null hypothesis of the Barlett's test (p-value: **0.039**) so a Welch's test was applied here as well (Appendix C). A Welch's ANOVA differs from the classic one-way ANOVA in that it does not assume groups have equal variances (it assumes standard deviations are unequal). As the mid group was not normally distributed for PC5 but met the equal variances assumption, a nonparametric Kruskal-Wallis test was used in that instance. For PCs that returned significant results in the ANOVAs, PC1 and PC 6, post-hoc Tukey's tests were applied to determine which groups varied from each other.

Assessment of the relationship of shape to both age and activity was done using correlation tests. Correlation analyses were performed to determine if any of the 38 PCs had a relationship to estimated age, addressing the first research question. To examine specifically the impact of activity on shape, correlations were performed between body mass adjusted F50J and PC score on each PC. PC1 was found to be related to estimated age in the age/pc score correlation tests and was regressed on age to produce a standardized variable where age-effects were removed from the analysis (Appendix B). Adjusting F50J and PC1 score and then performing the correlation test explores if activity has enough impact on shape that its effects show up with age and body mass effects on shape excluded from the data. All data distributions were checked for normality using the Shapiro-Wilk test. Data were normally distributed except for PC scores for PCs 1, 10, 12, 33 and 36. Spearman's correlation tests were run for this data, while Pearson's (Product-Moment) correlations were used for all others. P-values were adjusted for family-wise error using Holm's method. All statistical analyses were conducted in R version 3.6.3 and an alpha level of 0.05 or less was considered statistically significant for all tests administered.

Results

The PCA returned 38 principal components (Appendix B). Of these, only PC1, accounting for 57.4% of total shape variation, showed a correlative relationship with estimated dental age (Table 3; Appendix C). Examining PC scores, younger individuals sat on the negative end of the axis of variation, with increasing age associated with increasing PC 1 score (Figure 3).

Table 3: Variance explained and results of correlation test with age for the first 6 PCs (92. 5% of total shape variation). Reporting percentage of variance explained, rho and p-value results of correlation tests, and holm's adjusted p-value. Significant results bolded. For full results of PC score/estimated age correlations tests see Appendix C.

	% Variance Explained	**r (p-value)**	**Holm's p-value**
PC 1	57.4	0.56 **(0.0002)**	**0.008**
PC 2	13.0	0.24 (0.134)	1.0
PC 3	10.4	0.15 (0.367)	1.0
PC 4	5.7	0.25 (0.127)	1.0
PC 5	3.0	0.01 (0.926)	1.0
PC 6	2.9	0.17 (0.310)	1.0

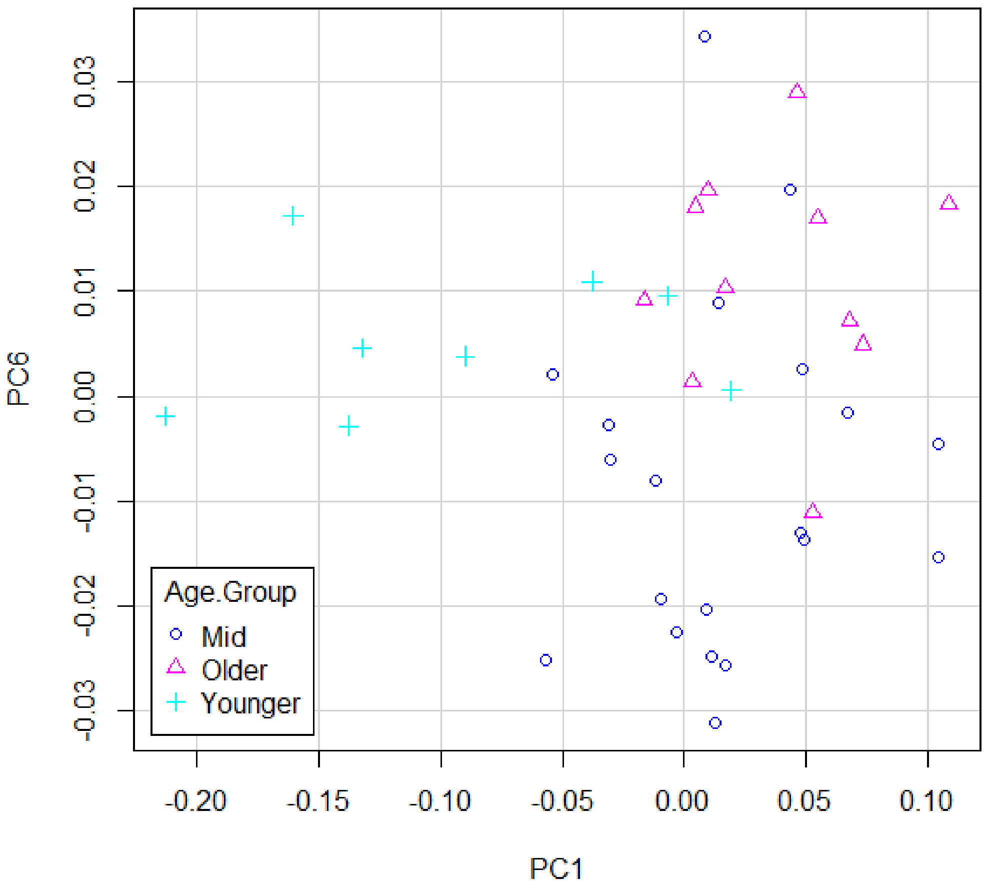

Figure 3: Bivariate plot PC1 and PC6 scores. Symbol colour groups specimens by estimated age categories linked to locomotor regime; Cyan = 1.5 – 4.5yrs (Younger = Toddling), blue = 4.6 – 12.9yrs (Mid = Mature Walking), pink 13+ yrs. (Old = Stabilized Gait).

Examining the graphical outputs and loading coefficients to define shape change along this axis indicates that variation on PC 1 concerns the entire area captured by the landmarks. The most identifiable shape changes appear to be related to the development of a distinct, elongated femoral neck as age increases (Figure 4).

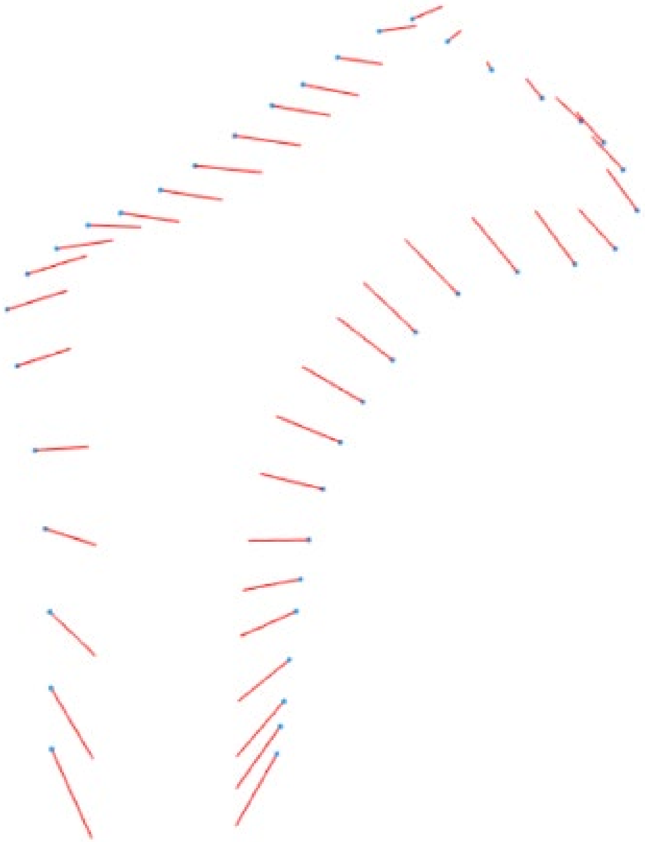

Figure 4: Shape change along PC1 axis. Posterior view.

The ANOVA indicated that mean PC1 and PC6 scores were significantly different between the researcher defined age groups (both tests producing a p-value of 0.002). For PC1, the Toddling group differed in shape from the two older groups, while for PC6, the Mature Walking group differed from the Stabilized Gait group (Appendix D, Tables D3 & D4). Examining the loading coefficients for PC6, shape variation appears to be more localized and is concentrated along the metaphyseal surfaces (Figure 5). However, this PC appears to also correspond to shifting along the anterior-posterior axis.

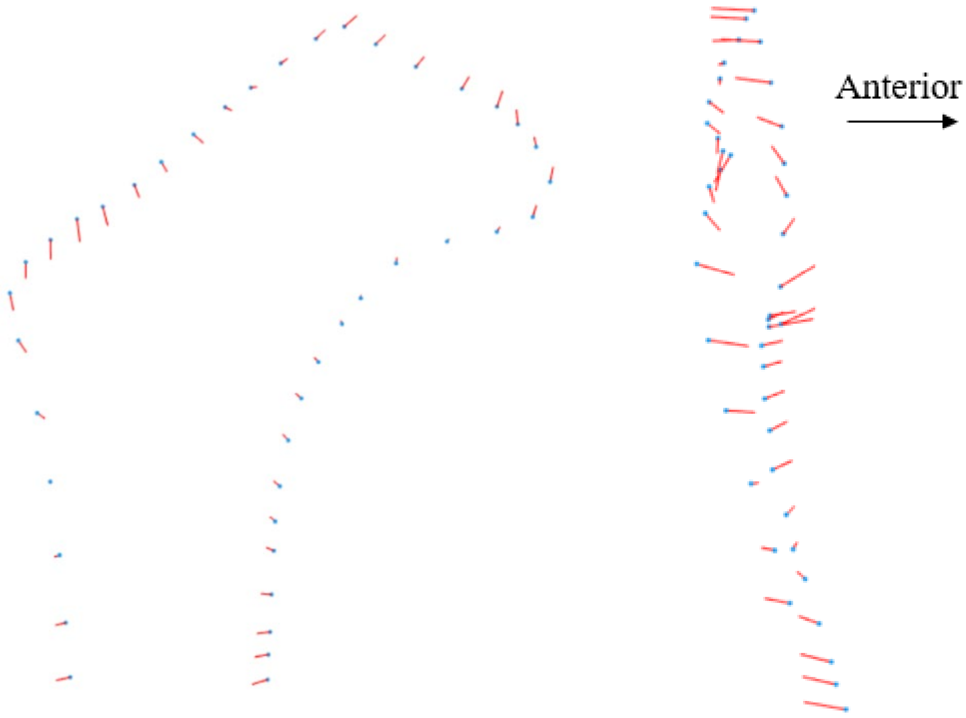

Figure 5: Visualization of change along PC6. Left - posterior view. Right - medial view.

Pertaining to my second research question, only PCs 8, 9, and 23 (accounting for 3.1% of shape variance) showed significant relationships with standardized F50J in the correlation tests (Table 4, Appendix E). After adjusting for family-wise error, only PC8 remained significant (1.3% total shape variation).

Table 4: Significant results for correlation tests between standardized J and PC score. Reporting rho, p-value, and Holm's adjusted p-value. Significant results bolded. For full results see Appendix E.

	r (p-value)	**Holm's p-value**
Adjusted PC 1	-0.22 (0.184)	1.0
PC 8	-0.56 (**0.002**)	**0.007**
PC 9	-0.33 (**0.043**)	1.0
PC 23	0.32 (**0.046**)	1.0

PC 8 score had a strong negative correlation with standardized J (Figure 6). Seemingly, as standardized J increases, there are corresponding changes at the femoral neck and additional changes to the metaphyseal surface which lies under the greater trochanter (Figure 7).

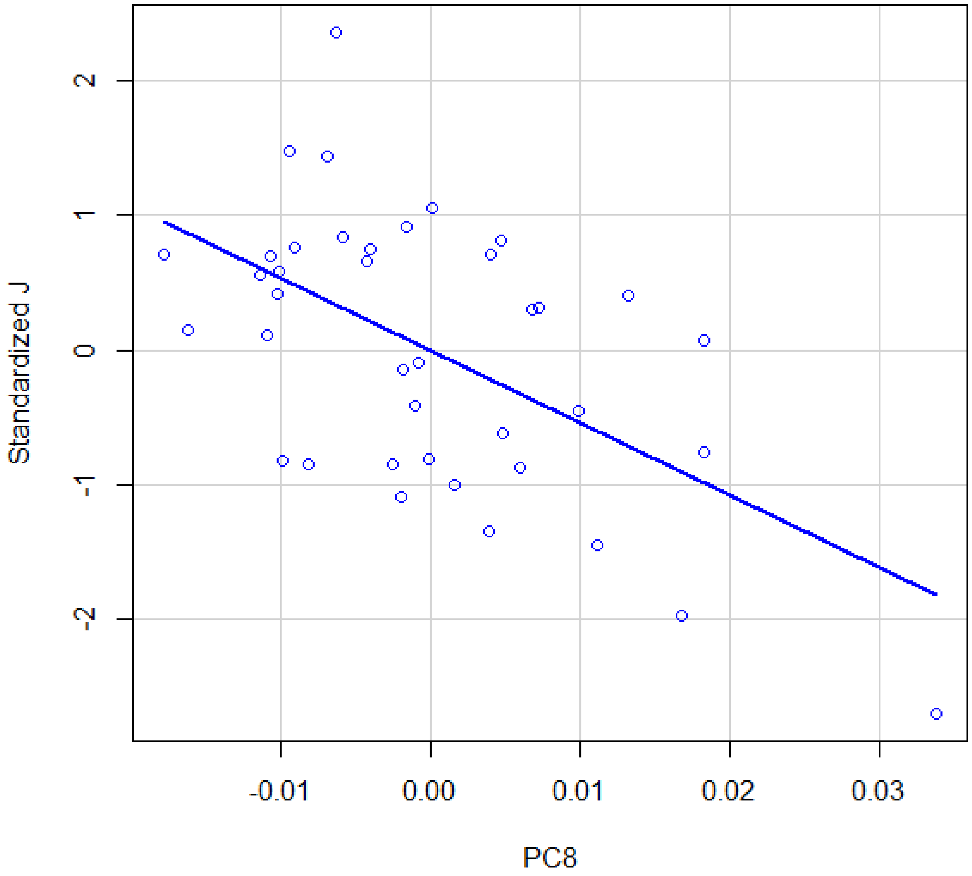

Figure 6: Bivariate plot of PC 8 score and standardized J - standardized activity value (standardized residuals from regression of log(F50J) on log(bodymass * femur length^2)).

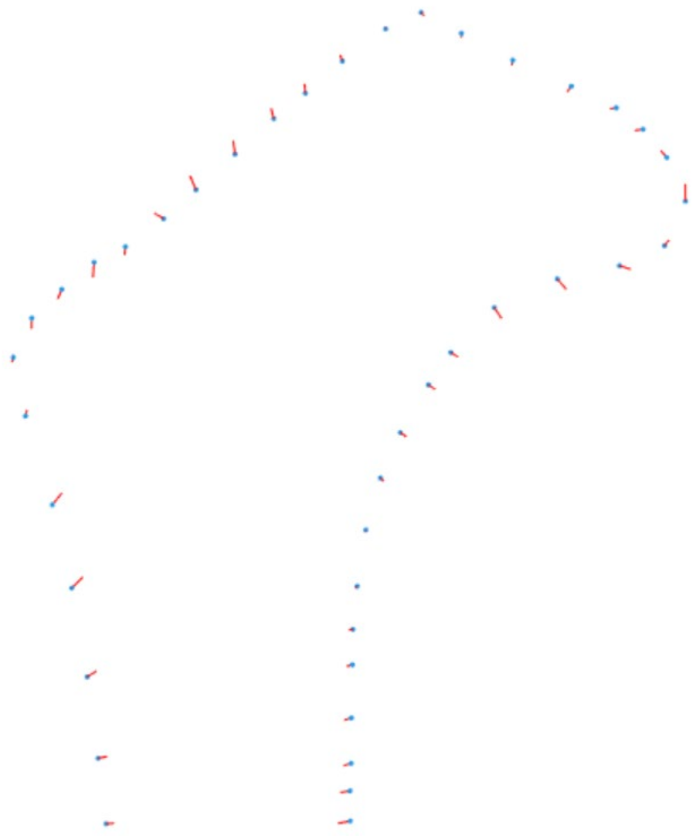

Figure 7: Visualization of change along PC8. Posterior view

Discussion: Ontological Shape Change

To explore the first research question, I determined if the PC score on any of the PCs correlated with age. PC1 accounted for a very large portion of shape variation (57.4%) and PC1 score was found to be strongly correlated with age (rho: 0.56, p-value: **0.0001**). This suggests that age-related shape change is a significant source of variation in the sample. As addressed above, this PC concerns the entire area captured by landmarks, with the most identifiable shape changes related to the development of a distinct, elongated femoral neck with increasing age (Figure 1). Disregarding changes occurring in the proximal shaft, loading coefficients are highest along the neck, indicating that a large amount of change in shape across ontogeny occurs in this region. As

I will discuss in my limitations, interpreting semi-landmark movement remains a difficult undertaking for beginners, which limited how descriptive I could regarding shape change along any of the PCs generated by the PCA.

Conducting an ANOVA test provided an idea of when during ontogeny these changes in shape is taking place. The test identified that the ontogenetic locomotory groups I have defined varied significantly in their PC scores (their shape/morphology) on PCs 1 and 6. The Toddling group (1.5 - 4.5 yrs.) varied significantly in mean PC1 score from the older two age groups (those 4.6yrs. +). This suggest that the proximal femoral metaphyseal regions of individuals below the age of 4.6 have are shaped in a way that is significantly different than those above this age. By extension, major shape change begins at or slightly before this time. I had expected shape within the Toddling group to be variable, considering the variety of locomotor style used by children within the span of this age-group. However, this potential variation did not obscure variation between the three groups, as the ANOVA results were significant.

Though it was the only PC that was found to have a relationship with age, PC1 was not the only PC found to vary significantly between the age groups. PC 6 separated out the middle (Mature Walking) and oldest (Stabilized Gait) groups and appears to be related to the metaphyseal surface. Stamos and Weaver (2020) have indicated that the topographic complexity of the distal metaphyseal surface increases with age (p. 470). To me, this suggests that the PC6 result could be an indicator of similar changes on the proximal surface. My results indicate the proximal metaphyseal surface may exhibit shape change in later childhood, which may be an increase in topographic complexity, as Stamos and Weaver suggested the distal surface experiences. As the groups used in this project are related to locomotor regime, it may be that some of this variation is related to the onset of fully mature bipedal locomotion and the changes in biomechanical loading that occur at this time. While this was not a direct part of the research questions asked in this project, it is unsurprising that locomotor regime would vary alongside shape, given the results of previous research (Stamos & Weaver, 2020; Stark, 2018; Swan et al., 2020).

Plasticity in Response to Biomechanical Loading

My second research question was answered by assessing the relationship between shape (PC score) and activity (F50J). Three PCs were found to have a significant relationship with J, but they accounted for limited variation (3.1% of total shape variation). After adjusting for family-wise error, only PC8 remained significant (1.3% of total shape variation). The strong negative correlation between PC8 score and J value does indicate that some relationship exists between metaphyseal shape and activity. However, the small percentage of variance explained by this PC suggests that the impact of activity on the shape of the region under study is minor, especially when compared to the large proportion of variation which is related to age.

My findings pertaining to this second research question were unexpected given Stamos and Weaver's (2020) work, which found that the metaphyseal surface responded plastically to changing loading scenarios across growth in multiple primate species, including humans. I believe this disconnect can be explained by the placement of landmarks used in my project. I mainly captured the 2D shape of the metaphyseal region, with limited emphasis being placed on the metaphyseal surface, while Stamos and Weaver capture only the metaphyseal surface but capture its entirety. Essentially, the two studies describe different but overlapping regions. Nonetheless, my conclusion is that the proximal metaphyseal region under study in this project demonstrates limited plasticity. This suggests that the region is fairly developmentally constrained, responding to loading in a more similar fashion to long bone epiphyses than diaphyses. As my landmarking procedures capture the 2D outline of the metaphyseal region, I believe these results may in part be due to the functional role of flaring of the metaphyseal region. The shape of the sides of the metaphyseal region is likely constrained by its role in transferring forces from the proximal epiphysis down to the shaft (Weinstein & Dolan, 2018). Considerable change in the flared shape of this region may increase fracture risk, which could be avoided by constraining the shape of the region.

Limitations and Future Research

Methodological

A key limitation of this study is that I did not calculate measures of error for the landmarking process. According to Hirst, White, and Smith (2018, pp. 283-284), there is no standardized method for calculating and reporting observer error in GM research and there are a variety of thresholds of error which are currently considered acceptable. One of the more popular methods for landmarking-error estimation is to repetitively place landmarks on the same specimen and run a PCA on the resulting configurations to assess intra-observer error is likely to have influenced the results of the study (Hirst, et al., 2018, p. 284). This was not done in this project due to time constraints. However, I suspect that landmarking error is low in this project due to the use of geometrically defined landmarks. Landmarks of this type should, in theory, likely have a decreased degree of error compared to biologically defined landmarks. Instead of visually identifying where points were, as would be done with biological points, I calculated at least an X or Y coordinate for each landmark on each individual using measurement tools built into Meshlab. Using this coordinate, I generated a planar section which defined the area of interest. In most cases, this area was miniscule and required a significant amount of magnification to locate.

This suggests that fixed landmark placement was quite accurate and would be highly repeatable. However, it would be advisable to conduct an error-assessment sub-study to confirm this, which appears to be fairly common practice (Hirst, et al. 2018).

Another area where error was likely introduced was during the production of the body-mass estimations that were used to adjust J. Error in body mass estimations comes from the measurements used in the estimation equations and from the equations themselves (Ruff, 2007). When the necessary measures had not already been calculated in other projects using these samples, measurements were taken off the 3D models. For some individuals in the PH collection, equations which consider the breath of the femoral head were used as this measurement was available from data derived by Libby Cowgill, which may have reduced error. This information was not available for the other individuals as the femoral head epiphyses are not present on the models. In cases where certain measurements could not be taken due to preservation issues approximations were made. When there were no equations for a particular age group it was decided to round down to the nearest age group that does have an established equation. All of these decisions may have introduced error. Finally, Ruff's equations are derived from the Denver growth study. Individuals in small-bodied populations (for example the LSA southern African population) may fall outside the range of the sample used to generate the equations, something which is generally advised against in statistical predictions (2007). However, as no population-specific body-mass estimations are available for use in this project, this was the only option that would allow J to be standardized.

An additional methodological issue I experienced was due to the use of semi-landmarks, which added a significant level of difficulty to the project. While advice on reading fixed landmarks is plentiful, I experienced issues interpreting the movement of my semi-landmarks, for which instruction seems to be lacking. Compared to fixed landmarking, semi-landmarking is newer and seemingly more computationally difficult (Slice, 2007). This decreased my level of confidence in describing shape change, resulting in the fairly general descriptions I give in this paper. This may have been remedied by using GM specific software. MorphoJ is an example that generates more GM specific plots than I could make in R, which may have helped with describing shape changes. However, R was necessary to generate the semi-landmarks, and formatting the outputs so the MorphoJ software could read them ended up being beyond the skills I could acquire in the timeframe I had for this project. More accessible information that guides beginners through semi-landmark analysis would be helpful for future scholars attempting to learn to use this valuable analytical method.

Finally, I suggest that the placement of the landmarks could have been improved to focus more on the area of interest. Using semi-landmarks vastly increased the shape data that could be derived from a difficult-to-landmark region. However, I was not able to capture the region's entire morphology as the landmarks mainly capture shape in two-dimensions and a significant segment of the proximal shaft. I also could not discuss the topography of the metaphyseal surface using these landmarks. This may have produced the differences between my results and that of Stamos and Weaver (2020). If I had been able to capture more of the metaphyseal surface and less of the shaft it is possible, even likely, that I would have found a stronger relationship between shape and activity. I suspect that applying areal landmarking to better capture the topography of the metaphyseal surface would produce a more nuanced view of the relationship of shape to age and activity during growth. As a result, I recommend future research use GM-based methods to approach the metaphyseal surface, with the aim of capturing changes in topography throughout growth. Additionally, there is room to apply this approach to other skeletal elements. Shape variation in the humerus would be particularly interesting to explore with the populations in this study given that at two of the populations (PH and NP) were heavily engaged in marine transportation.

Alternative Sources of Variation

There are a multitude of cultural and climatic factors likely influencing shape that I did not control for or discuss fully in this project. There is limited research on subadult specific activity in the populations under study, with very little archaeological evidence tied specifically to children. There appears to be little information regarding activities in which subadults in these populations engaged and when they began. As a result, I could not firmly integrate this information into the study as would be recommended when working with a biocultural approach to growth. While it would have been very interesting to ask questions about differences in shape which may have resulted from differences in habitual activities associated with subsistence activities, I could not confidently define this variable for each age group in each population. If I had considered this from the beginning of the project, and devised a way to include these variables, this would have introduced many more areas of integration with my secondary subfield. This approach may have provided an opportunity to examine if the same patterns of variation linked to subsistence type that have been seen in adults are visible in children (for examples see Macintosh & Stock, 2019; Stock & Pfeiffer, 2001).

Another source of variation that I did not integrate into the project was shape difference resulting from adaptation to different climates. Two of the populations (Point Hope and Sadlermiut) are cold-adapted, while two (Indian Knoll and LSA southern Africa) are not. Additionally, the four groups would have been exposed to a variety of environmental factors (terrain, resource availability etc.) which extend beyond Allen's and Bergmann's rules.

Environmental differences may produce morphological variation between groups which may already be evident in infancy, childhood, or adolescence.

As a result of what I did not do in this project, I call for research examining if subadults belonging to groups engaged in different subsistence strategies and displaying different climate-based adaptations show the same patterns of variation in shape that have been seen in adults. This would involve examining shape differences between same-age children from marine resource reliant cold-adapted populations (like the NP and PH populations) and terrestrial reliant non-arctic populations (like the LSA and IK populations). It would be interesting to see if the same patterns seen in adults, in terms of robusticity and morphology, are evident in the metaphyseal regions of children and when these patterns begin to develop during ontogeny.

Conclusion

Physical anthropology has long been interested in the development of the skeleton and how it responds to activity. However, shape change in metaphyseal regions throughout ontogeny has been largely understudied, despite these regions playing a key role in growth and development. In response to this, the application of GM and CSG derived data in this project allowed for an in-depth statistical analysis of the effects of activity and age on the shape of the proximal femoral metaphyseal region. Its results suggest that age-related shape change is significant, and that the region displays minimal plasticity in response to activity.

While these findings were interesting, there is much work to be done to understand how activity and age impact shape variation in this region of the femur. Particularly work focused on how the proximal metaphyseal surface responds to activity and how metaphyseal shape may vary in response to cultural and climatic variables is needed. Applying a biocultural approach to growth necessitates viewing the skeleton as an amalgamation of cultural, environmental, and biological facts (Zuckerman & Armelagos, 2011). The shape of metaphyseal regions, and bones in general, is likely the sum of a multitude of factors and their complex interactions. In accordance with this, variables from all these categories should be considered when approaching questions about ontogeny, variation, and growth. As a result, the relationship of shape to age and activity is likely very complex. Additionally, in this paper I attempted to address how, with important changes in the disciplines of biological anthropology and bioarchaeology surrounding repatriation and transparency, it is vital to consider how collections like those used in this project came to be available and why they are still in use. Addressing these issues helps to remove some of the historic silences in these disciplines. In conclusion, while this project did not fully answer its questions surrounding development and plasticity of the proximal femoral metaphyseal region, it did produce potential new avenues of research and served as an opportunity for me to apply methodologies which I would not have had a chance to learn otherwise.

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References

Alqahtani, S., Hector, M., & Liversidge, H. (2010). The London Atlas of Human Tooth Development and Eruption. *American Journal of Physical Anthropology*, *142*, 481–490. https://doi.org/10.1002/ajpa.21258

Auerbach, B. M. (2008). *Human skeletal variation in the New World during the Holocene: Effects of climate and subsistence across geography and time - Part I* [Doctoral dissertation., The Johns Hopkins University]. In *ProQuest Dissertations and Theses*. https://search.proquest.com/docview/304614898/abstract/CF1F9356D9DC4BE2PQ/1

Beauchesne, P., & Agarwal, S. C. (2018). The Bioarchaeology of childhood. In P. Beauchesne, S. C. Agarwal, & C. S. Larsen (Eds.), *Children and childhood in bioarchaeology* (pp. 1–24). Gainesville: University Press of Florida.

Büchler, L., Tannast, M., Siebenrock, K. A., & Schwab, J. M. (2018). Biomechanics of the hip. In K. A. Egol & P. Leucht (Eds.), *Proximal Femur Fractures* (pp. 9–15). Springer International Publishing. https://doi.org/10.1007/978-3-319-64904-7_2

Buikstra, J. E., & Ubelaker, D. H. (1994). *Standards for data collection from human skeletal remains*. Fayetteville, Arkansas: Arkansas Archaeological Survey Report Number 44.

Bardua, C., Felice, R. N., Watanabe, A., Fabre, A.-C., & Goswami, A. (2019). A practical guide to sliding and surface semilandmarks in morphometric analyses. *Integrative Organismal Biology*, *1*(1), obz016. https://doi.org/10.1093/iob/obz016

Cameron, M. E., & Stock, J. (2018). Biomechanics, habitual activity, and resilience among southern African hunter-gatherers and herders. In D. Temple & C. Stojanowski (Eds.), *Hunter-gatherer adaptation and resilience: A bioarchaeological perspective* (pp. 110–140). Cambridge: Cambridge University Press.

Chen, J.-H., Liu, C., You, L., & Simmons, C. A. (2010). Boning up on Wolff's Law: Mechanical regulation of the cells that make and maintain bone. *Journal of Biomechanics*, *43*(1), 108–118. https://doi.org/10.1016/j.jbiomech.2009.09.016

Cowgill, L. W. (2010). The ontogeny of Holocene and Late Pleistocene human postcranial strength. *American Journal of Physical Anthropology, 141*(1), 16–37. https://doi.org/10.1002/ajpa.21107

Cowgill, L. W. (2014). Postcranial growth and development of immature skeletons from Point Hope, Alaska. In C. E. Hilton, B. M. Auerbach, & L. W. Cowgill (Eds.), *The foragers of Point Hope* (pp. 212–232). Cambridge University Press. https://doi.org/10.1017/CBO9781139136785.014

Dabbs, G. R. (2011). Health status among prehistoric Eskimos from Point Hope, Alaska. *American Journal of Physical Anthropology*, *146*(1), 94–103. https://doi.org/10.1002/ajpa.21556

Davies, T., Shaw, C., & Stock, J. (2012). A test of a new method and software for the rapid estimation of cross-sectional geometric properties of long bone diaphyses from 3D laser surface scans. *Archaeological and Anthropological Sciences*, *4*(1), 277–290. https://doi.org/10.1007/s12520-012-0101-8

de la Cova, C. (2019). Marginalized bodies and the construction of the Robert J. Terry anatomical skeletal collection. In *Bioarchaeology of Marginalized People* (pp. 133–155). Elsevier. https://doi.org/10.1016/B978-0-12-815224-9.00007-5

d'Heurle, A., McCarthy, J., Klimaski, D. & Stringer, K. (2018). Proximal femoral growth modification: : Effect of screw, plate, and drill on asymmetric growth of the hip. *Journal of Pediatric Orthopaedics, 38*(2), 100–104. doi: 10.1097/BPO.0000000000000771.

Doershuk, L. J., Saers, J. P. P., Shaw, C. N., Jashashvili, T., Carlson, K. J., Stock, J. T., & Ryan, T. M. (2019). Complex variation of trabecular bone structure in the proximal humerus and femur of five modern human populations. *American Journal of Physical Anthropology*, *168*(1), 104–118. https://doi.org/10.1002/ajpa.23725

Frost, H. M. (2003). Bone's mechanostat: A 2003 update. *The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology*, *275A*(2), 1081–1101. https://doi.org/10.1002/ar.a.10119

Gosman, J. H., Hubbell, Z. R., Shaw, C. N., & Ryan, T. M. (2013). Development of cortical bone geometry in the human femoral and tibial diaphysis: Developmental cortical bone. *The Anatomical Record, 296*(5), 774–787. https://doi.org/10.1002/ar.22688

Hart, N., Nimphius, S., Rantalainen, T., Ireland, A., Siafarikas A., & Newton, R. U. (2017). Mechanical basis of bone strength: Influence of bone material, bone structure and muscle action. *Journal of Musculoskeletal & Neuronal Interactions*, *17*(3), 114–139.

Hayes, M, G., Coltrain, J, B., & O'Rourke, D, H. (2005). Molecular archaeology of the Dorset, Thule and Sadlermiut. In P.D. Sutherland (Ed.), *Contributions to the study of the Dorset Palaeo-Eskimo*. Mercury Series, Archaeology Paper 167. Canadian Museum of Civilization, Gatineau.

Herrmann, N. P. (2002). *Biological Affinities of Archaic Period Populations from West-Central Kentucky and Tennessee* [Doctoral dissertation, University of Tennessee, Knoxville]. University of Tennessee – Knoxville, Tennessee Research and Creative Exchange.

Hilton, C. E., Auerbach, B. M., & Cowgill, L. W. (2014). Introduction: Humans on the edge of the Alaskan Arctic. In C. E. Hilton, B. M. Auerbach, & L. W. Cowgill (Eds.), *The foragers* *of Point Hope* (pp. 1–8). Cambridge University Press. https://doi.org/10.1017/CBO9781139136785.004

Hirst, C. S., White, S., & Smith, S. E. (2018). Standardisation in 3D Geometric Morphometrics: Ethics, ownership, and methods. *Archaeologies*, *14*(2), 272–298. https://doi.org/10.1007/s11759-018-9349-7

Holland, E. J. (2007). *Ethnographic data to understand Sadlermiut childhood* [Master's thesis, University of Manitoba]. University of Manitoba.

Holliday, T. W., & Hilton, C. E. (2010). Body proportions of circumpolar peoples as evidenced from skeletal data: Ipiutak and Tigara (Point Hope) versus Kodiak Island Inuit. *American Journal of Physical Anthropology*, *142*(2), 287–302. https://doi.org/10.1002/ajpa.21226

Johnston, F. E. (1962). Growth of the long bones of infants and young children at Indian Knoll. *American Journal of Physical Anthropology*, *20*(3), 249–254. https://doi.org/10.1002/ajpa.1330200309

Justice, L., & Temple, D. (2018). Bioarchaeological evidence for cultural resilience at Point Hope, Alaska: Persistence and memory in the ontology of personhood in northern hunter-gatherers. In D. Temple & C. Stojanowski (Eds.), *Hunter-gatherer adaptation and resilience: A bioarchaeological perspective* (pp. 253–273). Cambridge: Cambridge University Press.

Kandzierski, G., Matuszewski, Ł., & Wójcik, A. (2012). Shape of growth plate of proximal femur in children and its significance in the aetiology of slipped capital femoral epiphysis. *International Orthopaedics*, *36*(12), 2513–2520. https://doi.org/10.1007/s00264-012-1699-y

Kelly, R. L. (2013). *The Lifeways of hunter-gatherers: The foraging spectrum*. Cambridge University Press.

Klingenberg, C. P. (2013). Visualizations in geometric morphometrics: How to read and how to make graphs showing shape changes. *Hystrix, the Italian Journal of Mammalogy*, *24*(1). https://doi.org/10.4404/hystrix-24.1-7691

Klingenberg, C. (2012a). *Chapter 2 – Data Types and Data Acquisition* [Lecture Notes]. Analysis of Organismal Form, University of Manchester.

Klingenberg, C. (2012b). *Chapter 7 – Principal Components: Exploring the Geometry of Multidimensional Morphospaces* [Lecture Notes]. Analysis of Organismal Form, University of Manchester.

Kurki, H. K., & Harrington, L. A. 2017. A 3D geometric morphometric study of the illium during growth and the influence of habitual activity in the Later Stone Age Foragers of Southern Africa. Paper presented at: APAA 2017.

Laurent, M., Antonio, L., Sinnesael, M., Dubois, V., Gielen, E., Classens, F., & Vanderschueren, D. (2014). Androgens and estrogens in skeletal sexual dimorphism. *Asian Journal of Andrology*, *16*(2), 213–222. https://doi.org/10.4103/1008-682X.122356

Liebmann M. (2008). Postcolonial cultural affiliation: essentialism, hybridity, and NAGPRA. In M. Liebmann & U. Z. Rizvi (Eds.), *Archaeology and the Postcolonial Critique* (pp. 73–90). Lanham, MD: AltaMira Press.

Lewis, M. E. (2018). Children in bioarchaeology: Methods and interpretations. In M. A. Katzenberg & A. L. Grauer (Eds.), *Biological Anthropology of the Human Skeleton* (pp. 117–144). John Wiley & Sons, Inc. https://doi.org/10.1002/9781119151647.ch4

Macintosh, A. A., Pinhasi, R., & Stock, J. T. (2017). Prehistoric women's manual labor exceeded that of athletes through the first 5500 years of farming in Central Europe. *Science Advances*, *3*(11), 1–13. https://doi.org/10.1126/sciadv.aao3893

Macintosh, A. A., & Stock, J. T. (2019). Intensive terrestrial or marine locomotor strategies are associated with inter- and intra-limb bone functional adaptation in living female athletes. *American Journal of Physical Anthropology*, *168*(3), 566–581.

Martini, F. H., Tallitsch, R. B., & Nath, J. L. (2018). *Human anatomy* (9th ed.). NY, NY: Pearson.

Merbs, C. F. (2018). The discovery and rapid demise of the Sadlermiut. In C. M. Stojanowski & D. H. Temple (Eds.), *Hunter-Gatherer Adaptation and Resilience: A Bioarchaeological Perspective* (pp. 302–327). Cambridge: Cambridge University Press.

Meyers, J. L. (2018). *The relationship between proximal long bone shape and activity among four hunter-gatherer populations* [Master's thesis, University of Victoria]. University of Victoria Electronic Thesis and Dissertations.

Nadell, J. A., & Shaw, C. N. (2016). Phenotypic plasticity and constraint along the upper and lower limb diaphyses of *Homo sapiens*: Plasticity and constraint along limbs. *American Journal of Physical Anthropology*, *159*(3), 410–422. https://doi.org/10.1002/ajpa.22889

Nash, S. E., & Colwell, C. (2020). NAGPRA at 30: The Effects of Repatriation. *Annual Review of Anthropology*, *49*(1), 225–239. https://doi.org/10.1146/annurev-anthro-010220-075435

Osipov, B., Temple, D., Cowgill, L., Harrington, L., Bazaliiskii, V. I., & Weber, A. W. (2016). Evidence for genetic and behavioral adaptations in the ontogeny of prehistoric hunter-gatherer limb robusticity. *Quaternary International, 405*(B), 134-146. https://doi.org/10.1016/j.quaint.2015.09.093

Pfeiffer, S., & Harrington, L. (2018). Regional continuity and local challenges to resilience among Holocene hunter-gatherers of the Greater Cape Floristic Region, South Africa. In C. M. Stojanowski & D. H. Temple (Eds.), *Hunter-Gatherer Adaptation and Resilience: A Bioarchaeological Perspective* (pp. 26–46). Cambridge: Cambridge University Press. https://doi.org/10.1017/9781316941256.002

Ruff, C. (2007). Body size prediction from juvenile skeletal remains. *American Journal of Physical Anthropology*, *133*(1), 698–716. https://doi.org/10.1002/ajpa.20568

Ruff, C. B. (2000). Body size, body shape, and long bone strength in modern humans. *Journal of Human Evolution*, *38*(2), 269–290. https://doi.org/10.1006/jhev.1999.0322

Ruff, C. B., Trinkaus, E., Walker, A., & Larsen, C. S. (1993). Postcranial robusticity in Homo. I: Temporal trends and mechanical interpretation. *American Journal of Physical Anthropology*, *91*(1), 21–53. https://doi.org/10.1002/ajpa.1330910103

Schlager, S., Jeggeris, G., & Ian, D. (2020). *Morpho: Calculations and Visualisations Related to Geometric Morphometrics. R package version 2.8.* https://cran.r-project.org/web/packages/Morpho/index.html Schlager, S., Jeggeris, G., and Ian, D. 2020.

Slice, D. E. (2007). Geometric morphometrics. *Annual Review of Anthropology*, *36*(1), 261–281. https://doi.org/10.1146/annurev.anthro.34.081804.120613

Stamos, P. A., & Weaver, T. D. (2020). Ontogeny of the distal femoral metaphyseal surface and its relationship to locomotor behavior in hominoids. *American Journal of Physical Anthropology*, *172*(3), 462–474. https://doi.org/10.1002/ajpa.24036

Stark, S. Y. (2018). *The shape of childhood: A morphometric growth study of the Anglo-Saxon to post-medieval period* [Doctoral dissertation, University of Southampton]. University of Southampton Institutional Repository. http://eprints.soton.ac.uk/id/eprint/422263.

Stock, J., & Pfeiffer, S. (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*, *115*(4), 337–348. https://doi.org/10.1002/ajpa.1090

Stock, J. T., & Pfeiffer, S. K. (2004). Long bone robusticity and subsistence behaviour among Later Stone Age foragers of the forest and fynbos biomes of South Africa. *Journal of Archaeological Science*, *31*(7), 999–1013. https://doi.org/10.1016/j.jas.2003.12.012

Swan, K. R., Ives, R., Wilson, L. A. B., & Humphrey, L. T. (2020). Ontogenetic changes in femoral cross-sectional geometry during childhood locomotor development. *American Journal of Physical Anthropology*, *173*(1), 80–95. https://doi.org/10.1002/ajpa.24080

Tardieu, C. (2010). Development of the human hind limb and its importance for the evolution of bipedalism. *Evolutionary Anthropology: Issues, News, and Reviews*, *19*(5), 174–186. https://doi.org/10.1002/evan.20276

Tardieu, C., & Trinkaus, E. (1994). Early ontogeny of the human femoral bicondylar angle. *American Journal of Physical Anthropology*, *95*(2), 183–195. https://doi.org/10.1002/ajpa.1330950206

Trigger, B. G. (1984). Alternative archaeologies: Nationalist, colonialist, imperialist. *Man*, *19*(3), 355–370. https://doi.org/10.2307/2802176

Trouillot, M. (1995). *Silencing the past: Power and the production of history*. Beacon Press.

Watkins, R. (2018). Anatomical collections as the anthropological other: Some considerations. In P. K. Stone (Ed.), *Bioarchaeological analyses and bodies: New ways of knowing anatomical and archaeological skeletal collections* (pp. 27–47). Springer International Publishing. https://doi.org/10.1007/978-3-319-71114-0_3

Weinstein, S. L., & Dolan, L. A. (2018). Proximal femoral growth disturbance in developmental dysplasia of the hip: What do we know? *Journal of Children's Orthopaedics*, *12*(4), 331–341. https://doi.org/10.1302/1863-2548.12.180070

Zelditch, M., Swiderski, D., & Sheets, H. D. (2012). *Geometric morphometrics for biologists: A primer* (2nd ed.). Elsevier/Academic Press.

Zuckerman, M. K., & Armelagos, G. J. (2011). The origins of biocultural dimensions in bioarchaeology. In S. C. Agarwal & B. A. Glencross (Eds.), *Social bioarchaeology* (pp. 13–43). Wiley-Blackwell. https://doi.org/10.1002/9781444390537.ch2

Appendix A: Polar Second Moment of Area (J) Values

Reporting standardized activity values (standardized residuals from regression of log(F50J) on log(bodymass * femur length^2), Imax, Imin, and F50J.

Individual	Standardized residuals	Imax	Imin	F50J
ALB199	-0.45487064	9501.31792	6993.44	16494.76
ALB295	0.29896542	4288.91143	3262.5	7551.413
IK138	-1.97784482	3201.06219	2372.33	5573.388
IK172	-1.44444804	2659.23127	2064.95	4724.186
IK219	-0.84382148	6868.13099	5923.74	12791.88
IK232	-0.87724003	3648.07104	2505.68	6153.753
IK47	-1.34666983	6023.83043	4846.12	10869.95
IK472	-0.84669787	5449.46953	4727.24	10176.71
IK785	-0.75977994	2991.41678	2429.58	5420.996
MMK222	0.83386411	6896.13305	4402.68	11298.81
MMK230	-0.99690782	2053.12438	1837.26	3890.383
MMK238	1.4795944	2909.6593	2448.57	5358.225
MMK246	0.14446244	785.88179	763.465	1549.346
MMK248	2.35905375	7199.05122	6360.57	13559.62
NMB1641	0.06909081	1633.4778	1572.45	3205.929
NMB1642	-0.61447095	1725.45469	1290.12	3015.575
NP151	-0.09459525	6383.48514	4286.21	10669.7
NP198	0.39949689	14145.72377	9158.07	23303.79
NP220	-0.82323453	3839.51866	3058.72	6898.234
NP222	-0.81550838	257.83634	177.569	435.4056
NP223	0.92084291	688.61389	440.409	1129.022
NP231	0.57882216	5705.68766	4021.05	9726.737
NP232	0.11035615	3145.77574	2067.41	5213.181
NP238	0.66451078	3259.88589	2336	5595.891
NP278	-2.69946001	141.61735	101.028	242.6451
NP301	-1.08657135	6024.67677	4231.35	10256.03
NP76	0.71664242	4876.9044	3598.26	8475.167
NP77	1.05908251	782.82271	572.208	1355.03
NP78	0.71609853	2606.7641	1853.53	4460.292
PH304	0.74940429	17917.11974	11103.8	29020.94
PH321	1.44105056	23654.79614	17914.3	41569.14
PH342	0.41941386	5612.40715	5053.1	10665.51
PH343	0.56345061	6941.65085	4731.73	11673.38
PH344	0.81007046	8250.46332	6875.51	15125.97
PH361	0.31515998	15857.18347	10909.1	26766.3
PH419	0.69884414	5442.03333	4914.83	10356.86
PH88	-0.15120191	13654.85768	9865.4	23520.26
UCT346	0.76610439	1343.09756	1180.44	2523.541
UCT437	-0.41214202	1246.74305	1025.46	2272.204

Appendix B: Principal Component Scores

Individual	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
ALB199	5.50E-02	-2.56E-02	2.00E-02	-2.98E-02	-7.32E-03	1.70E-02	-2.28E-03	9.85E-03
ALB295	1.04E-01	-7.05E-03	1.69E-02	1.83E-02	1.30E-02	-1.53E-02	1.29E-02	6.76E-03
IK138	1.04E-01	-4.26E-02	1.47E-02	1.83E-02	-3.92E-03	-4.51E-03	-4.36E-03	1.68E-02
IK172	4.78E-02	-4.41E-04	6.10E-03	-1.74E-02	8.97E-04	-1.31E-02	8.18E-03	1.12E-02
IK219	6.80E-02	3.20E-02	-2.70E-02	-5.27E-02	-2.66E-02	7.22E-03	8.51E-03	-8.10E-03
IK232	4.89E-02	-1.88E-02	4.70E-02	-9.65E-03	-1.22E-02	-1.36E-02	8.19E-03	6.02E-03
IK47	1.09E-01	-4.03E-02	-5.03E-02	-9.26E-03	9.82E-03	1.83E-02	6.10E-03	3.92E-03
IK472	6.70E-02	-3.53E-02	7.89E-03	1.18E-02	3.02E-04	-1.52E-03	-6.70E-03	-2.49E-03
IK785	1.69E-02	-4.28E-02	2.40E-02	-1.63E-03	2.13E-03	-2.57E-02	3.27E-03	1.82E-02
MMK222	7.31E-02	-2.31E-02	-2.82E-02	-6.58E-03	2.49E-02	4.96E-03	-2.05E-02	-5.85E-03
MMK230	4.87E-02	3.23E-04	-1.38E-02	-4.40E-03	1.77E-02	2.55E-03	-2.54E-02	1.66E-03
MMK238	1.93E-02	-4.61E-02	1.34E-02	-1.79E-02	5.54E-04	5.39E-04	1.64E-02	-9.41E-03
MMK246	-6.98E-03	-7.54E-02	-1.12E-03	8.38E-05	1.35E-02	9.64E-03	8.89E-03	-1.61E-02
MMK248	5.27E-02	1.64E-03	6.93E-03	-1.31E-02	-3.02E-03	-1.11E-02	-3.21E-02	-6.30E-03
NMB1641	1.25E-02	-3.11E-03	-6.24E-02	-2.07E-02	-1.72E-02	-3.11E-02	1.72E-02	1.83E-02
NMB1642	1.10E-02	6.79E-02	-3.04E-02	-6.57E-04	-6.57E-03	-2.48E-02	-4.68E-03	4.78E-03
NP151	-5.72E-02	4.36E-02	2.96E-02	-1.88E-03	-5.51E-04	-2.52E-02	2.14E-03	-8.29E-04
NP198	4.30E-02	8.90E-02	-4.62E-03	1.02E-02	4.99E-02	1.98E-02	7.19E-03	1.32E-02
NP220	-1.64E-02	8.18E-04	1.64E-02	2.68E-02	-1.23E-04	9.21E-03	1.24E-03	-9.91E-03
NP222	-1.32E-01	1.80E-02	4.08E-02	-4.66E-02	2.48E-02	4.54E-03	7.90E-03	-1.19E-04
NP223	-2.13E-01	-5.05E-02	6.18E-04	-1.19E-03	2.24E-02	-1.84E-03	3.86E-03	-1.55E-03
NP231	-3.11E-02	4.17E-03	1.47E-02	3.16E-02	8.99E-05	-2.73E-03	8.70E-03	-1.01E-02
NP232	-3.01E-02	9.66E-03	-4.43E-02	6.58E-03	-4.59E-03	-6.08E-03	-1.61E-02	-1.09E-02
NP238	-5.38E-02	-4.13E-02	7.45E-04	3.61E-02	-1.30E-02	2.12E-03	1.60E-02	-4.22E-03
NP278	-1.60E-01	6.21E-03	-1.57E-02	1.96E-02	-1.22E-02	1.72E-02	-1.59E-02	3.38E-02
NP301	9.64E-03	1.66E-02	-3.43E-02	1.31E-03	-1.01E-02	1.96E-02	4.29E-04	-1.92E-03
NP76	-9.98E-03	4.55E-02	-1.76E-02	1.81E-02	9.60E-03	-1.94E-02	1.28E-02	-1.78E-02
NP77	-1.38E-01	-6.82E-03	-3.73E-02	-3.54E-02	2.82E-03	-2.80E-03	1.19E-03	1.30E-04
NP78	-8.99E-02	-2.33E-02	-2.03E-02	2.09E-02	-5.98E-03	3.84E-03	-1.33E-02	4.03E-03
PH304	3.35E-03	4.01E-02	1.94E-02	2.24E-02	-5.18E-03	1.34E-03	1.66E-02	-3.98E-03
PH321	1.67E-02	3.47E-02	4.77E-02	1.41E-02	-2.33E-02	1.04E-02	-1.17E-02	-6.87E-03
PH342	1.36E-02	-1.77E-02	-5.41E-03	1.66E-02	-3.55E-03	8.95E-03	-9.60E-03	-1.02E-02
PH343	-3.38E-03	4.24E-03	4.87E-02	-2.79E-02	1.50E-02	-2.25E-02	-1.41E-02	-1.14E-02
PH344	-1.15E-02	1.36E-02	6.12E-02	1.65E-02	-1.32E-02	-8.07E-03	-1.19E-02	4.67E-03
PH361	4.60E-02	1.61E-02	2.81E-03	3.10E-02	3.17E-03	2.90E-02	1.23E-02	7.23E-03
PH419	9.28E-03	4.26E-03	-5.93E-02	1.93E-02	9.30E-03	-2.03E-02	-1.43E-04	-1.06E-02
PH88	4.39E-03	2.23E-02	-8.58E-04	6.66E-03	7.11E-04	1.81E-02	4.30E-03	-1.83E-03
UCT346	-3.79E-02	1.35E-02	-1.10E-02	-4.31E-03	-4.79E-02	1.10E-02	9.35E-04	-9.08E-03
UCT437	8.00E-03	1.59E-02	2.43E-02	-4.52E-02	-3.96E-03	3.43E-02	3.58E-03	-9.74E-04

Individual	PC9	PC10	PC11	PC12	PC13	PC14	PC15	PC16
ALB199	1.25E-02	5.08E-03	4.20E-03	-2.54E-03	-1.15E-02	-2.08E-03	-4.00E-03	-1.44E-03
ALB295	4.34E-03	-1.02E-03	-3.27E-03	-2.85E-03	1.39E-02	2.74E-03	3.55E-04	7.14E-03
IK138	-6.35E-03	-1.16E-02	-4.46E-04	-5.76E-03	-3.85E-03	9.10E-04	4.88E-03	3.83E-03
IK172	1.08E-02	9.57E-03	-2.43E-03	-3.09E-03	7.57E-03	-2.82E-03	1.57E-03	-6.12E-03
IK219	4.94E-03	-9.04E-03	4.68E-03	-5.29E-03	-1.95E-03	-3.33E-03	1.19E-03	7.49E-04
IK232	-3.22E-03	3.41E-04	-6.22E-03	1.08E-02	1.44E-03	-1.02E-02	9.67E-03	9.48E-05
IK47	-7.78E-03	-3.07E-03	7.40E-03	-2.34E-04	1.28E-04	-3.11E-03	2.56E-04	2.38E-03
IK472	2.19E-03	-1.27E-02	-5.62E-04	-9.72E-04	-3.81E-03	6.13E-03	-4.62E-03	-2.89E-03
IK785	-8.43E-03	7.10E-03	-1.75E-05	-1.90E-03	-3.20E-03	2.78E-03	-5.58E-03	-7.43E-03
MMK222	6.90E-03	-5.87E-03	1.45E-03	-5.17E-03	4.12E-03	-4.91E-03	-3.89E-03	4.80E-03
MMK230	4.98E-03	2.92E-02	-1.04E-02	2.28E-03	-2.52E-03	3.04E-03	3.81E-03	6.14E-03
MMK238	-1.14E-02	-2.43E-03	-2.44E-04	1.04E-02	8.58E-04	8.18E-03	6.02E-03	3.21E-03
MMK246	1.54E-02	-4.52E-03	-5.25E-04	2.97E-03	1.62E-03	5.85E-05	2.10E-03	-1.71E-03
MMK248	-1.27E-02	-2.22E-03	4.28E-03	3.76E-04	1.20E-02	-1.96E-04	-3.57E-03	-1.61E-03
NMB1641	-3.34E-03	1.34E-03	-7.65E-05	-2.18E-03	-5.80E-03	2.86E-03	-2.60E-03	-7.66E-04
NMB1642	6.74E-03	4.93E-03	4.86E-03	-3.20E-03	-1.59E-03	-1.06E-03	8.65E-03	1.35E-03
NP151	1.50E-02	-4.87E-03	6.45E-03	5.93E-03	-1.18E-03	8.49E-03	-9.66E-04	7.84E-03
NP198	-6.54E-03	-7.31E-03	-7.92E-03	2.99E-04	-6.37E-03	2.73E-03	-1.39E-03	-2.62E-03
NP220	1.33E-02	-3.58E-03	5.69E-03	-5.19E-03	-9.71E-04	1.74E-03	4.13E-03	-3.06E-03
NP222	2.35E-03	-5.42E-04	9.63E-03	-8.04E-03	2.86E-03	-1.13E-03	4.11E-03	-1.80E-04
NP223	-8.43E-03	-3.22E-04	-2.02E-04	-4.73E-03	-3.58E-03	8.81E-04	6.16E-03	-1.31E-03
NP231	1.27E-02	9.73E-03	-3.08E-03	-1.18E-03	-5.82E-04	-1.36E-03	-6.92E-03	-1.63E-03
NP232	-1.04E-02	1.57E-03	4.82E-03	-2.62E-03	-4.41E-03	1.27E-03	-2.57E-03	-6.27E-04
NP238	-6.54E-03	1.35E-02	9.50E-03	-4.73E-03	2.16E-03	-4.14E-03	-9.46E-03	4.15E-03
NP278	6.38E-03	-6.33E-03	7.50E-03	1.12E-02	7.08E-03	-4.74E-03	-2.07E-03	-5.00E-04
NP301	4.13E-03	-8.42E-03	-5.63E-03	4.80E-03	6.67E-03	9.44E-04	-3.87E-04	-7.86E-03
NP76	-9.36E-03	-2.73E-03	-2.65E-03	-5.28E-03	4.31E-03	-7.43E-03	4.54E-04	1.40E-04
NP77	4.56E-06	-5.57E-03	-1.54E-02	-2.59E-03	1.90E-03	6.58E-04	-6.44E-03	5.68E-03
NP78	-5.13E-03	-3.45E-03	-5.40E-03	-1.18E-03	-2.92E-03	-8.24E-04	6.48E-03	5.24E-03
PH304	-8.66E-03	-2.03E-03	-5.94E-03	8.40E-03	-2.10E-03	-5.05E-06	-6.20E-03	2.64E-03
PH321	-8.38E-03	-5.83E-04	1.13E-02	-1.20E-03	-5.03E-03	2.08E-03	2.60E-03	5.27E-03
PH342	3.27E-03	-7.07E-04	-9.76E-03	1.63E-03	-4.11E-03	1.45E-03	3.78E-03	-5.05E-03
PH343	-1.45E-03	-4.00E-03	-9.39E-04	9.74E-03	-7.49E-03	-1.20E-02	-6.73E-03	-1.60E-03
PH344	-2.24E-04	-6.15E-03	-6.81E-03	-1.05E-02	2.64E-03	6.22E-03	-1.20E-03	-5.85E-03
PH361	3.82E-03	9.21E-04	1.16E-03	-3.18E-04	-3.33E-03	-5.88E-03	-8.18E-04	4.54E-03
PH419	5.19E-03	1.98E-03	1.16E-02	1.12E-02	-1.10E-03	6.13E-03	1.34E-03	-5.59E-03
PH88	-1.16E-02	1.20E-02	4.42E-03	-1.53E-03	2.71E-03	-3.04E-03	5.47E-03	-8.51E-03
UCT346	2.17E-03	2.06E-03	-1.35E-02	-1.85E-03	-1.52E-05	-6.42E-04	9.03E-04	5.15E-04
UCT437	-7.15E-03	9.63E-03	2.37E-03	4.07E-03	5.46E-03	9.59E-03	-4.52E-03	6.61E-04

Individual	PC17	PC18	PC19	PC20	PC21	PC22	PC23	PC24
ALB199	6.92E-03	-4.08E-03	3.71E-03	-4.48E-04	4.54E-03	3.55E-04	1.08E-03	4.43E-03
ALB295	7.32E-03	-2.05E-03	-5.28E-05	-1.54E-03	6.88E-04	-6.58E-04	-4.78E-06	-2.72E-04
IK138	-4.98E-03	3.18E-03	5.06E-03	-1.90E-03	-6.27E-04	-6.09E-03	-1.29E-03	6.83E-04
IK172	-6.68E-03	-2.96E-03	-1.86E-03	-3.12E-03	-3.36E-03	-3.51E-03	-6.12E-05	-2.30E-03
IK219	5.49E-03	7.13E-03	2.25E-03	6.54E-03	-4.07E-03	-1.36E-03	2.93E-03	-2.62E-03
IK232	1.22E-03	2.07E-03	6.38E-04	-9.76E-05	-4.64E-03	2.46E-03	-3.45E-04	1.36E-03
IK47	1.55E-03	-8.13E-03	-3.99E-03	-9.51E-04	-1.71E-03	-2.30E-03	-3.68E-03	-2.28E-04
IK472	-6.23E-03	-2.09E-04	1.63E-03	3.93E-04	-6.72E-04	2.07E-03	-3.82E-03	-1.39E-03
IK785	-1.69E-04	6.28E-04	1.81E-03	4.88E-03	-2.14E-03	4.33E-03	-9.48E-04	-1.57E-03
MMK222	1.56E-03	-2.96E-03	-3.45E-03	1.67E-03	-2.68E-03	3.65E-03	2.40E-03	1.79E-03
MMK230	1.02E-03	4.14E-03	1.75E-03	1.35E-03	-1.25E-03	3.19E-03	-1.49E-03	-6.96E-04
MMK238	3.65E-03	-1.74E-03	-2.89E-04	2.45E-03	3.00E-03	7.19E-04	-4.62E-04	-2.59E-03
MMK246	-4.48E-03	2.77E-03	6.65E-04	-1.29E-03	2.89E-03	5.77E-05	4.32E-03	-2.59E-04
MMK248	-1.25E-03	4.95E-04	6.84E-03	6.35E-04	5.42E-03	7.63E-05	4.19E-03	-9.05E-04
NMB1641	-1.74E-03	9.79E-04	-1.25E-03	-3.22E-03	3.21E-03	4.23E-03	2.29E-03	1.56E-03
NMB1642	-6.90E-03	-2.52E-03	-2.90E-03	4.57E-03	6.59E-03	-2.98E-03	-8.81E-04	-1.03E-03
NP151	7.60E-04	-5.00E-03	-3.02E-03	3.71E-03	-3.25E-03	5.91E-05	1.21E-03	2.52E-04
NP198	1.78E-03	1.19E-03	1.93E-03	-1.41E-03	-9.99E-04	-1.29E-03	3.75E-03	-4.60E-03
NP220	4.33E-04	1.93E-03	3.82E-04	1.46E-03	5.64E-03	3.47E-03	-3.73E-03	-3.03E-03
NP222	-5.20E-03	3.52E-04	2.86E-03	-4.85E-03	-3.02E-03	2.04E-03	7.01E-04	2.88E-03
NP223	3.88E-03	-1.73E-03	9.66E-04	4.28E-03	-1.01E-03	-1.02E-03	-2.21E-04	-1.33E-03
NP231	-6.53E-04	-3.45E-03	6.61E-03	-4.47E-04	-3.08E-03	-2.31E-03	-3.85E-04	-8.24E-04
NP232	-6.24E-04	-1.56E-03	-1.25E-03	8.58E-04	-6.38E-03	-1.08E-03	-1.37E-03	5.90E-04
NP238	-1.59E-03	3.75E-03	-3.82E-03	1.26E-03	-1.74E-04	-1.74E-03	3.25E-03	-2.91E-03
NP278	2.86E-03	7.90E-04	2.94E-03	2.49E-03	9.27E-05	-1.47E-03	-1.55E-03	-6.57E-05
NP301	-4.32E-03	-1.45E-03	-2.90E-03	8.19E-04	-2.20E-03	6.61E-03	-8.44E-04	-6.05E-04
NP76	9.75E-04	3.07E-03	3.89E-03	2.44E-03	8.75E-04	1.30E-03	-4.91E-03	4.34E-03
NP77	1.69E-03	-7.57E-04	1.38E-03	-3.42E-03	3.74E-03	-7.76E-04	-3.60E-03	-4.10E-04
NP78	-4.20E-03	2.28E-03	-4.74E-03	-2.97E-03	-1.26E-04	1.39E-03	4.52E-03	8.85E-04
PH304	-4.52E-03	-3.55E-03	1.65E-03	2.17E-03	1.35E-03	7.43E-04	3.59E-03	4.32E-03
PH321	-6.95E-04	-3.46E-03	2.60E-03	-5.72E-03	-1.58E-03	3.74E-03	-9.14E-04	-1.83E-03
PH342	-1.62E-03	-2.68E-03	9.55E-05	4.81E-03	-8.41E-04	-5.04E-03	1.47E-03	3.95E-03
PH343	-1.01E-04	1.12E-03	-6.31E-03	-2.41E-03	2.84E-03	-2.54E-03	-1.86E-03	-2.94E-03
PH344	7.76E-03	3.57E-03	-8.70E-03	-1.16E-03	-4.22E-05	-1.11E-03	2.27E-04	2.64E-03
PH361	-6.09E-04	5.94E-03	-2.93E-03	1.64E-04	1.86E-03	1.93E-03	-2.15E-03	9.99E-04
PH419	6.05E-03	6.16E-03	9.83E-04	-7.43E-03	-1.51E-03	-2.44E-03	-2.88E-04	2.07E-03
PH88	4.45E-03	-5.56E-03	-1.95E-03	-1.16E-03	3.33E-03	8.24E-05	1.66E-03	2.60E-04
UCT346	2.62E-03	-2.76E-03	1.96E-03	-4.72E-03	-1.04E-03	-1.19E-03	1.11E-04	-3.22E-03
UCT437	-5.43E-03	5.05E-03	-3.20E-03	1.32E-03	3.41E-04	-3.63E-03	-2.89E-03	2.59E-03

Individual	**PC25**	**PC26**	**PC27**	**PC28**	**PC29**	**PC30**	**PC31**	**PC32**
ALB199	2.61E-03	4.28E-04	3.21E-04	6.77E-04	-2.54E-03	-1.11E-04	3.42E-03	1.90E-04
ALB295	-1.24E-03	4.12E-03	2.05E-03	3.21E-03	-1.16E-03	-2.22E-03	-6.27E-04	1.42E-03
IK138	-7.18E-04	-3.68E-03	-4.75E-04	2.57E-03	-1.87E-03	3.03E-03	-1.44E-03	6.49E-05
IK172	-2.75E-03	-8.06E-04	-2.16E-03	1.14E-03	5.13E-04	-7.20E-04	4.40E-03	-2.54E-03
IK219	-1.37E-03	5.42E-04	-5.51E-05	2.31E-03	1.28E-03	-5.33E-04	-2.01E-04	4.04E-04
IK232	3.72E-03	-7.99E-04	1.90E-03	-3.94E-03	5.35E-04	2.31E-04	-7.91E-05	-9.39E-05
IK47	6.26E-04	2.65E-03	1.88E-03	-2.76E-03	1.75E-03	4.61E-04	-5.16E-04	1.20E-03
IK472	4.20E-03	1.29E-03	-9.74E-04	1.86E-03	2.72E-03	-3.70E-04	-5.00E-04	-2.98E-04
IK785	-3.61E-03	-3.29E-04	2.18E-03	-1.04E-03	1.57E-03	4.40E-04	9.84E-04	2.57E-03
MMK222	-3.21E-03	-4.15E-03	-1.69E-03	-2.51E-03	7.50E-04	1.21E-03	-9.60E-04	-1.88E-03
MMK230	-3.64E-04	4.87E-04	-1.23E-03	1.75E-03	-9.99E-05	4.07E-04	-1.36E-03	3.39E-04
MMK238	6.30E-04	-8.98E-04	-3.24E-03	6.52E-05	-2.09E-03	-1.45E-03	2.74E-04	-2.86E-03
MMK246	-2.13E-04	1.17E-03	-4.84E-03	-1.33E-03	1.45E-03	-3.09E-04	-9.76E-05	3.50E-03
MMK248	3.18E-03	1.57E-04	2.50E-03	-9.89E-04	1.07E-03	-3.27E-04	8.61E-04	-1.17E-03
NMB1641	-3.75E-04	2.08E-03	-2.03E-03	-1.27E-03	-1.05E-03	-5.34E-06	-3.05E-03	-1.93E-03
NMB1642	1.82E-03	-1.74E-03	2.47E-04	-1.68E-03	6.10E-04	-2.42E-03	-4.73E-04	1.74E-03
NP151	2.42E-03	-1.22E-03	6.23E-04	5.09E-04	3.73E-05	3.89E-03	7.23E-04	3.89E-04
NP198	1.03E-03	7.57E-04	-3.17E-04	-2.86E-03	-1.38E-03	4.01E-04	6.65E-04	2.06E-04
NP220	-3.74E-03	2.83E-03	3.37E-03	-1.50E-03	-2.39E-04	2.57E-03	1.01E-04	-2.29E-03
NP222	3.28E-04	1.31E-03	2.32E-03	7.82E-04	-5.37E-04	-9.19E-04	-2.74E-03	-3.73E-04
NP223	1.31E-04	-1.66E-03	5.75E-04	1.06E-03	1.55E-03	-1.21E-03	6.82E-04	-5.75E-04
NP231	3.66E-03	4.88E-04	-9.99E-04	-1.21E-03	2.40E-04	-5.78E-04	-2.01E-03	-1.05E-03
NP232	1.97E-03	3.33E-03	-1.49E-03	1.51E-03	-3.86E-04	-1.59E-03	8.08E-04	-6.14E-04
NP238	1.42E-03	-1.99E-03	1.54E-03	-1.05E-03	-3.44E-03	3.49E-04	-1.73E-04	2.95E-04
NP278	-1.69E-03	1.87E-03	-3.25E-03	-2.92E-04	-2.74E-04	-2.45E-04	-9.83E-04	-9.58E-05
NP301	1.88E-03	-2.77E-03	1.77E-03	2.85E-03	-4.61E-03	-4.81E-04	-5.62E-05	1.26E-03
NP76	-2.15E-04	1.46E-03	-3.76E-03	-9.75E-04	-1.99E-03	2.06E-03	2.23E-03	7.04E-04
NP77	-1.98E-04	-4.14E-03	1.60E-03	-2.42E-04	4.82E-04	-6.44E-04	8.90E-04	1.07E-03
NP78	8.33E-04	4.25E-03	1.52E-03	1.09E-03	1.05E-04	1.52E-03	3.19E-03	9.76E-05
PH304	-4.14E-03	-1.79E-05	6.99E-04	2.19E-03	3.41E-03	-4.47E-04	9.41E-05	-5.15E-04
PH321	-4.03E-03	-1.91E-03	-2.23E-03	-1.43E-03	-1.09E-03	-2.81E-03	8.16E-04	1.59E-03
PH342	-3.46E-03	5.46E-04	3.00E-03	-1.32E-03	-2.90E-03	-2.08E-03	-1.67E-03	-4.82E-04
PH343	-1.55E-03	1.66E-03	2.57E-05	2.48E-03	-1.24E-03	2.15E-04	-1.43E-03	7.78E-05
PH344	1.52E-03	-6.36E-04	-2.40E-03	-1.61E-03	9.38E-04	-1.22E-03	-7.51E-04	-3.87E-06
PH361	2.22E-03	-2.21E-03	1.35E-03	1.58E-03	3.22E-03	-2.63E-03	4.81E-04	-1.55E-03
PH419	-1.15E-03	-2.65E-03	2.61E-03	-6.26E-05	1.15E-03	-1.88E-04	8.15E-04	1.48E-04
PH88	1.10E-03	-1.94E-03	-1.74E-03	3.81E-03	1.82E-03	3.28E-03	-1.81E-03	7.45E-04
UCT346	-7.50E-04	9.51E-04	8.14E-04	-1.31E-03	1.64E-03	1.95E-03	-8.22E-04	2.88E-05
UCT437	-5.46E-04	1.17E-03	-1.41E-05	-2.07E-03	7.47E-05	1.50E-03	3.20E-04	2.59E-04

Individual	PC33	PC34	PC35	PC36	PC37	PC38
ALB199	-3.75E-04	8.99E-05	8.69E-05	-4.81E-04	-1.90E-04	8.59E-04
ALB295	2.90E-04	1.88E-03	-1.46E-04	2.03E-05	-1.73E-04	6.28E-04
IK138	1.36E-03	-7.28E-04	-6.05E-05	-4.67E-05	8.20E-05	6.13E-04
IK172	-6.18E-04	-4.06E-04	2.20E-04	7.36E-04	-1.69E-04	-3.22E-04
IK219	-4.42E-04	-1.59E-04	6.29E-04	1.42E-04	1.16E-03	-5.84E-04
IK232	-5.64E-04	8.73E-04	-5.76E-04	1.15E-03	8.56E-04	9.87E-04
IK47	-5.79E-05	-2.50E-03	1.45E-03	2.60E-04	1.65E-04	-6.60E-04
IK472	-3.89E-03	1.73E-03	4.26E-04	-1.82E-04	-5.13E-05	-7.20E-05
IK785	1.19E-03	-9.32E-06	-1.39E-03	-1.42E-03	-2.03E-04	-8.05E-04
MMK222	5.81E-05	1.66E-03	-2.89E-04	-1.29E-03	9.51E-05	6.74E-04
MMK230	-1.09E-03	-1.68E-03	8.42E-04	4.54E-04	-7.07E-05	6.00E-05
MMK238	-7.04E-05	-1.06E-03	-1.19E-03	-1.81E-03	3.31E-04	-5.37E-04
MMK246	9.27E-04	-6.44E-04	-8.12E-04	9.34E-04	-5.86E-04	2.82E-04
MMK248	8.16E-04	-8.00E-04	4.35E-04	7.83E-04	-7.95E-04	-5.36E-04
NMB1641	7.42E-04	8.39E-04	9.02E-04	1.36E-03	-4.48E-04	-3.23E-04
NMB1642	-1.43E-04	3.47E-04	-1.29E-04	-1.44E-03	3.47E-04	9.37E-04
NP151	3.61E-04	-3.65E-04	-3.16E-04	1.10E-03	-1.12E-03	-1.04E-03
NP198	-5.16E-04	1.83E-04	-3.34E-04	1.43E-04	-2.39E-04	2.78E-04
NP220	3.66E-04	-5.83E-04	-6.47E-04	1.05E-03	1.06E-03	8.98E-04
NP222	-1.07E-03	-1.32E-03	-9.59E-04	-1.16E-03	-4.24E-04	-2.30E-04
NP223	8.32E-04	1.12E-03	2.83E-03	7.76E-04	-1.09E-03	1.05E-03
NP231	2.50E-03	4.05E-04	1.13E-03	-9.77E-04	2.09E-03	-8.19E-04
NP232	1.57E-03	-2.29E-04	-3.14E-03	9.39E-04	1.11E-05	1.64E-03
NP238	-2.43E-03	-3.70E-04	-1.55E-04	2.13E-04	-1.27E-04	4.26E-04
NP278	-8.41E-04	-1.78E-04	-2.70E-04	-2.62E-04	3.10E-06	-7.43E-05
NP301	1.24E-03	-7.82E-04	1.30E-03	-1.78E-04	-7.56E-05	5.20E-04
NP76	-6.42E-04	-1.03E-04	6.30E-04	-4.34E-04	-8.81E-04	-7.28E-04
NP77	-5.20E-04	-1.03E-04	-1.57E-03	1.17E-03	1.62E-03	-5.38E-04
NP78	3.69E-04	7.70E-04	5.26E-04	-1.41E-03	1.55E-03	-1.16E-03
PH304	-7.43E-04	-1.70E-03	6.60E-04	-5.30E-06	7.56E-04	1.51E-03
PH321	8.90E-05	8.87E-04	8.71E-04	9.57E-04	3.19E-04	-6.87E-04
PH342	-1.14E-03	8.21E-04	-7.47E-04	8.64E-04	-7.22E-04	-1.73E-03
PH343	7.04E-04	2.65E-04	6.35E-04	-2.91E-04	-3.03E-04	-1.11E-04
PH344	-1.48E-04	-1.96E-03	5.75E-04	-3.99E-05	4.98E-04	1.34E-04
PH361	1.84E-03	6.34E-05	-1.00E-03	1.61E-04	-1.76E-03	-1.28E-03
PH419	-5.38E-04	1.35E-04	4.17E-04	-7.59E-04	6.43E-05	1.77E-04
PH88	-4.92E-04	1.35E-03	-1.25E-03	6.24E-04	8.09E-04	-7.24E-04
UCT346	-1.55E-04	9.81E-05	-2.96E-04	-1.61E-03	-2.56E-03	7.46E-04
UCT437	1.23E-03	2.16E-03	7.21E-04	-5.05E-05	1.67E-04	5.38E-04

Appendix C: Full Correlation Results – Age/PC Score

Spearman's Rank Correlations applied for PCs 1, 10, 12, 33 and 36 due to non-normal distribution. All other tests Pearson's (Product-Moment) correlations. Adjustment for family-wise error using Holm's method. Significant results bolded.

PC	r	p-value	Holm's p-value
1	0.5619	**0.0002**	**0.0076**
2	0.2432	0.1357	1.00
3	0.1486	0.3667	1.00
4	0.2485	0.1271	1.00
5	0.0155	0.9255	1.00
6	0.1667	0.3104	1.00
7	-0.0898	0.5867	1.00
8	-0.1423	0.3875	1.00
9	-0.0298	0.8569	1.00
10	-0.1601	0.3303	1.00
11	0.2191	0.1802	1.00
12	0.0546	0.7414	1.00
13	-0.1178	0.4752	1.00
14	-0.136	0.4092	1.00
15	-0.1044	0.527	1.00
16	-0.0577	0.727	1.00
17	0.1396	0.3968	1.00
18	-0.1273	0.4398	1.00
19	0.016	0.9229	1.00
20	0.0397	0.8104	1.00
21	-0.0001	0.9993	1.00
22	0.1721	0.2949	1.00
23	0.0458	0.7821	1.00
24	0.0541	0.7436	1.00
25	-0.0997	0.546	1.00
26	-0.1684	0.3054	1.00
27	0.1874	0.2532	1.00
28	0.1212	0.4622	1.00
29	0.0729	0.6592	1.00
30	0.0484	0.7696	1.00
31	0.0393	0.812	1.00
33	0.1253	0.4472	1.00
32	-0.0655	0.6918	1.00
34	-0.0114	0.9452	1.00
35	0.106	0.5207	1.00
36	0.1357	0.4099	1.00
37	0.1359	0.4095	1.00
38	-0.0591	0.7208	1.00

Appendix D: Full Results for ANOVA tests.

For the following tables/graphs, Y or young = Toddling, M or mid = Mature Walking, O or older = Stabilized Gait.

Table D1: Full Normality, Homogeneity of Variance and ANOVA test results. Significant results are bolded.
*: This measure is close to significant. Welch's ANOVA was applied to be conservative. A regular ANOVA returns a p-value >0.001 and a F value of 17.18.
**: Levene's Test of Homogeneity of variance used instead due to non-normal distribution of Mid group
***: Nonparametric Kruskal-Wallis test applied due to non-normal distribution of Mid group
****: Welch's ANOVA applied.

PC	Shapiro-Wilk W	Shapiro-Wilk p-value	Barlett's k-squared	Barlett's p-value	ANOVA results
1	Y: 0.95958 M:0.95791 O: 0.95386	Y: 0.8061 M: 0.5031 O: 0.6935	6.8245	0.05435*	**p: 0.00248** F: 9.0441
2	Y: 0.92936 M: 0.92546 O: 0.92833	Y: 0.5103 M: 0.1262 O: 0.3942	0.95665	0.6198	p: 0.154 F: 1.968
3	Y: 0.96431 M: 0.96783 O: 0.95712	Y: 0.85 M: 0.7086 O: 0.7354	1.2109	0.5458	p: 0.831 F: 0.186
4	Y: 0.93345 M: 0.95218 O: 0.95136	Y: 0.548 M: 0.4015 O: 0.6614	0.67196	0.7146	p: 0.462 F: 0.789
5	Y: 0.90329 M: 0.85194 O: 0.9613	Y: 0.3092 **M: 0.0057** O: 0.7878	0.8803 **	0.4234 **	P: 0.6278 KW^2: 0.93108 ***
6	Y: 0.9455 M: 0.9344 O: 0.96394	Y: 0.6659 M: 0.1875 O: 0.8196	6.4877	**0.03901*******	**p: 0.002499** F: 7.9336

Table D2: PC 1 Post-Hoc Test Results – Tukey Contrasts. Reporting Adjusted P-values.

	Mature Walking	Stabilized Gait
Stabilized Gait	0.5257	-
Toddling	**0.00003**	**0.0001**

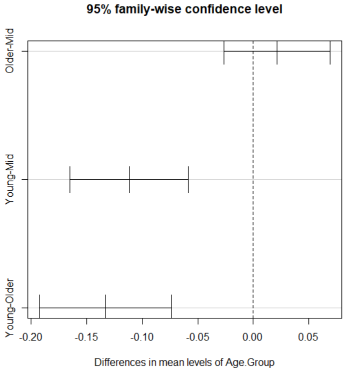

Figure D1: Graph of the 95% confidence interval of the means for PC1 for each age group. Lines that do not cross zero indicate a significant result. Young-Old, and Young-Mid are significant pairings.

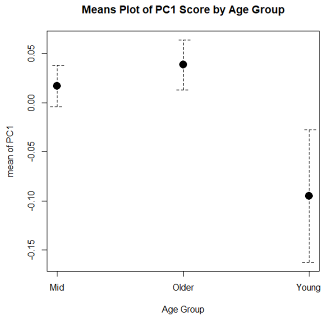

Figure D2: Means plot of PC1 Score by Age Group. The dot represents the means for each age group. The whiskers represent the 95% confidence interval of the means.

Table D3: PC6 Post-Hoc Test Results – Tukey Contrasts. Reporting Adjusted P-values.
*I acknowledge that this is close to being significant.

	Mature Walking	**Stabilized Gait**
Stabilized Gait	**0.001**	-
Toddling	0.0574*	0.614

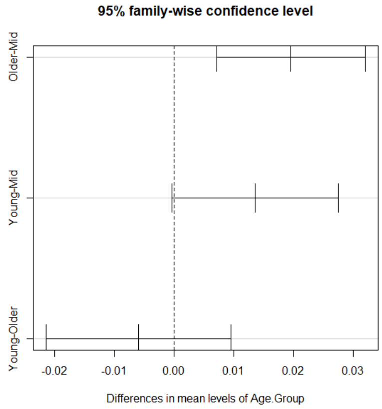

Figure D3: Graph of the 95% confidence interval of the means for PC6 by Group Pairs. Lines that do not cross zero indicate a significant result. Only Old-Mid is a significant pairing. As was noted in Table D3, the pairing of the youngest and mid group is almost significant (p-value = 0.0574).

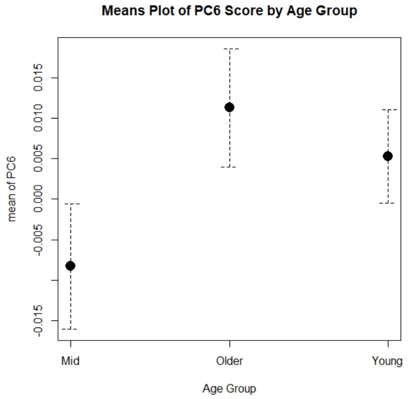

Figure D4: Means plot of PC6 Score by Age Group. The dot represents the means for each age group. The whiskers represent the 95% confidence interval of the means.

Appendix E: Full Correlation Results – Activity/PC score

Spearman's Rank Correlations applied for PCs 10, 12, 33 and 36 due to non-normal distribution. All other tests Pearson's (Product-Moment) correlations. Adjustment for family-wise error using Holm's method. Significant results bolded.

PC	r	p-value	Holm's p-value
Age-Standardized 1	0.1297	0.4314	1.00
2	0.0624	0.7059	1.00
3	0.0757	0.6471	1.00
4	0.098	0.5528	1.00
5	0.0387	0.8153	1.00
6	-0.1427	0.3863	1.00
7	-0.569	0.7309	1.00
8	-0.5586	**0.0002**	**0.0068**
9	-0.3259	**0.0429**	1.00
11	-0.1377	0.4032	1.00
13	0.0156	0.925	1.00
14	0.1166	0.4795	1.00
15	-0.1881	0.7309	1.00
16	0.1671	0.3093	1.00
17	0.2247	0.1691	1.00
18	-0.0428	0.7958	1.00
19	-0.0129	0.9377	1.00
20	-0.1596	0.3318	1.00
21	0.2418	0.138	1.00
22	0.0676	0.6828	1.00
23	0.3259	**0.0429**	1.00
24	0.0071	0.966	1.00
25	0.0404	0.8072	1.00
26	-0.1123	0.4962	1.00
27	0.0218	0.895	1.00
28	-0.1585	0.3351	1.00
29	0.0425	0.7972	1.00
30	-0.2186	0.1813	1.00
31	0.1133	0.4923	1.00
32	-0.1269	0.4413	1.00
34	0.1323	0.4219	1.00
35	0.023	0.8895	1.00
37	-0.0911	0.5812	1.00
38	-0.1309	0.427	1.00

Congratulations on an excellent paper, Isabelle—well-conceptualized, well-written, and clearly explained. While I know that addressing the ethical component was a challenge, I think it was important for you to do so and I think you did a good job of articulating the dilemma. Very well done!

78/80 (98%)