THESIS

BONE MINERAL DENSITY IN HABITUAL CLIMBERS: AN ANALOGUE FOR EARLY HOMININS?

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ABSTRACT

BONE MINERAL DENSITY IN HABITUAL CLIMBERS: AN ANALOGUE FOR EARLY HOMININS?

Functional loading history of limb morphology has given researchers insights into past human locomotor behavior and general physical capabilities, given the assumption that, during life, loads have positive dose-dependent effects on bone structure (Wallace et al., 2012). Identifying if, and then, when during human evolutionary history habitual climbing was an important part of the early hominin locomotor pattern is key to conceptualizing the transition to obligate bipedalism.

Given Wolff's law we can assume that repetitive function has the ability to change the morphology of bone growth (Ruff et al. 2006, Wallace et al. 2012). With this we can expect individuals who practice frequent recreational rock climbing to be more robust at specific muscle attachment locations when compared to individuals who do not rock climb for recreation. It was further predicted that the climbers would possess larger arm musculature and an increased total bone mineral density (BMD), as well as increased BMD of the shoulders when compared to active and non-active individuals.

A sample of 32 individuals, male and female, including rock climbers, active individuals and non-active individuals were asked to participate in a survey and self-assessment of physical activity that included climbing abilities, a push up test, standard body anthropomorphic measurements, and a DEXA scan. As a result, increased average total BMI standardized BMD was found among the practiced rock climbers when compared to the active and non-active

individuals. Additionally, increased average BMI standardized shoulder BMD was found among the rock climbers when compared to the active and non-active individuals. It is the intention that this preliminary research be used as a proxy for how a locomotor behavior effects bone development and shows that in a modern sample population positive relationships between activity and BMD can be found.

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CHAPTER ONE

Introduction

Early hominin locomotor patterns are critical to understanding the transition to obligate bipedalism because locomotor patterns are inferred from bony morphology. Understanding bony morphology and identifying new characteristics related to previously understood morphology, such as bone mineral density in relation to muscle use and function at the shoulder joint, allows researchers a new perspective on functional morphology. This thesis focuses on the modern human shoulder in rock climbers and looks for relationships between climbing behavior and bone mineral density at the deltoid muscle in order to examine the general notion that hominoids retained an arboreal component to their anatomy. Hominoid locomotor patterns vary depending on the morphology of the fossils examined and can reflect on a variety of behaviors including suspension, knuckle-walking, and vertical climbing. Historically there have been two main arguments, with each depicting the transition to obligate bipedalism very differently. The Savannah hypothesis states that bipedalism evolved in a savannah environment, where walking bipedally to acquire resources on the ground was more efficient compared to walking quadrupedally (Potts 1998, Harcourt-Smith 2007, Jolly 1970, Wheeler 1994). This hypothesis usually suggests that the precursor to bipedalism was a knuckle-walking morphology (Crompton et al. 2008, Richmond et al. 2001, Begun et al. 2007). Alternatively, the Mosaic landscape hypothesis[1] argues for the presence of dispersed trees over a varied woodland-like environment, where the development of a bipedal stance and locomotion was dependent on orthograde arboreal behavior and was primarily used as a method of resource acquisition in the trees (Potts

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[1] Mosaic landscape hypothesis is the term I chose to represent this category of hypotheses. In the literature it can also be called the forested/woodland hypothesis or the mosaic woodland hypothesis among others depending on author, see Potts 1998 for a general description of these variations.

1998, Stern and Susman 1983, Stern 2000, McHenry and Berger 1998). This hypothesis relies more on the reconstructions of the paleoenvironment and takes into account the landscape early hominins had to function within, it also implies an arboreal component as part of the locomotor pattern to pre-obligate bipedalism (Potts 1998, Stern and Susman 1983, Stern 2000, McHenry and Berger 1998, Crompton et al. 2008). It is important to note that each hypothesis is dependent on environmental reconstruction, and that environmental reconstruction varies from site to site and between researchers. With increased data accuracy, recent research in paleoenvironmental reconstructions suggests a more diverse paleolandscape. This in turn suggests that the mosaic landscape hypothesis may be the correct theory for the origins of bipedal walking. In conjunction with the partially wooded environment described by the mosaic landscape hypothesis, this thesis argues for the presence of an arboreal component in the early hominin locomotor pattern and fits the same morphologic realities present in early hominins.

Skeletal evidence provides a tool for examining locomotor patterns of the past, which in turn offer support for paleoenvironmental reconstructions that suggest mosaic environments. The primary specimen which demonstrates a distinctive early hominin locomotor patterns was Lucy, or AL288-1, the adult *Australopithecus afarensis* skeleton from Hadar, Ethiopia (Potts 1998, Stern and Susman 1983, Stern 2000, McHenry and Berger 1998). Lucy was distinctive in that she transformed the way locmotor patterns of early hominins were perceived. Her limb proportions are more similar to a modern chimpanzee than to a modern human, her scapular positioning is more superior compared to modern humans, and her phalanges are an intermediate length between modern humans and chimpanzees (Stern and Susman 1983, Lovejoy 1988, Potts 1998, Richmond et al. 2001, Stern 2000, Ward 2013, Larson 2013, Green and Alemseged 2012). These morphologies imply that she relied more on her arms during locomotion than previously thought, if the Savannah hypothesis were correct (Potts 1998, Stern and Susman 1983, Stern 2000, McHenry and Berger 1998). By adding the arboreal component into the early hominin repertoire it is logical to question the type of arboreality, i.e. suspensory, vertical climbing, or hand assisted bipedailty, and to what extent early hominins, including Lucy, relied on it.

Understanding secondary characteristics seen in the fossil record, such as the suspensory shoulder of hominoids, is critical to conceptualizing the transition to bipedalism because it highlights a suite of morphologic traits that were necessary to survival but did not hinder the development of a bipedal hominin (Sylvester 2006). Emphasis is placed on the shoulder girdle because it is actively engaged in all arboreal activities, including suspensory and vertical climbing. In modern humans, rock climbing mimics some of the muscular responses seen in arboreal hominoids and provides a proxy to study the effects that climbing may have on bone remodeling at the shoulder. This study provides an additional way of examining skeletal characteristics in living humans and could provide further insight for inferring relationships between behavior and skeletal morphology.

Effective morphology in a transitional landscape requires a suite of characteristics that are functional in multiple environments. For hominins it is argued that the onset of bipedality should be coupled with a loss of upper body suspensory adaptations (Sylvester 2006), however a general arboreal component to their locomotor behavior does not appear to have been lost (White et al. 2009, Green and Alemdeged 2012, Thrope et al. 2007). Understanding morphologic characteristics through time in the hominin record helps to better illustrate the foundations of evolutionary progression. The background presented here explores the idea of a tree dwelling hominoid ancestor as well as argues that early hominins were likewise a set of tree reliant species, with an emphasis on vertical climbing adaptations of the shoulder.

Identifying whether habitual climbing was an important part of early hominin locomotor patterns is key to conceptualizing the transition to obligate bipedalism, because bipedalism is a primary characteristic in defining what it means to be a human (Sylvester 2006, Richmond et al. 2001, Gebo 1996, Larsen and Repcheck 2008, Conroy 1997). The morphology concerned with bipedalism has been extensively studied (see Harcourt-Smith and Aiello 2004, Robson and Wood 2008, Schmitt 2003, Videan and McGrew 2002, Young et al. 2010, and Washburn 1967 for a few examples); however, factors contributing to how the transition to bipedalism occurred causes further contention between scholars and are beyond the scope of this research. Rather than identifying the timing and location of the emergence of bipedalism in the fossil record, the goal of this research is to identify a secondary set of morphological factors that could represent plesiomorphic characters of an arboreal locomotor strategy. While this strategy is not a defining trait of hominins, it does represent an aspect of a locomotor pattern key to the hominin transition out of the trees and onto a terrestrial landscape. The plesiomorphic traits associated with the shoulder girdle are important to examine in modern humans because they represent a locomotor pattern that was imperative for early hominin survival and that could therefore give us insight into early hominin behavior, especially during the transition into obligate bipedalism (Sylvester 2006, Crompton et al. 2012).

The hominoid shoulder girdle is relatively similar across taxa and represents a joint equipped for suspensory adaptations (Ward 2013, Larson 2013). The shoulder joint is flexible to allow for full abduction of the arm, while being stable enough to prevent dislocation during hanging or swinging (Freeman and Herron 1998, Sylvester 2006). The glenoid fossa is laterally facing with the scapula positioned on the posterior ribcage, a position that enables joint extension. Due to the presence of these characteristics in all hominoids as well as in fossil hominins, namely *Australopithecus afarensis* (Ward 2013, Larson 2013), it is important to examine how bone responds to function in the modern human shoulder in order to infer probable past behavior, and to increase the number of morphological features examined to support the general notion of a locomotor pattern that retained a substantial arboreal component. Here modern human rock climbers are examined as a proxy for early hominin behavior and morphology because both information on shoulder anatomy, as well as behavioral characteristics related to rock climbing are recorded; in turn providing a way to relate form to function in a modern human sample. Understanding the bones, joints, muscle attachments and muscle functions are imperative to interpreting the methods of data collection, because the bony landmarks created by muscle attachments of the shoulder are used as boarders when creating the region of interest for the study.

The only way to truly conceptualize the relationship between morphological form and behavioral function is to observe contemporary modern human behaviors and examine the resulting morphology (Wallace et al. 2012, Sylvester 2006, Green and Alemseged 2012). Animal model based experiments have illustrated that limb loading exercises or activities, such as running, have the potential to promote bone formation and enhance bone structure and strength (Wallace et al. 2012, Biewener and Bertram 1994, Barak et al. 2011). Typically, large muscles have been correlated with a large surface area at the attachment site and can be observed in bones with robust size and shape characteristics that were loaded greatly during life, whereas bones that appear more gracile were not as forcefully loaded (Ruff et al. 2006). Because it is well understood that bone responds to the functional environment (Goodship and Cunningham 2001), it is possible to measure bone density at the attachments sites of muscles engaged during climbing in a modern human sample to create a proxy for bony morphology related to these behaviors in our ancestors.

Using a modern human sample (n=32) and a Dual-Energy X-ray Absorptiometry (DEXA) bone mineral density scanner, this study is interested in finding relationships between frequency in use of the deltoid muscle when rock climbing based on a self-assessment survey and bone mineral density (BMD) at the deltoid attachment site on the humerus. If positive correlations are found, DEXA may be a useful tool when examining functional adaptation in the fossil record.

Hypothesis

This study aims to examine the relationships between the tensions forces seen in suspensory hanging and vertical climbing and bone remodeling, measured in bone mineral density (BMD), at the shoulder. It is assumed that humans today do not participate in routine vertical climbing to the degree that our hominin ancestors did (Green 2012), because food gathering in trees is no longer a component of subsistence strategies among populations in the developed world. Therefore, in modern humans it is not expected that the muscle origins and attachments associated with the upper arm and shoulder muscles would reflect habitual climbing abilities. Habitual climbing is defined as an acquired and routine pattern of behavior based on frequency and duration.

However, given Wolff's[2] law we can assume that repetitive function has the ability to change the trajectory of bone growth (Ruff et al. 2006, Wallace et al. 2012). It is well supported

[2] Wolff's law generally states, "bone adapts to its mechanical environment during life… [and that] … the mechanical load applied to living bone influences the structure of bone tissue" (Ruff et al. 2006:484-485). Wolff's law as a principle of bone deposition is commonly used as evidence supporting that bone morphology is used to examine differences in the mechanical stress placed on bone in past environments, and therefore aids in the identification of past behaviors (Ruff et al. 2006).

that large muscles require large attachment sites on the bone (Sylvester 2006, Green et al. 2012, Wallace et al. 2012, Ruff et al. 2006). It is also well accepted that through increasing activity duration and frequency bone mineral density (BMD) also increases (Sylvester et al. 2006, Wallace et al. 2012, Gosman et al. 2013, Tingart et al. 2003). Therefore the initial expectation is that individuals who practice frequent recreational rock climbing will have increased BMD when compared to both active individuals and non-active individuals. This is expected because of the frequency, intensity and duration that results from rock climbing as an extreme level of activity when compared to other activity types and non-active behavior. Therefore, the initial hypotheses are as follows:

H_{0A}: There is no significant difference in BMI standardized bone mineral density (BMD) among rock climbing, active, and non-active groups, regardless of sex.

H_{1A}: There is a significant difference in BMI standardized bone mineral density (BMD) among rock climbing, active, and non-active groups, regardless of sex.

Secondarily it is predicted that increased arm use and strength is needed in rock climbing due to the continuous shoulder abduction required for the action. It is expected that individuals who practice frequent recreational rock climbing will have an increased bone mineral density at specific muscle attachments located on the proximal humerus that are related to shoulder abduction when compared to individuals who do not climb. This is expected because in modern humans it is assumed that isometrically holding the arms abducted in a hanging or suspensory position requires more shoulder strength than adducting the arms down in a relaxed position. If the initial null hypothesis is rejected then the following secondary hypotheses will be addressed.

H_{0B}: There is no significant difference in BMI standardized shoulder bone mineral density (BMD) among rock climbing, active, and non-active groups, regardless of sex.

H_{1B}: Changes in BMI standardized shoulder bone mineral density (BMD) can be partially attributed to habitual shoulder specific activities in males and females.

The two sets of hypotheses can be thought of as paired hypotheses rather than independent of one another, because it is expected that a change in over all bone mineral density would be accompanied by a change in shoulder region specific bone mineral density. This prediction has previously been seen in various other anatomical regions including the proximal femur, lumbar spine, and phalanges (Nichols et al. 1994, Sylvester et al. 2006).

Chapter Synopses

Chapter two begins by describing the hominoid pattern. Hominoid locomotor patterns associated with the shoulder joint that highlight the similarities in hominoid shoulder anatomy will be discussed. Chapter two reviews the anatomy of the shoulder and upper arm in modern humans; the modern human anatomical survey is restricted to the shoulder girdle and proximal humerus because of the specific morphologies that are being compared in the fossil record. Additionally a brief summation of human biomechanics, bone biological and histological principles, including Wolff's Law, will be provided; this includes the differentiation of bone density and bone robusticity.

Chapter three provides a synopsis of the hominin fossil record, beginning with *Sahelanthropus tchadensis*, and continuing forward in time until *Australopithecus afarensis*. Lastly, Chapter three offers insight into theories surrounding the transition from an arboreal ancestor to a bipedal hominin and specifically focuses on how climbing proficiency was a critical locomotor behavior in the early hominin repertoire.

Chapter four describes the materials and methods that provide the foundation to test the hypotheses, as well as defines the statistical tests and terms used during analysis. Chapter five summarizes the statistical results found on the sample groups bone mineral densities (BMD), and discusses the applicability of the results to implying functional loading mechanisms and behaviors. Chapter six is a discussion of the implications of this research, offering insight into interpretations for functional loading and behavioral morphology in living humans. In turn this research will be applied to potential interpretations on fossil morphology and hence behavioral implications within the fossil record. Lastly, Chapter seven provides a brief conclusion that summarizes of the background research reflected upon during the introduction and discussion. The conclusion also speaks to future research and application of this type of data analysis.

CHAPTER TWO

This chapter provides relevant background information necessary for contextualizing the research project to follow. Chapter two explains the modern hominoid locomotor and shoulder girdle pattern first in order to explain the similarities in anatomy and function across extant taxa and to illuminate that the differences among each member fall on a continuum of traits and reliance on arboreal components. Next, Chapter two contextualizes the research with modern human musculoskeletal anatomy and function first in order to understand the parts that make up the region of interest, the shoulder.

Chapter Two will review modern human shoulder girdle musculoskeletal anatomy and mechanics, as well as bone structure and the differences between bone robusticity and density. Here a modern human anatomical survey of the shoulder will be provided as regional context for the location of interest throughout the study, because shoulder girdle anatomy is important when discussing climbing adaptations in our ancestors. Chapter two is imperative to understanding the modern sample used in the pilot study to follow, where in contrast Chapter three explains the theoretical approach, fossil basis, and functional morphology that led to the project on a whole.

Modern hominoid locomotor patterns

One way to begin to understand patters of selective pressure on locomotor morphology is to examine modern hominoid locomotor patterns and the resulting skeletal modifications that occur as a result of the forces applied to the bones during movement. The superfamily hominoidea includes two major locomotor categories, terrestrial and arboreal, and can be further broken into subcategories. Under a terrestrial locomotor pattern there are several forms of quadrupedal movement including knuckle-walking (chimpanzees and gorilla), palmigrady (orangutans), and plantigrady (most other primates), whereas arboreal locomotion can be divided into brachiation (orangutan, gibbons), arboreal quadrupedalism (chimpanzees), and arboreal bipedalism (gibbons), (Almecija et al. 2007, Richmond et al. 2001, Crompton et al. 2008). Lastly, there is a review of vertical climbing and how the shoulder facilitates climbing actions.

The varying types of locomotion can be understood through kinematics, or the forces and movements that enable locomotion. In both terrestrial and arboreal quadrupedalism, as seen in chimpanzees, large forces from the gluteus maximus, medius and minimus propel the animal's center of mass forward, exerting a caudal force and causing the hindlimb to extend at the hip (Larsen and Repcheck 2008, Videan and McGrew 2002, Fleagle et al. 2013). It is further argued that during quadrupedalism chimpanzee forelimbs function as a steering wheel, and help guide the direction of movement (Fleagle et al. 2013). Furthermore, the chimpanzee utilizes forelimb suspensory adaptations including: highly mobile shoulder joints, shallow rib cages, short spines, full elbow extension, and long arm proportions relative to leg proportions (Fleagle et al. 2013). These adaptations allow for efficient mobility and suspensory hanging in an arboreal setting (Larsen and Repcheck 2008, Reed et al. 2013). This summation of chimpanzee suspensory traits will be used throughout the background as a comparison for hominin shoulder morphology and is of upmost relevance to understanding variation within the shoulder because it highlights suspensory morphology seen in the shoulder.

Secondly, modern gibbons express suspensory traits used for brachiation. Brachiators utilize their suspensory morphology including long arms and phalanges, highly flexible shoulders and elbows, short spines, and shallow torsos, which allow them to efficiently swing below tree branches (Larsen and Repcheck 2008). Additionally, brachiators are commonly associated with above-branch bipedalism, which is a scenario in which they use their arms as supports and balances while walking bipedally through the trees (Thrope et al. 2007a, b, Crompton et al. 2008). This gibbon behavior has recently been used as a model for hominin bipedalism and has been subjected to much debate (Crompton et al. 2007, Crompton and Thorpe 2008, Thorpe et al. 2007a, Crompton et al. 2012, Begun et al. 2009). It is argued here that understanding the various behaviors and resulting morphology of gibbon bipedalism is useful for acquiring a holistic understanding of the functional morphology of hominoids in arboreal settings.

Lastly, vertical climbing among hominoids requires a long reach, and as a result hominoids have forelimbs that are longer than their hindlimbs, flexible and agile joints, and generally have more highly developed flexors, pronators, supinators, and abductor muscles as opposed to extensors (Hildebrand and Goslow 2001). Suspensory locomotion requires a relatively short back, long arms, laterally facing shoulders with the shoulder blades flat against the back, long phalanges, and a broad chest (Conroy 1997, Larsen and Repcheck 2008). This set of characteristics is respectively brought up throughout this thesis as they are defining characteristics of arboreality in general, and are pertinent to interpreting fossil morphology, even though the focus is placed on the modern human shoulder.

More specifically, shoulder morphology can be divided into four main adaptive categories; sitting and lying, quadrupedal, suspensory, and vertical climbing. Sitting and laying behavior is not particularly relevant to this study but it is important to understand that individuals that are sedentary and spend most the their day sitting or lying deliver no loading forces through the shoulder joint and do not require either a highly mobile or stable shoulder joint (Sylvester 2006). Therefore when examining the shoulder joint the absence of stable, mobile, or force produced morphology may suggest an immobile joint. The quadrupedal shoulder possesses a proximally flattened humeral head that is shorter than the greater and lesser tubercles, glenoid fossae that are comparatively large and scapulae that are laterally situated on the thorax (Sylvester 2006). An arboreal and terrestrial quadrupedal shoulder must provide increased stability under pressure forces when locomoting as well as create an effective lever system for the muscles required to locomote on all limbs (Sylvester 2006).

In contrast, and relevant to the current research, are both suspensory and vertical climbing shoulder morphologies. Suspensory shoulder morphology allows the forearm to fully abduct and is characterized by a large highly curved humeral head that rises above the greater and lesser tubercles, a relatively small flat glenoid fossa, and scapulae that are dorsally positioned on the thorax (Sylvester 2006). This suspensory shoulder morphology is generalized, and details about arboreal morphology will be to follow. Lastly, vertical climbing puts the shoulder joint under tension forces, where the deltoid muscle is contracting on the deltoid tuberosity allowing the arm to laterally abduct. Tension forces do not require a highly stable or a highly mobile shoulder joint to the point of full abduction, as in suspensory locomotion (Sylvester 2006). Vertical climbing morphology is more extensive then the tension forces just described. The following sections feature arboreal locomotion and vertical climbing in more detail.

Modern Human Musculoskeletal Anatomy and Mechanics

Here modern human shoulder musculoskeletal anatomy and function is reviewed. The differences between extant apes and human musculoskeletal anatomy will not be discussed past the previous section because this research is not a comparative anatomy study, and is focused solely on modern human shoulder anatomy form and function. However, it is important to acknowledge that all hominoids share the same general shoulder anatomy with minor differences reflecting each group's preference of locomotor pattern.

The shoulder girdle in modern humans consists of the scapula, clavicle, and proximal humerus, where the glenoid fossa of the scapula articulates with the humeral head, and the acromion process of the scapula articulates with the acromial end of the clavicle. The glenoid fossa faces laterally with the subscapular fossa lying flat against the posterior side of the rib cage. The scapular spine protrudes posteriorly and is the originating location for the posterior end of the deltoid muscle as well as the insertion site for the trapezius muscle. The clavicle articulates at the acromion process of the scapula, acting as a support for arm muscle attachments, and is the lateral origin of the deltoid muscle as well as an insertion for the trapezius muscle. *Figure 2.1* shows the articulations and muscle origins and insertions of the shoulder girdle, as discussed. It provides a visual representation and reference for the following discussion of muscles attachments and locations for the rest of the musculoskeletal anatomy section. (All anatomical descriptions were derived from the images presented in *Figure 2.1* and the anatomical atlas where they were referenced, Netter 2010, and are supported by Veeger and van der Helm 2007).

The three posterior rotator cuff muscles are *supraspinatus*, *infraspinatus*, and *teres minor*. All of these muscles originate on the posterior side of the scapula, insert on the greater tubercle of the humerus, and are responsible for laterally rotating the shoulder by way of rotating the humeral head. The fourth rotator cuff muscle, the *subscapularis*, originates on the anterior side of the scapula and inserts on the lesser tubercle of the humerus. When contracted, it causes the shoulder to rotate medially, again by way of rotating the humeral head. The *coracobrachialis* is an important shoulder flexor and medial rotator originating on the coracoid process of the scapula and inserting approximately halfway up the humeral shaft on the medial and slightly anterior side of the humerus. (Netter 2010, Veeger and van der Helm 2007).

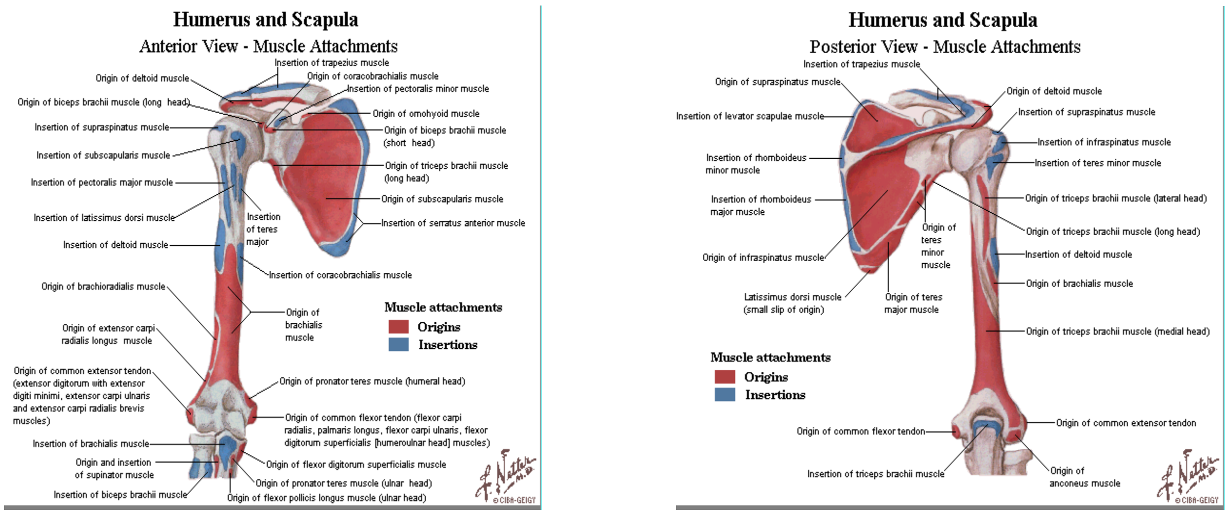

Figure 2.1. Origins and insertions for the muscles of the shoulder girdle (Netter 2010). *Figure 2.1* provides a reference for the muscles and bones associated with the shoulder girdle and gives a visual representation of the anatomy discussed in this chapter.

The muscle requiring the most attention for the purpose of this research is the deltoid because the insertion point of the deltoid muscle, deltoid tuberosity on the proximal humerus, is a prominent bony landmark used in the data collection process. The deltoid is a tri-headed muscle that originates from three locations, one at the scapular spine, a second at the acromion, and a third on the clavicle (Netter 2010, Veeger and van der Helm 2007). All three muscular heads insert on the deltoid tuberosity, which is located on the lateral side of the humerus at midshaft (Netter 2010, Veeger and van der Helm 2007). At this same mid-humeral location there are a number of elbow flexor originations, including the *brachialis* and *brachioradialis* muscles, which allow the elbow to flex and the forearm to supinate when contracted (Kahn et al. 2001). The deltoid is key to the current research because it is an arm abductor and is partially responsible for lifting the arm above the head, a position assumed to be critical in vertical climbing. *Figure 2.2* shows the actions that muscle contractions have on the shoulder joint. Arrows indicate the direction of contraction and hence the direction that the shoulder will move toward. This creates a visual representation of the above stated movements of the shoulder joint in response to muscle action. (All muscle action statements were derived from *Figures 2.1* and *2.2*, and are supported by Hamill and Kuntzen 2008, Netter 2010, and Veeger and van der Helm 2007).

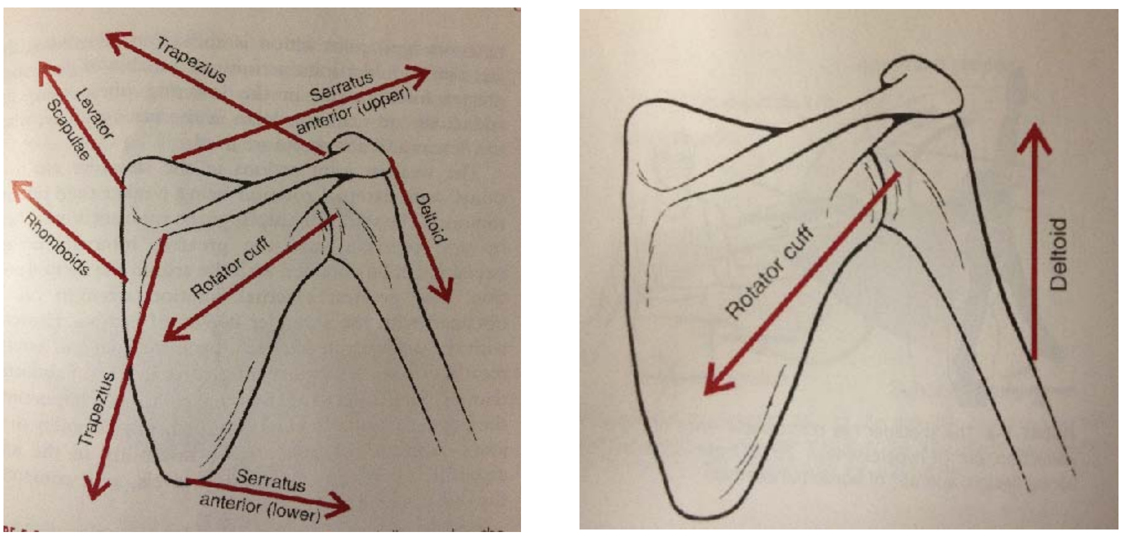

Figure 2.2 Muscles of the shoulder girdle and their direction of action on the shoulder joint (Hamill and Kuntzen 2008). *Figure 2.2* illustrates muscle contractions and their corresponding action in the shoulder joint. It shows the complexities of shoulder movement and can be used as a visual reference to the muscle action description provided above.

A laterally directed glenoid fossa of the scapula and a longer, more laterally twisted clavicle allows for freer mobility to raise the arm and helps to facilitate vertical climbing (Veeger and van der Helm 2007). The laterally facing glenohumeral joint combined with the strut-like support provided by the clavicle allows the humerus to be used as a large lever arm for the muscles used while vertically climbing, e.g. the *serratus anterior*, *latissmus dorsi*, and rhomboids (Veeger and van der Helm 2007). It is important to keep in mind that while the glenohumeral joint is of focus here, the scapulothorasic gliding plane is also critically important in shoulder stabilization (Veeger and van der Helm 2007). While climbing and suspending are dependent on having a flexible shoulder, flexibility without any sort of stabilization could result in injury and decreased fitness. The scapulothorasic gliding joint, therefore, acts as an important shoulder stabilizer.

Complete shoulder mobility is characterized by the movements of several joints including, the glenohumeral joint allowing 120 degrees of elevation, the axillary humeral rotation of 135 degrees relative to the scapula, and scapular rotation along the thorax responsible for approximately one third of total arm elevation, making general shoulder mobility an incredibly integrated processes (Veeger and van der Helm 2007). The muscles and joints of the shoulder girdle interact in a complex way making a full mechanical analysis of the shoulder difficult and beyond the scope of this paper. Still, it is important to conceptually understand the powerful integration found within this joint, as it allows us to apply hominoid functional morphology onto hominin fossil morphology.

Based on strict bony morphology, there is a negative trade-off between shoulder joint stability and mobility (Veeger and van der Helm 2007). Trade-offs are defined as “an inescapable compromise between one trait and another that makes it impossible for any population of organisms to evolve optimal solutions to all agents of selection at once” (Freeman and Herron 1998:297). In the case of the hominoid shoulder the tradeoff is between joint stability and joint mobility, where quadrupedism necessitates high stability and suspension necessitates high mobility (Sylvester 2006). Both mobile hominoid shoulders and stable hominoid shoulders are extremes on a continuum of phenotypic expression, and hence movement towards one extreme requires movement away from the other; in other words, enhanced shoulder stability must reduce shoulder movability and vice versa (Sylvester 2006). Recognizing morphology as a continuum of traits is critical when attempting to conceptualize functional morphology in living populations because it reflects on modern human climbing as an ancestral ability and highlights the purpose of using the shoulder as the region of interest for the flowing study. Applying modern behavior to fossils is critical to our understanding of fossil behavior because hominins possess morphology and behavior on a continuous scale ranging from arboreality to bipedalism.

The next section focuses on principles of bone structure, robusticity and density as a way to increase understanding on the methods chosen in the current research. Understanding concepts of functional morphology and locomotor behavior is not useful in and of itself, therefore by adding bone biology and density conclusions regarding activity and bone deposition from a live sample of humans can be drawn.

Bone Structure: Robusticity vs. Density

This final section focuses on bone structure and the differences and similarities between bone robusticity and bone density. Histologically bone is very different from other tissues in the human body. Bone is rigid due to a matrix of inorganic salts, collagen fibers, proteins, and minerals (Jee 2001, Majeska 2001, Boskey 2001). Bone is composed of 65% mineral and 35% organic matrix cells and water, where the organic matrix consists of 90% collagen and 10% non-collagenous proteins (Jee 2001, Majeska 2001, Boskey 2001). The mineral content of bone acts as a reserve for calcium ions and an extracellular fluid composition of ionized calcium concentration (Jee 2001, Boskey 2001). Most importantly, bone has the ability to self-repair and change its mass, shape, and composition in order to endure mechanical requirements from voluntary physical activity without breaking (Jee 2001, Goodship and Cunningham 2001). It is this principle that the research in this pilot study is based on.

Long bones have a standard structure with an epiphysis, a metaphysis, and a diaphysis that are made up of both cancellous (trabecular) and cortical bone (Jee 2001). Cortical bone is the dense layer of outer bone that makes up for approximately 80% of skeletal mass in the adult human body, the other 20% of skeletal mass is from the trabecular bone, or the spongy inner lattice of bone (Jee 2001). Both cortical and trabecular bone is made up of either woven or lamellar bone types. In humans woven bone is deposited more or less at random as a sort of scaffold for the lamellar bone deposits that begin around the age of 2 to 3 years old (Jee 2001). In cortical bone lamellae are deposited in adjacent directions, with each lamellae made up of osteon segments (Jee 2001). In adults it is assumed that bone deposition is primarily made up of cortical bone deposits adding thickness to the outer layer of long bones, largely where there are high compression forces (Goodship and Cunningham 2001, Cowin 2001, Hart 2001), where in contrast trabecular bone deposition is thought to follow direct force patterns applied to the bone (Whalen et al. 1988, Gosman et al. 2013).

For the present study it is assumed that bone density is dependent on the cortical bone thickness and bony remodeling in the humeral shaft, because it has been demonstrated that cortical thickness and bone mineral density of the proximal humerus are highly correlated (Tingart et al. 2003). Bone density is often related to the visual presence or absence of a heavy, strong or rigid bone, bone density is defined as grams of bone calcium per centimeter squared (g/cm^2), or bone mass per unit of selected area (Mazess et al. 1990, Tingart et al. 2003). Notably, robustness is also a measure of bone weight, strength and rigidity per size (Shackleford 2007). The problem with robusticity is that it is often a qualitative measure of how large or thick the feature in question appears to the observer. For example, it is common to use robusticity scales in sexing individuals based on skeletal morphologies present on the human cranium or pelvis (see Bass 1995 for further information). This results in researcher bias because individuals can perceive scales differently. On the other hand, density is a quantitative measurement taken via standardized equipment (in this study a Dual-energy X-ray Absorptiometry, DEXA, scanner was used). This allows the researcher to get specific numeric measurements that could correspond to an observer's qualitative scale of robusticity. The present research is not concerned with numerically labeling robusticity scales; however, it is important to understand that the two terms, while related, are very different in definition and use throughout this study.

Chapter Two Summary

Chapter two gives a brief explanation of the modern human shoulder girdle musculoskeletal anatomy and bone physiology was described. Human mechanics of the shoulder related to vertical climbing were addressed for a contextual background to the research that will be presented to follow. A discussion of bone structure and the difference between robusticity and density for the purposes of this study was addressed. All concepts presented are critical to the interpretation and collection of the data presented in the following pilot study. Chapter three begins by focusing on patterns associated with arboreal and vertical climbing behavior in hominoids, in relation to should girdle morphology as described in Chapter two. Additionally, Chapter three addresses the theoretical backgrounds, fossil material, and locomotor patterns relevant to the study. In summation, Chapter two focused on modern human musculoskeletal anatomy and mechanics related to the shoulder girdle. Additionally, it presented information on bone biology and the difference between bone robusticity and bone density.

CHAPTER THREE

Chapter three provides a synopsis of the fossil record, as well as appropriate anthropological theory relevant to the origins of bipedalism, including arboreal and vertical climbing behavior and the relevant morphology in order to understand why the region of interest for the pilot study was chosen. Chapter three begins with an examination of anthropological theory regarding early hominin bipedalism. The transition away from arboreal behavior and towards bipedalism allows us to focus on the morphology necessary for arboreal adaptations and climbing proficiency as a critical component to the acquisition of resources for early hominins. Next a fossil overview will examine hominin taxa from *Sahelanthropus tchadensis* to *Australopithecus afarensis*; however, the attention is focused on *Au. afarensis* morphology. *Au. afarensis* shifted how researchers regarded the time and place for the transition to bipedalism, as the anatomy indicates that an open savannah was not the landscape in which bipedalism arose. Instead *Au. afarensis* shifted the context in which bipedalism arose to an arboreally inclined landscape (Potts 1998, Behrensmeyer and Reed 2013). This change in thought is important because it allows us to reexamine secondary morphology not directly related to bipedalism, like the shoulder, when looking for characteristics associated with the transition away from an arboreal ancestor instead of focusing solely on the bipedal hindlimbs. In turn understanding shoulder morphology may aid in developing a clearer picture as to how hominins moved through their environment.

Theories surrounding early bipedalism

The chronology, location, landscape, specific morphological pattern and exact locomotor behavior of habitual bipedalism in early hominins are not entirely known. The fossil record creates challenges, some of which are related to a correct description of the onset of bipedalism.

Numerous arguments attempting to identify the selective pressures responsible for the evolution of bipedality in hominins have been put forth, which include: vigilance (Dart 1925, Darwin 1871); the transporting of food, tools or infants (Washburn 1960, Hewes 1961, Sinclair et al. 1986); seed eating (Jolly 1970); provisioning (Lovejoy 1981); terrestrial efficiency (Rodman and McHenry 1980); increased foraging efficiency (Wrangham 1980); feeding posture (Hunt 1994); the hylobatian model (Tuttle 1975, Tuttle 1981); thermoregulation (Wheeler 1991); and the locomotor decoupling hypothesis (Sylvester 2006). Even though not all of the competing hypotheses are detailed here it is important to understand the shear number of theories demonstrates how difficult the transition to obligate bipedalism is to understand.

The focus here is on two main opposing hypotheses that describe the transition in locomotor behavior from arboreality towards bipedality in early hominins, and focuses on an arboreal and climbing ancestral hominin compared to a largely quadrupedal and terrestrial one (Kieth 1923, Morton 1926, Gregory 1926, Richmond et al. 2001, Wood Jones 1916, Osborn 1927, Lovejoy 2009, Tuttle 1975, Thrope et al. 2007, Crompton et al. 2008, Sylvester 2009). The literature regarding arboreal behavior is discussed here in order to understand the importance of a mosaic landscape in the transition to bipedalism. Terrestrial quadrupedism will not be addressed as an alternative because this thesis is not concerned with the hindlimb; however it is noted that varying hypotheses are present in the literature (Washburn 1967). Additionally, the arboreal theory is offered to provide insights on the use of the shoulder in theoretical hominin behavior.

Arboreality is intrinsically a locomotor characteristic that encompasses all modes of movement within and among the trees (Cartmill 1975). This includes vertical climbing, brachiating, hanging, as well as quadrupedal and bipedal movements within the trees.

Meanwhile, brachiating, which is a specific form of arboreal locomotion, was defined by Sir Arthur Keith in 1923 as the movement from branch to branch by way of fully abducted shoulders resulting in an erect and orthograde posture of the torso (Keith 1927, Avis 1962). Neither arboreal locomotion in general, or more precisely brachiation, specify much about the function of the hindlimb, and for the simplification of this research, hindlimb form and function will be largely ignored. That is not to minimalize the significance of the hindlimb in the evolution of bipedalism, but instead will allow us to examine secondary locomotor patters and morphology that were also significant to early hominin locomotor behavior.

By the 1970s this debate was split between hypotheses. The first hypothesis focused on a species that was a terrestrial intermediate between non-human and human primates as described by Washburn (1967). The second hypothesis focused on the hominin ancestor being largely arboreal due to environmental and morphological support (Carmill 1975, Avis 1962, Richmond et al. 2001, Wood Jones 1916, Osborn 1927, Straus 1949, Lovejoy 2009, Tuttle 1975, Thrope et al. 2007b, Crompton et al. 2008, Sylvester 2009). For example the discovery of AL288-1 in 1974, an adult australopithecine female, shifted the research focus to the second hypothesis and caused researchers to reconsider an arboreal component to the early hominin adaptive strategy, likely as a method of resource acquisition in the trees, largely due to her chimpanzee-like limb proportions (Stern 2000, Johansen et al. 1982, Potts 1998, Richmond et al. 2001).

Arboreal locomotion

When considering arboreal locomotion as a component to early hominin behavior it is important to define what it means to be arboreal. The arboreal locomotor hypothesis argues that bipedality evolved from pronograde adaptations for locomoting mostly quadrupedally above branches (Richmond et al. 2001). In this hypothesis, arboreal traits in the hands, feet, fingers and toes of both the last common ancestor and its descendants would have been maintained (Larson and Repcheck 2008, Richmond et al. 2001). The hand and foot digit lengths would need to be intermediate between a climbing ancestor such as chimps and modern humans, because of the use of both suspensory and climbing patters as well as terrestrial ones (Richmond et al. 2001). In addition, a smaller to mid-range body size would have been selected for, since arboreal locomotion is generally more difficult for larger apes than it is for smaller ones (Richmond et al. 2001, Crompton et al. 2008). This in turn coincides with numerous physical adaptations that the most recent common ancestor is predicted to have had, such as relatively long flexible forelimbs, an intermediate lumbar spine that allows a side-to-side bending motion, a relatively low center of gravity, wide hips, a broad thorax with laterally facing shoulders, mobile arm and wrist joints with longer fingers and well developed pollux and hallux (Larsen and Repcheck 2008, Richmond et al. 2001).

Many of these traits are seen in *Ardipithecus ramidu*s, a 4.4 mya hominin found in Aramis Ethiopia by Tim White and colleagues (Lovejoy et al. 2009). *Ar. ramidus* is believed to practice some form of arboreality in combination with terrestrial bipedality because the reconstruction of the *Ar. ramidu*s pelvis is said to represent a bipedal gait, while her limb proportions, flexible joints and opposable hallux represent an arboreal adaptation (Klages 2011, Lovejoy et al. 2009). *Table 3.1* demonstrates the general characteristics of the arm and shoulder necessary for arboreal locomotion. *Table 3.1* shows that there is little difference morphologically between the traits needed to efficiently suspend versus brachiate; and that in most cases suspensory adaptations appear to allow for brachiation and vise versa.

Table 3.1. General arboreal characteristics. *Table 3.1* illustrates the general traits of arboreal groups and sows little variation between suspensory and brachtion adaptations.

Body part	Characteristic	Function
Hands and feet	Long phalanges, well developed pollux and hallux	Brachiation
Thorax	Broad	Suspension
Shoulders	Laterally facing glenoid fossa, flexible joints	Suspension and brachiation
Wrist and elbow	Mobile	Suspension

(Richmond et al. 2001, Larsen and Repcheck 2008, Thrope et al. 2007)

Additionally, Thorpe and colleagues (2007a) argued that hand assisted bipedality over flexible branches, where the majority of the body mass is centered over the hind limbs rather than over all four appendages equally, as seen in orangutans, was a precursor to terrestrial bipedalism. This method of arboreal locomotion allows for a larger body size without compromising the supports used to traverse through the trees (Crompton and Thorpe 2007). This is significant because most early hominins are considered to have a relatively large body size for most arboreal adaptations (Crompton et al. 2010). Thorpe and colleagues (2007a) argue that the extended hip angles of orangutans are much more similar to human hip angles than any other ape relatives and therefore hominins likely also evolved bipedalism out of the need to locomote over flimsy tree branches (Crompton and Thorpe 2007, Thorpe et al. 2007a,b, Crompton et al. 2010). It can be argued that using orangutans as a proxy for hominin behavior is less useful than using chimpanzees or modern humans because orangutans are phylogenetically farther removed from the hominin lineage (Begun et al. 2007). However, there is no decidedly right or wrong model for hominin evolution and perhaps the correct model is a combination of many modern analogies.

Therefore, Thorpe and colleague's (2007a,b) research highlights key aspects of morphologic evolution that are plausible, such as the hip and knee angles, that can be used as a proxy for inferring hip and knee angles of past hominins. To accompany this model it has been suggested that hand assisted arboreal bipedality is a part of a continuum of orthrograde type behaviors that, if habitual, would decreases the number of adaptations necessary for habitual bipedality and permanent orthograde posture (Crompton et al. 2008). Orthograde behaviors are pertinent to understanding body posture while bipedal and can be seen in many other behavioral and locomotor strategies including feeding behavior in the trees (Hunt 1996), above branch bipedalism (Crompton et al. 2007, Crompton and Thorpe 2007, Thorpe et al. 2007a,b, Crompton et al. 2010), and vertical climbing, which will be discussed next (Crompton et al. 2010, Richmond et al. 2001, Fleagle et al. 1981).

Vertical Climbing

Vertical climbing requires an orthograde body position in order to physically see the path up the desired substrate. For example, reaching and grasping substrate superiorly to pull with the forelimbs while simultaneously pushing with the himblimbs causing a cranial propulsive force requires an upright torso parallel to the surface, otherwise the individual would push themselves off of the substrate. The vertical climbing model generally states that early hominins practiced a locomotor behavior adapted to vertical climbing, described as the movement previously explained (Richmond et al. 2001). It would include considerable fore- and hindlimb mobility, suspensory postures such as relative orthogrady, and the use of multiple and often vertical supports (Richmond et al. 2001, Hunt et al. 1996, Stern 2000). This hypothesis is most concerned with the positioning of the torso relative to the branches, specifically that the torso is roughly retracted vertically 45 degrees or greater from the branch, which will be considered a defining characteristic of vertical climbing (Stern 2000, Richmond et al. 2001).

The vertical climbing model describes a relatively large body mass that is supported by the presence of highly mobile joints, in particular the hip, shoulder, knee, elbow, wrist and ankle, and elongated and curved fingers and toes (Richmond et al. 2001). Body mass is most important because vertical climbing helps to control balance on top of branches where a horizontal position, as found in arboreal quadrupedism, would compromise balance on a larger bodied individual (Richmond et al. 2001, Larsen and Repcheck 2008, Pontzer and Wrangham 2004). Currently it can be seen that modern humans possess torso morphology resembling that of a climbing ancestor, such as laterally facing scapulae that allow for a wide range of motion at the glenohumeral joint, which is essential for reaching and pulling movements, as well as primary functions of the forelimbs in vertical climbing.

Evidence from the fossil record that supports vertical climbing in early hominins is demonstrated by the australopithecines, which possessed general morphology intermediate to modern ape-like arboreality and *Homo*-like climbing ability (Ward 2013). This is significant because it highlights an intermediate phase of mobility in and out of the trees, in addition to a reliance on an arboreal landscape for resources such as food and shelter. For example, australopithecines possess higher brachial indices compared to humans but less than that of modern apes, longer and more curved fingers and toes relative to *Homo*, and a cranially oriented glenoid fossa, all features implying that *Australopithicus* was more adept to climbing compared to *Homo* but less adept when compared to apes (Ward 2013, Stern 2000, Larson 2013, Green and Almseged 2012). The morphological evidence of the shoulder girdle provides additional support to climbing abilities and behavior but does not provide support as to the proficiency or frequency that climbing was used.

The discussion over the use of vertical climbing as a part of the australopithecine toolkit depends on the selective pressures that forced them away from arboreal reliance and into bipedal reliance. It can be agreed that morphology related to vertical climbing and arboreal locomotion was retained through *Australopithecus* and to some extent early *Homo* and modern humans (Ward 2013, Crompton et al. 20008, Crompton et al. 2010, Larson 2013, Green and Almseged 2012), but deciphering whether or not climbing morphology experienced selective pressure allowing its retention or if the characteristics were simply just not selected against is still unclear (Ward 2013). One way of examining morphological changes in the hominin record is to look at the fossil morphology in sequence and try to infer behavioral adaptations as they progress through time.

Identifying fossils

The following section provides an overview of hominin fossil morphology of the postcrania in sequence time in order to track morphologic changes along with their implied behaviors. The cranial fossils and morphology are excluded from this review because the focus of this thesis is on the shoulder girdle. Cranial morphology, while important, does not necessarily play a key role in locomotor patterns in either living or fossil hominins. The hominin record is always changing due to new findings, both fossil and genetic. *Figure 3.1* shows a hominin phylogeny to offer a visual reference for the provided fossils. It is important to keep in mind that the structure of hominin phylogenies can vary based on their creator and the one provided is merely for reference.

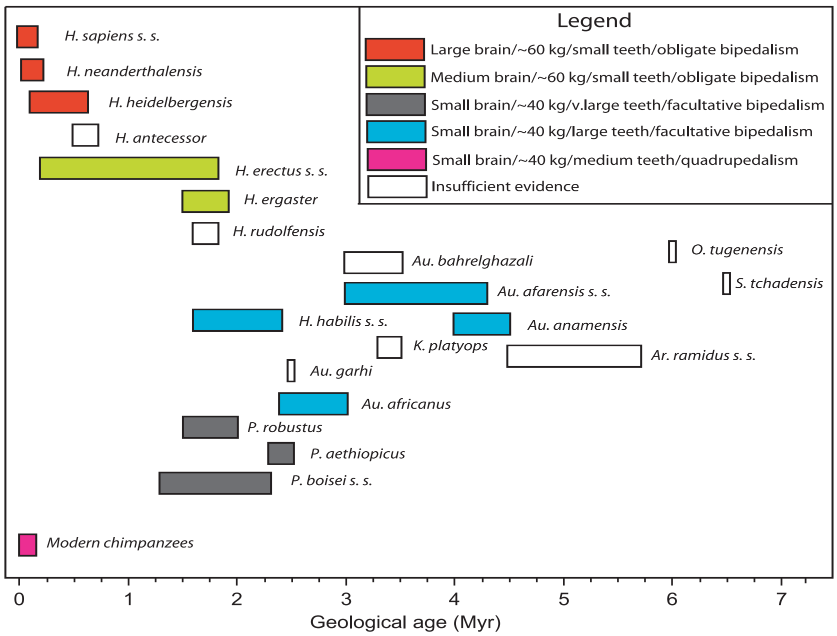

Figure 3.1. Hominin phylogeny with split groups based on brain size, body mass, post-canine tooth size estimates, and locomotor mode (Robson and Wood 2008). *Figure 3.1* is provided as a visual reference of hominin phylogeny.

Since this research is concerned with shoulder girdle morphology related to climbing adaptations in the fossil record, a recount begins with *Sahelanthropus tchadensis* at 7-6 million years ago and ends with *Australopithecus afarensis* at 3.7 million years ago, because it is well understood that these groups of taxa are associated with a wooded environment (Burnet et al. 2002, Haile-Selassie 2001, Conroy 1997, Lovejoy et al. 2009, Senut et al. 2001, Richmond and Jungers 2008). Additionally, morphology of *Australopithecus afarensis* is emphasized because of the relatively complete skeletal record for australopithecines in general (Stern 2000, Ward 2013, Larson 2013), but also because of the intensive analysis on the australopithecine shoulder girdle (Ward 2013, Larson 2013, Green and Almseged 2012).

Sahelanthropus tchadensis

Sahelanthropus fossils were recovered from the Toros-Menalla 266 fossiliferous area of the Djurab Desert of northern Chad. They have been dated at between 7 and 6 million years ago (mya) and are composed of a cranium and partial mandible (Burnet et al. 2002, Guy et al. 2005). *Sahelanthropus* shows a mosaic of characteristics that reflect both apes and early hominins including a basicranium similar to bipedal hominins, a U-shaped dental arcade, and small endocranial volume (Burnet et al. 2002). *Sahelanthropus* does not have any post-cranial fossils to consider, making any comparative analysis or argument for climbing behavior difficult, if not impossible.

Orrorin tugenensis

Orrorin was recovered from the Lukeino Formation, Tugen Hills, Kenya and is dated to roughly 6 million years ago, mya (Senut et al. 2001). *Orrorin* is composed of 13 known fossils, including cranial, dental and postcranial bones, from at least five separate individuals (Senut et al. 2001). *Orrorin's* proximal femur is characterized by a spherical and anteriorally positioned head, an elongated and oval shaped neck, and a lesser trochanter that is medially situated with robust muscle insertions (Senut et al. 2001). The proximal femur possesses several osteological morphologies that can be related to bipedalism including various muscle attachment sites and the general size and shape of the head and neck (Senut et al. 2001). In general the proximal femur is more similar to humans then it is to australopithecines or African apes and biomechanically suggests a locomotive repertoire related to facultative bipedalism – the use of bipedalism when necessary but not requiring bipedal movements for locomoting all of the time (Senut et al. 2001, Richmond et al. 2008).

Orrorin has a distal humeral shaft and a proximal manual phalanx. The humeral shaft shows a strong straight lateral crest, an important insertion point for the brachioradialis muscle (Senut et al. 2001). This muscle is often linked to climbing as it supinates and flexes the elbow joint (Richmond et al. 2008). Additionally, the phalanx is curved, another trait found in climbing primates, both extinct and extant, including early australopithecines (Senut et al. 2001, Richmond et al. 2008). The forelimb morphology suggests that *Orrorin* was well adapted to arboreal climbing or behaviors that evolved from an orthograde vertical climbing repertoire (Senut et al. 2001, Richmond et al. 2008), and is important because it illustrates climbing morphology early on in the hominin clade.

Ardipithecus ramidus kadabba

Ardipithecus ramidus kadabba is a composed of a set of fossils believed to be a subspecies of *Ardipithecus ramidus* recovered from the Middle Awash area of Ethiopia and dated to 5.8-5.2 mya (Haile-Selassie 2001). Subspecies distinction is derived from variant molar cusp patterns that are more primitive than *Ar.* ramidus (Haile-Selassie 2001). *Ardipithecus ramidus kadabba* is composed of various dentition, hand and foot phalanges, and clavicle, humerus and ulna fragments (Haile-Selassie 2001). Phalanx morphology suggests similarities to *Au. afarensis*, however, the phalanx is longer and generally larger than *Au. afarensis* (Haile-Selassie 2001). The humerus fragment is larger than most *Au. afarensis* but smaller than *Ar. ramidus* (Haile-Selassie 2001), indicating an intermediate body mass. Both the ulnar shaft and the humerus show an elongation of the shaft as well as a curvature that is more distinct from later hominins, as well as a clavicle that is absolutely more robust than other fossils or modern chimpanzees (Haile-Selassie 2001). Both traits are most often related to climbing or arboreal adaptations in australopithecines (Ward 2013), and are therefore important to consider when tracing ancestral or divergent traits through the hominin lineage.

Ardipithecus ramidus

Ardipithecus ramidus was found in Aramis, Ethiopia in the Gaala Vitric Tuff Complex dated to 4.4 mya (Conroy 1997). *Ardipithecus ramidus* is most well known for its unique foot morphology, including an opposable hallux and an os peroneum[3] bone that showcases its primitive nature (Lovejoy et al. 2009). It shows that the evolutionary track of the human foot is more closely related to monkeys than to African apes and that *Ar. ramidus's* foot morphology is in fact more primitive than other early hominins because it more closely resembles that of arboreal monkeys rather than apes or humans (Lovejoy et al. 2009, Crompton et al. 2010).

Additional postcranial remains include a complete left arm (humerus, radius and ulna), all from the same individual that shows a mosaic of characteristics (Conroy 1997). *Ardipithecus* possesses short metacarpals with no knuckle-walking groove, a flexible hamate and a capitate that has a palmarly rotated head, characteristics that promote a more flexible wrist (Lovejoy et al. 2009). Therefore, it has been found that the wrist joint of *Ardipithecus* possessed greater mobility when compared to modern apes, additionally, the joint in the palms and fingers are more flexible refuting any relationship to knuckle-walking (Lovejoy et al. 2009).

It has been further argued that the positions of the articular facets of both the radius and ulna do not support either knuckle-walking or suspensory locomotor adaptations (Lovejoy et al. 2009, Crompton et al. 2000). Lovejoy and colleagues (2009) instead relate these morphological characteristics to primitive fine motor manipulative skills that relied heavily on triceps

[3] Os peroneum bone – In humans it is highly variable and not often present, but is a small sesamoid bone that sits in the *fibularis longus* tendon and articulates with the cuboid; common in arboreal monkeys (Lovejoy et al. 2009, Netter 2010)

movement, a claim that goes beyond locomotor behavior and attempts to allude to intelligence. *Ardipithecus* possesses a robust anterior deltoid crest (White et al. 2009). This trait is typically associated with powerful arm musculature; however, the trait is underdeveloped in modern apes, known for suspensory locomotion, and absent in brachiating gibbons indicating that the trait is a primitive development that has been modified by positional use and not loading mechanics (Lovejoy et al. 2009). That is not to say that positional use, for example maintaining an abducted arm position, does not require constant isometric muscle contraction. Instead, it is interpreted that positional use implies a more passive type of muscular loading acting on the bone in contrast to active mechanical loading as with active compression or torsion forces seen in various locomotor strategies (Larson 2013).

Australopithecus anamensis

Australopithecus anamensis is known from two sites on East Lake Turkana (Allia Bay and Kanapoi) and is dated to 4.2-3.2 mya. It shows a mosaic suite of ape and hominin characteristics (Conroy 1997). The only postcranial element from Allia Bay is a left radius. The radius was nearly complete when found in 1988 and since then an additional fragment was found that articulates to the proximal end just under the radial tuberosity, but does not join the proximal and middle portion of the shaft (Heinrich et al. 1993, Ward et al. 2001). The radius possesses both ape and hominin characteristics. Ape-like traits include a relatively long radial neck, wide distal metaphysis and a large brachioradialis crest. Other features, such as the radial neck robusticity in relation to the radial head and the crescent shape of the distal end distinguish KNM-ER 20419 as a hominin (Heinrich et al. 1993). The radiocarpal joint has a larger surface for a radio-lunate articulation, indicating that the wrist was adapted for increased adducting associated with climbing adaptations (Heinrich et al. 1993).

Interestingly most features associated with the forelimb elements of *Au. anamensis* can also be associated with some form of arboreality and vertical climbing (Ward 2013). Namely, the large brachioradialis crest and the large radio-lunate articular surface aid in supporting the theory that *Au. anamensis* was at least partially equipped for arboreal resource foraging, be it through true arboreal and suspensory behaviors or vertical climbing. Regardless of the method of locomotion, *Au. anamensis's* morphology supports a hominin ancestry that to some extent relied on an arboreal landscape (Ward et al. 2001, Ward 2013).

Australopithecus afarensis

Australopithecus afarensis is the most known east African early australopithecine, and was present from about 4-3 mya ago (Conroy 1997). The most well-known *afarensis* fossils are AL-288-1, "Lucy", and the Laetoli footprints; both of which date to 3.7mya (Reed et al. 2013). The *afarensis* postcranial fossils show a mixture of ape and human like morphologies (Conroy 1997, Stern and Susman 1983).

AL-288-1's humerofemoral index is larger than that of a modern human, indicating that *Au. afarensis* possessed unique body proportions with a longer humerus in proportion to their lower limbs than in modern humans (Conroy 1997, Jungers 1982). This is further confirmed by the discovery of upper limb elements from Hadar that indicate that *Au. afarensis* had relatively long forearms and an ulna/humerus index closer to that of a modern chimpanzee than to a modern human (Conroy 1997, Kimbel and Delezene 2009). The brachial indices of *Au. afarensis* are important because it places *Au. afarensis* within chimp-like limb proportions, a trait that is commonly linked to some degree of arboreal dependency.

Of particular interest in this study is the shoulder morphology of AL-288-1. AL-288-1 has unique shoulder morphology that is more similar to orangutans then to either chimpanzees or humans (McHenry 1986). AL-288-1 has orangutan like angles between its glenoid fossa and the axillary boarder of its scapula, as well as a narrow glenoid fossa, and a narrow humeral head in the mediolateral direction with a wide intertubecular groove (McHenry 1986). These traits indicate a non-human like scapulohumeral joint, and when compositely considered the scapula identifies as more orangutan-like compared to chimpanzees (McHenry 1986). Orangutans are known for their exceptional arboreality and suspensory lifestyles, and along with the similarities in scapular morphology should be considered as a potential proxy for behavioral adaptation in *Au. afarensis*.

Furthermore, a juvenile 3.3 mya *Au. afarensis* partial skeleton from the Dikika research area of Ethiopia, DIK-1-1, preserved a distal humerus showing a wide and deep olecranon fossa and phalanges that are long and curved, in agreement with previous stated australopithecine morphology (Alemseged et al. 2006). Interestingly, DIK-1-1 preserved nearly complete right and left scapulae (Alemseged et al. 2006), showing a very different morphology from AL-288-1. The humerus and phalangeal features tend to argue for an arboreal behavioral pattern, although the new scapular morphology does raise questions as to what extent. It is also important to remember that DIK-1-1 is a three-year-old juvenile and questions as to the ontogeny of the skeleton need to be considered when inferring behavior from the morphology.

The overall shape of the scapulae resembles both juvenile and adult gorilla morphology with an infraspinous fossa intermediate to that of human and chimpanzee (Alemseged et al. 2006). Additionally, the glenoid fossae orientation and corresponding scapular spine directions are intermediate between laterally facing as in humans and superiorly oriented as in chimpanzees, again aligning with gorilla orientations (Alemseged et al. 2006). The DIK-1-1 scapulae were tested in relation to its ontogeny in order to understand its locomotor function

(Green and Alemseged 2012). It was found that the scapular orientation would remain relatively stable through ontogeny indicating that a more cranially oriented glenoid fossa and scapular spine when compared to humans would be present in an adult DIK-1-1 shoulder (Green and Alemseged 2012). The shape of the infraspinous fossa is narrow compared to glenoid fossa size and resembles juvenile orangutans and gorillas (Green and Alemseged 2012). It was shown that there is an ontogenetic relationship in infraspinous fossa breadth indicating that there is a functional link between morphology and locomotion acting on scapular development (Green and Alemseged 2012). The relevance of the DIK-1-1 scapular morphology is clear in that it highlights aspects of ontogeny reflecting a dynamic locomotor regime with reliance on an arboreal or climbing component.

The functional relevance of the positioning of the glenoid fossa and scapular positioning on the rib cage are not entirely agreed upon; however, both do seem to indicate a behavior where the arms are frequently held above the head that would be most consistent with vertical climbing and or arboreality in general (Alemseged et al. 2006, Green and Alemseged 2012). A functional argument for the morphology seen in *Au. afarensis* shoulders does not necessarily argue for the presence of selective pressures actively maintaining locomotor efficiency in the trees.

Chapter Three Summary

Chapter three provided information pertinent to the understanding of the fossil record, in particular fossils known to have mosaic or semi-forested environmental reconstructions that span the transition into habitual bipedalism. Significant theory regarding the origins of bipedalism and the use of vertical climbing as an adaptive strategy for early hominins were examined. Information regarding the use of climbing as a mode of locomotion for early hominins was discussed with particular emphasis on the retention of upper limb general arboreal, and climbing specific characteristics though time was addressed. Specifics regarding *Australopithecus afarensis* morphology, especially related to the shoulder, were discussed in order to provide a benchmark for the hypothesis and research that this thesis is centered around. *Table 3.2* is a summary of the fossil information presented above. It is provided as a quick guide and reference for each taxa and gives the dates, locality and type specimen for each, as well as general features that were discussed above.

Chapter three revealed the significance of examining the shoulder as a region of interest for fossil hominins when considering arboreal and climbing behaviors as past locomotor patterns. Due to the increasing descriptions of modern hominoid locomotor patterns, specifically arboreal and climbing behaviors, it is important to understand the different types movements acting on the shoulder joint across taxa and locomotor pattern. Understanding locomotor patterning is important when considering the trajectory of bone deposition, and for this study the trajectory of bone mineral density as a measure of bone deposition in relation to activity and behavior.

The current research examines a living group of human rock climbers in order to relate bone density to shoulder activity and function with the assumption that through the use of the deltoid muscle cortical bone on the proximal humerus at the deltoid tuberosity will increase, and hence increase bone density. The techniques present in this study provide a new way of examining the effects of activity on bone deposition and resorption on a living sample, giving additional characteristics that can be added to the list of relevant features for identifying fossil behavior. If there is a positive correlation between bone density and activity then this method of analysis could provide information relevant to the fossil record. The following chapter details the materials and methods used to collect and analyze bone mineral density data with respect to rock climbing frequency and intensity in order to address the hypotheses stated in the Introduction chapter of this thesis.

Table 3.2. Summary of the fossil information presented in Part Two. *Table 3.2* is to be used as a quick guide reference for the fossils discussed in Part Two of Chapter Two.

Taxa	**Age**	**Locality**	**Type specimen**	**Elements present**	**Traits**
Sahelanthropus tchadensis *	7-6 mya	Toros-Menalla	TM 266-01-060-1	Crania and dentition	Parallel to substrate foramen magnum position
Orrorin tugenensis *	6 mya	Tugen Hills, Kenya	BAR 1000'00	Dentition, upper and lower limbs	femora showing generalized bipedal traits
Ardipithecus ramidus kadabba **	5.2-5.8 mya	Middle Awash Ethiopia	ALA-VP 2/10	Dentition and postcrania	Robust clavicle, generally larger, curved phalanges and distal humerus
Ardipithecus ramidus **	4.4 mya	Aramis Ethiopia	ARA-VP-6/500	Cranial and postcranial	Flexible wrist, robust humerus, opposable hallux
Australopithecus anamensis ***	4.2-3.2mya	E. Africa	KP 29281	Cranial and post cranial	Radius with both ape and hominid traits
Australopithecus afarensis ***	4-3mys	E. and S. Africa	AL-288	Cranial and postcranial	Chimp like limb proportions

(*Robson and Wood 2008, Guy et al. 2005, Burnet et al. 2002, Senut et al. 2001; ** Lovejoy et al. 2009, Conroy 1997, Haile-Selassie 2001; *** Conroy 1997, Jungers 1982).

CHAPTER FOUR

Materials and Methods

This thesis aims to address two initial expectations; 1. individuals who practice frequent recreational rock climbing will have increased bone mineral density (BMD) when compared to active individuals and non-active individuals, and 2. individuals who practice frequent recreational rock climbing will have an increased bone mineral density (BMD) at specific muscle attachments located on the proximal humerus that are related to shoulder abduction when compared to individuals who do not rock climb. Chapter four presents the sample used in this study, along with details about inclusion and exclusion criteria for selecting the sample. It elaborates on the methods of data collection, survey analysis, DEXA software and necessary procedures. Additionally, the statistical tests and methodology used to evaluate the study hypotheses are explained. Colorado State University's Internal Review Board (IRB) approved all methods; these include participant selection, survey questions, data collection, body measurements and analysis. All individuals were required to sign an informed consent form before participation could begin. All data collected was compiled in a master spreadsheet by individual's ID number, and did not include their name or any identifiable information. Lastly, all information was kept secure by the lead researcher, Aymee Fenwick.

Participants

A mixed sex sample (n=32) was selected based on study qualifiers. Participating adults were recruited through recruitment flyers and word of mouth communication. Fifteen males and seventeen females participated, including rock climbing, active and non-active individuals from both sexes. *Table 4.1* provides a description of the sample per sex and activity level based on the self-assessment survey of physical activity. All included participants were clinically healthy to their knowledge and none had known disorders that affected bone mineral density or general bone health, and were between the ages of 18 and 35 years old. Included females were not pregnant to their knowledge, and no included participants were on prescription or non-prescription drugs that could enhance or diminish activity level or performance for the duration of the study. All included volunteers were physically able to complete a timed push-up test. Exclusion criteria encompassed participants outside of the age range or those that had a known health condition that would interfere with the data collection, such as known bone disease. Participants involved in any prescription or non-prescription drugs that knowingly enhanced or diminished activity performance were also excluded. The following subsections provide detailed information about each aspect of data collection and analysis and are divided based on experiment design.

Table 4.1. Description of activity in participants used in study, categories based on the participants' self-assessment of their activity based on the survey data.

Sex	**Rock Climbers**	**Active**	**Non-active**	**Total**
Male	6	3	8	17
Female	7	3	5	15

Survey

To begin the study, each participant received and completed a questionnaire. The questionnaire took roughly 20 minutes on average to complete, and covered questions about climbing skill, general activity and physical performance, participation in exercise, and general health with special regards to bone health and female menopause. All surveys were reviewed for content and completion before being evaluated for physical activity or general health. The purpose of each survey was to establish the sample groups within the population of volunteers.

The survey was broken into four parts, three participant sections and one researcher section. Participant sections included; Health and Wellness, Climbing Skills, and Other Physical Activity. Each section has a series of yes and no questions as well as frequency and difficulty follow up questions in regards to each activity. Frequency was evaluated on a day scale (1-7 days) and a time scale (1- >20 hours), where as difficulty was evaluated on a 1-5 (easy to very difficult) scale. *Appendix 1* is an example of a blank survey given to participants for the completion of this study, followed by a coded survey, indicating how the survey was scored.

Based on the activity presented in the survey for each participant, three groups were created; rock climbing individuals, active individuals, and non-active individuals. In reality these groups were somewhat arbitrarily created because skill and activity level occurs on a spectrum scale; however, they are critical for the evaluation of bone mineral density with respect to activity. Information regarding sex, age, medication use, previous injury to joints and bones, known disease, and for females stage of menstruation in reference to menopause were asked on the survey to establish a good health record before completing the Dual Energy X-ray Absorptiometry (DEXA) scan.

Anthropometry

Standard anthropometric measurements were taken as a way to scale for natural variation in size. Anthropometric measurements taken included; height, weight, upper arm length and arm circumference. These measurements were used in creating body size corrections per individual. Each participant's total body BMD and shoulder BMD were scaled by dividing by that participant's body mass index (BMI), correcting for both height and weight effects on BMD. By using this correction the measurements used for statistical analysis were therefore unitless. BMD (g/cm^2) divided by BMI (kg/cm^2) cancels all units in the equation $[\left(\frac{g}{cm^2} * \frac{cm^2}{kg}\right) x\ 1000]$. This correction was chosen because both BMD and BMI are body density measurements where BMI looks at a total body density without discriminating between what type of tissue is contributing more or less to the total value. In contrast BMD specifically measures how much bone mineral content in contrast to organic material is available per individual.

All anthropometry measurements were collected according to standard guidelines for measuring and recording anthropometric data (Center for Disease Control 2007). All arm circumference and arm length data were collected in centimeters using a standard flexible cloth measuring tape. Height measurements were collected using a stadiometer and all weight measurements were collected on a calibrated electronic scale in kilograms. All measurements were calculated into means for each activity group per sex. *Table 4.2* provides a description of the sample used in the present study. In *Table 4.2* each group is composed of sex and activity level, while each recorded value is a mean of that group providing a description of each groups age (years), height (cm), weight (kg), and right and left arm lengths and circumferences (cm). *Table 4.2* also shows that the means for right and left arm measurements were symmetrical, adding to researcher consistency.

Push-up Test

The push-up test was conducted in the same room as the DEXA scan to avoid participant inconvenience. Participants were asked to perform as many correctly positioned push-ups as they comfortable could in a 15 second period. A correct push-up was defined by having hands shoulder width apart and flat on the floor, torso in a flattened plank position, with legs fully extended and feet together. This test was designed to stimulate similar muscle groups in the shoulder and upper arm that would be engaged in a climbing task (without the use of an indoor or outdoor rock climbing wall or a pull-up bar). It also serves as a check for questions on the survey that ask about strength and frequency of muscle use. The push-up test is the way in which the researcher could verify participant honest on their survey about their personal perception of their own strengths, as well as test participant strength and endurance. However participant push-up measurements were not directly used in the overall analysis.

Table 4.2. Description of sample used in the present study.

Activity by Sex	Mean Age	Mean Height (cm)	Mean Weight (kg)	Mean RUAL (cm)	Mean RAC (cm)	Mean LUAL (cm)	Mean LAC (cm)
Female Active	28.00	151.89	63.33	32.33	27.83	32.33	27.83
Female Non-active	26.38	167.69	63.76	34.38	27.06	34.50	27.06
Female Rock Climbers	23.67	167.13	58.03	34.33	26.42	34.33	26.42
Male Active	25.00	178.50	80.47	36.67	33.33	36.67	33.33
Male Non-active	28.60	176.75	68.28	34.60	28.60	34.60	28.60
Male Rock Climbers	22.71	180.97	74.78	37.57	31.21	37.57	31.21
Total Means	**25.44**	**171.44**	**67.33**	**35.13**	**28.75**	**35.16**	**28.75**

RUAL= Right upper arm length, RAC= Right arm circumference at bicep, LUAL= Left upper arm length, LAC= Left arm circumference at bicep.

Dual Energy X-ray Absorptiometry (DEXA)

Dual-energy X-ray Absorptiometry (DEXA) is a method of measuring absolute value in bone mineral content and calculates measures of bone mineral density (Sievanen et al. 1992). It has been found that bone mineral density (BMD) is less sensitive to subject repositioning when compared to bone mineral calcium (BMC), especially when examining highly 3-dimensional bone sites (Sievanen et al. 1992). DEXA is a noninvasive scanning technique that utilizes x-rays to perform a whole body scan. It is sensitive enough to discern lean muscle mass from fat mass, from bone calcium on a gram per centimeter-squared scale. The software allows for regional differentiation of body mass into standardized segments including right and left segments of the arms, ribs, and legs, as well as thoracic and lumbar spine, pelvis and head components. Additionally, subregions (regions of interests) can be manually created through using the DEXA software in order to focus on specific bony landmarks. The DEXA scanner omits less than one tenth the radiation of a chest x-ray, even when examining whole body scans. DEXA scans are sufficient at measuring calcium balance on the individual level; in fact, given multiple measurements, a change of 15 grams in skeletal calcium could be measured on an individual case with $p < 0.05$ (Mazess et al. 1990).

Here bone mineral density (BMD) is defined as an area density expressed in g/cm^2 representing the bone mass per unit of selected area (Mazess et al. 1990). In addition, bone mineral content (BMC) is representative of actual skeletal mass and the amount of mineral, calcium, content of the total bone mass as a constant proportion of the total bone compound, calcium hydroxyapatite (Mazess et al. 1990). For this analysis a DEXA is used as a way to assess and quantify BMD at a specific location on the skeleton in order to get at the density, mass per cubic centimeter, of the desired bone at the deltoid muscle's origin and insertion locations. This gives a quantifiable way to determine the amount of bone laid down at the region of interest throughout the study.

To determine the differences in bone mineral density (BMD) between modern human rock climbers, active, and non-active individuals, participants were asked to partake in a survey and self-assessment of physical activity and climbing abilities. Additionally, a bone mineral density measurement, in the form of a Dural Energy X-ray Absorptiometry (DEXA) scan, was taken on the whole body. Shoulder regions were built on each scan to get at specific shoulder region measurements per individual. Correlations and relationships between BMD and shoulder muscle use were then assessed.

This study focuses on the potential relationships between bone mineral density and the frequency of muscle use at the shoulder, specifically at the deltoid tuberosity on the humerus. Here BMD is defined as an area density expressed in g/cm^2 representing the bone mass per unit of selected area (Mazess et al. 1990). For this analysis a DEXA scan was used as a way to assess and quantify BMD at a specific location of the skeleton in order to get at the density, measured as mass per cubic centimeter, of the humerus as it functions as part of the shoulder girdle. This gives a quantifiable way to determine the amount of bone laid down at the attachment site of the deltoid muscle throughout the study.

The DEXA scan provided quantifiable information on each individual's percent body fat (BF), body mass index (BMI), bone mineral density (BMD), and bone mineral content (BMC) on both a total body and shoulder region scale. *Table 4.3* describes the mean DEXA measures for each activity group per sex. Each recorded value is a mean for each groups body fat, BMI, total BMD, total BMC, shoulder region BMD, and shoulder region BMC. This data was processed and assessed for each individual before being compiled into its designated group based on the survey categories as described earlier. The measurements provided in *Table 4.3* are some of the values used for data analysis and statistical significant testing that will be further explained in the results chapter of this thesis. Presently, *Table 4.3* provides a description of the measurements obtained through DEXA scanning for the over all sample.

Post scanning, individuals were given their personal DEXA scan data. No diagnosis or health related analysis was provided as the primary researcher is not trained nor has the appropriate credentials to provide medical advice or opinions. If the primary researcher noticed a significantly low BMD or BMC value, the primary researcher consulted with the participant and scans were again provided.

To complete a DEXA, participants were asked to wear lose fitting or workout clothing. No metal of any kind should have been worn, however earrings, small jewelry, pants zippers, buttons, and bra hooks were ignored due to symmetries across measurements between the right and left sides of the body per individual. The individuals were asked to lie down on the DEXA scanner bed with their limbs inside the marked outline on the table, and each participant was positioned on the table by the primary researcher in a safe and monitored manner.

Figure 4.1 shows the body positioning that the participants were required to lie in while the DEXA scanner was running. *Figure 4.1* shows a mock scan, and the volunteer showed in the image was positioned in order to create a step-by-step scan procedure for this thesis. Participants were asked to stay very still throughout the scan, as movement would obstruct the x-rays and hence produce a distorted image resulting in a rescan of the participant. Once the individual was comfortable the researcher started the DEXA scan using the attached computer and required software (HOLOGIC 13.1). Each scan took approximately ten minutes per individual, assuming there was no interruption or distortion of the image. After the scan was completed individuals were asked to carefully sit up and step down off the scanner in a slow and controlled manner, to avoid any discomfort of injury.

Table 4.3. Mean DEXA measures for each activity group per sex.

Activity by Sex	Mean Total %BF	Mean BMI	Mean Total BMD	Mean Total BMC	Mean Shoulder BMD	Mean Shoulder BMC
Female Active	35.47	28.10	1.07	1991.79	0.81	127.93
Female Non-active	34.88	22.70	1.12	2188.74	0.90	151.46
Female Rock Climber	26.48	20.72	1.16	2243.65	0.93	156.40
Male Active	21.83	25.27	1.17	2719.53	1.08	222.69
Male Non-active	20.90	21.86	1.11	2390.27	0.95	172.67
Male Rock Climber	16.70	22.91	1.22	2814.74	1.12	240.51
Mean Totals	**25.98**	**22.99**	**1.15**	**2398.76**	**0.97**	**179.65**

%BF= percent body fat, BMI= Body mass index, BMD= Bone mineral density, BMC= Bone mineral content

Each scan was saved to the computer system attached to the DEXA scanner, shown to the participant, and a printed copy was provided as a souvenir and thank you from the primary researcher. *Figure 4.2* shows the lead researcher, Aymee Fenwick, viewing and processing a DEXA scan output. The computer for processing scans was directly attached to the scanner itself and possessed the correct software for density and body composition analysis. All scan data was saved in printed format as well as inputted into a master spreadsheet, saved to the lead researcher's external hard drive and kept in a secure location.

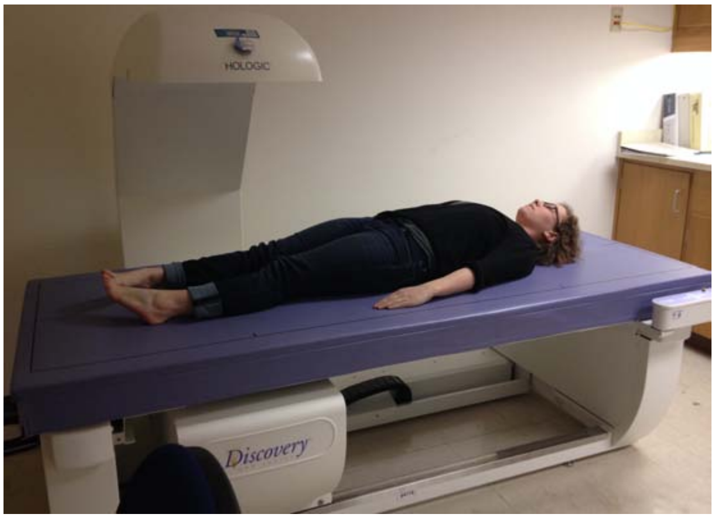

Figure 4.1. Volunteer modeling proper body position while taking a DEXA scan

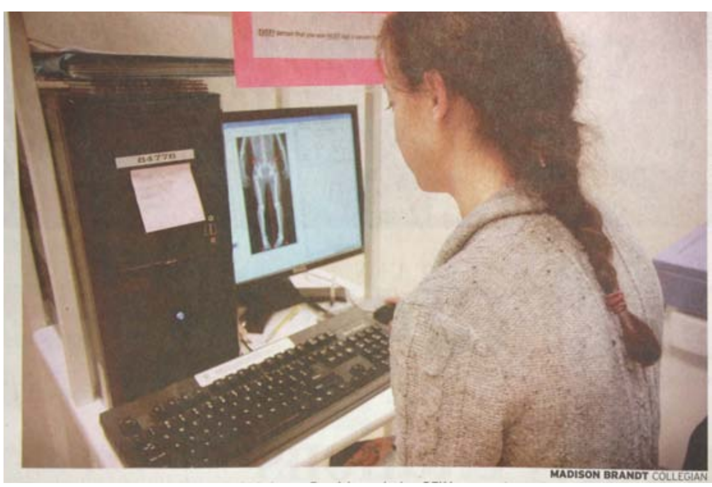

Figure 4.2. Aymee Fenwick viewing and processing the DEXA output. Photo by: Madison Brandt.

DEXA processing and computing was completed at the Human Performance Clinical Research Laboratory (HPCRL) at CSU. The scan is was designed to take whole body scans and divide each scan into standard body regions (cranium, right arm, left arm, right ribs, left ribs, vertebra, pelvis, right leg, and left leg). Additionally two shoulder regions were created using the *Region of Interest* function in the DEXA HOLOGIC 13.1 software. A five point shape was created based on bony landmarks easily seen on the scan results including the *glenoid fossa* and deltoid tuberosity, as well as the proximal and anterior curves of the flesh shoulder. *Figure 4.3* provides an example of the DEXA scan output. It is a representative scan and was not used in the data analysis as the body positioning is slightly off. *Figure 4.3* shows the body regions created by the HOLOGIC 13.1 DEXA scanner software as well as R1 and R2, the two regions created by the lead researcher for specific shoulder density analysis relevant to the hypotheses of this thesis.

The main purpose of collecting DEXA data for this study was to see whether there are relationships between total body and shoulder region BMD within a single individual and then between the individuals' in different activity subsets. It was predicted that the non-active individuals would possess lower BMD in the shoulder region when compared to the rock climbing individuals of both sex. It was further predicted that statistical analysis would illuminate trends in both the intra- and inter-group populations as well as within the sample population as a whole.

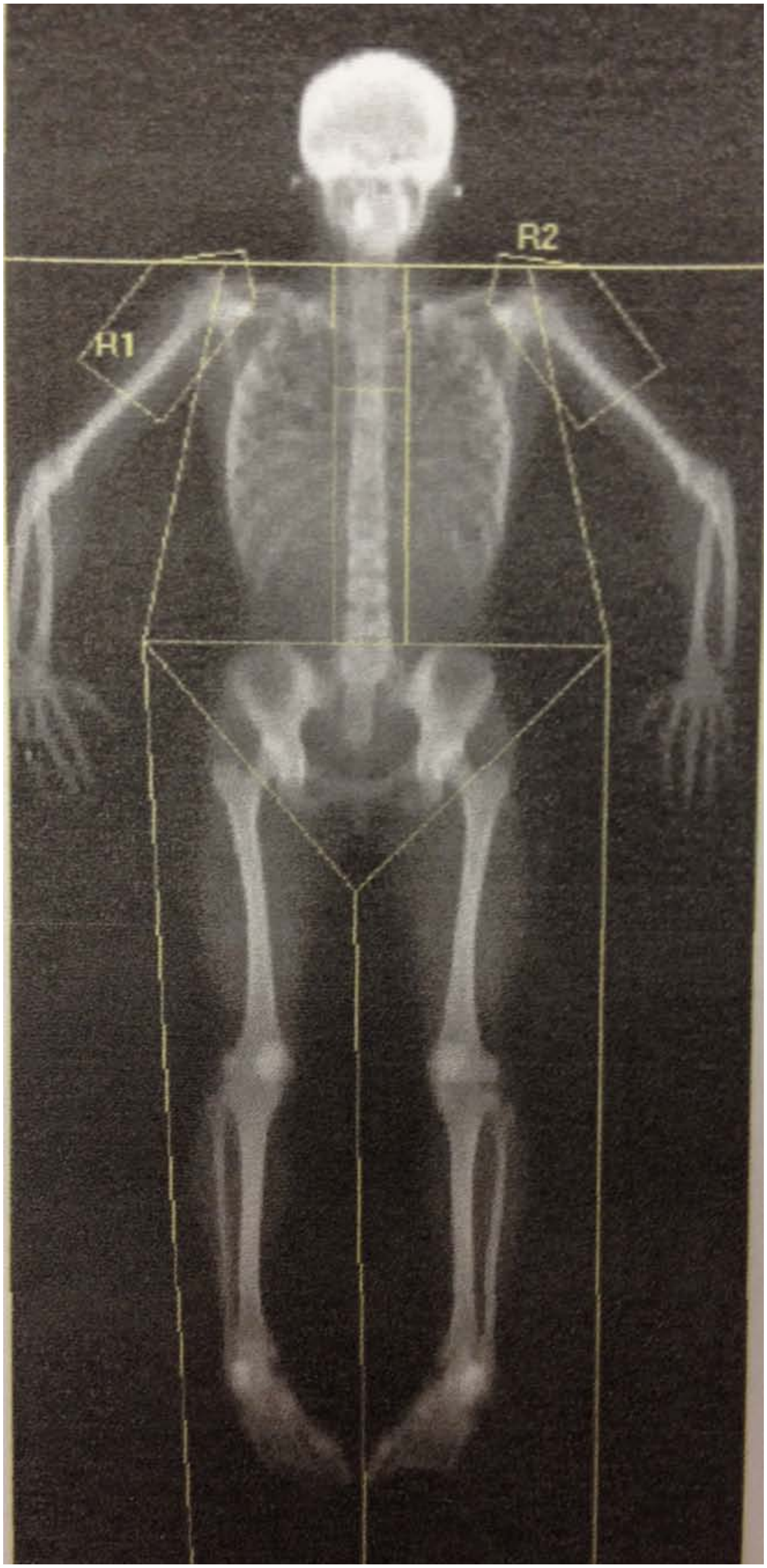

Figure 4.3. DEXA scan output. The image shown is not a true participant of the study due to consent form limitations. Scan shows regions around both shoulders created specifically should the purposes of this study.

Explanation of rock climbing

An understanding of the types of rock climbing as well as how rock climbing routes are scaled and graded was required in order to properly process the survey data. All forms of rock climbing involve using the climbers' body to lift and propel themselves up a rock face or wall, mainly using the hands and feet. Modern sport rock climbing allows materials for safety and protection, but not for assistance up the vertical face; and, the type and degree of safety measures vary depending on the type of climbing (Maddox personal communication 2014).

There are three major types of rock climbing including traditional climbing, sport climbing, and bouldering (Maddox and Preuit personal communications 2014). Sport climbing requires the climber to attach themselves to bolts located at fixed locations in a designed route up the wall or traverse. Traditional climbing requires the climber to fixate the protective stays, i.e. camelots or nuts along a route as the climber ascends. Traditional climbing focuses more on safety and efficiency rather than on difficulty, as is often the goal in sport climbing (Sylvester 2006). Bouldering utilizes shorter pieces of rock with limited or no protection against falls. Bouldering typically is categorized as lower height and lower danger with greater emphasis focused on difficulty and technique (Sylvester 2006). In general gym climbing can be either bouldering or sport climbing practiced on artificial rocks and walls with manmade hand and foot holds and is often used as training for outdoor climbing activities (Preuit and Maddox personal communication 2014). The present study collected data from individuals who practiced mostly sport climbing and bouldering, with some experience with traditional climbing, ice climbing and mountaineering; however, all participants practiced in a climbing gym.

Rock climbing route are scaled based on difficulty and are given a grade. Size of the hand- and foot-holds, distance between holds, degree of overhang of the rock, and frictional coefficient of the rock all contribute to the grade a route will be given (Sylvester 2006, Preuit personal communication 2014, Eng 2010). Therefore, climbs with large hand- and foot-hold, that are close together on a rough or frictional surface are rates as easier than climbs with small hold, far apart on a smooth surface. In North America sport and traditional climbing routes are rated using the Yosemite Decimal System, a scale ranging from 5.0 to 5.25 with 5.10 to 5.15 adding a, b, and c sub-grades to more accurately describe difficult, where lower numbers indicate easier routes (Eng 2010, Preuit personal communication 2014). Additionally in North America, bouldering routs are graded using the Sherman V-scale and range from V0 to V16 with lower numbers reflecting easier routes (Eng 2010, Preuit personal communication 2014). This information was critical when evaluating the surveys for the type of climbing and difficulty each participant was associated with.

Variables

Variables from the survey, DEXA scan and push-up test were pooled for each participant and compiled into a master spreadsheet consisting of 32 total variables. (*Appendix 2* is the master datasheet composed of all the data received from both the DEXA scans and the surveys for each participant. It shows all of the variables per individual without discrimination for which variables were used in the analysis.) Of the 32 variables 15 were considered in the final analysis (age, sex, height, weight, activity group, activity group per sex, total body fat, BMI, shoulder body fat, total BMD, total BMC, shoulder BMD, shoulder BMC, total BMI standardized BMD, shoulder BMI standardized BMD). Descriptive statistics on the 15 considered variables was completed in order to compare variable means within the sample. Again, *Table 4.2* and *Table 4.3* show the mean values for each category per variable. Of the 15 considered variables only three, activity group per sex, total BMI standardized BMD, and shoulder BMI standardized BMD were used in further significance testing.

Statistics

Statistical methods were performed using R version 3.0.2 (Venables, Smith, and R Core Team 2013) and were aimed at investigating the null hypotheses that no significant difference in BMI standardized total BMD among rock climbing, active and non-active groups, regardless of sex exists; and secondarily, that no significant difference in BMI standardized shoulder BMD among rock climbing, active, and non-active groups, regardless of sex exists.

Multiple regression analysis (MRA) was completed to organize variables by significance on BMD. This is how the three testable variables were chosen, though arbitrarily as MRA only showed relationships between BMD, BMC (p-value < 0.001) and region area (p-value < 0.001).

For significance testing, all BMD measurements per individual were standardized using the individual's BMI. Standardizing by individual's BMI provided a more holistic body standardization procedure and included both height and weight for each individual, in essence normalizing per individual's total density. Kruskal-Wallis one-way analysis of variance test were used because of a limited sample size (female n=17, male n=15, total n=32), with a non-normal distribution of means. When significances (p-value < 0.05) appeared it was argued that the groups differ from each other. Kruskal-Wallis one-way analysis of variance tests are comparable to an ANOVA on a normally distributed sample (Venables, Smith, and R Core Team 2013), but do not assume a normal distribution.

The reliability and reproducibility of the procedures in this study are attributed to 1) the standardization of the survey, 2) the standardization of the DEXA scans and DEXA software used to process and analyze each scan, and 3) all anthropometric measurements and the push-up test were administered by a single researcher. Each participant received the same survey and each individual was processed using the same HOLOGIC version 13.1 software installed on the computer connected to the DEXA scanner. Additionally the same DEXA scanner was used for each participant, administered by a single researcher.

A Kruskal-Wallis one-way analysis of variance was calculated for each activity group per sex and the total and shoulder BMI standardized BMD variables for each groups, resulting in six paired tests. Kruskal-Wallis one-way analysis or variance tests whether or not two means are identical without assuming a normal distribution (Venables, Smith, and R Core Team 2013). Kruskal-Wallis tests produce both Chi-squared and p-values, of which p-value was used to determine statistical significance. A p-value of less than 0.05 indicates that the medians are statistically different from one another, whereas a p-value or greater than 0.05 indicates that the medians are not statically different from one another.

Chapter Four Summary

Chapter four examined details about the sample presented in this pilot study. Next, chapter four discussed the methods used in data collection, processing, and statistical tests used though out the remainder of the study. The study and protocol were approved by CSU's IRB. Participants were selected based on general health and age standards. Survey data was taken to assign participant groups and determine frequency, duration and difficulty of activities per individual, with particular interest on rock climbers. Anthropometric measurements, height, weight, upper arm length, and upper arm circumference, were taken on each individual by a single researcher to avoid bias. One researcher on a single DEXA scanner at CSU's HPCRL administered all DEXA scans. All scans were process and the *Regions of Interests* were created on one computer with the same HOLOGIC 13.1 software, by a single researcher. Push-ups were monitored and timed for safety and consistency. Statistical analysis was chosen due to constricted sample size and non-normal distributions. A Kruskal-Wallis one-way analysis of variance was used to determine statistical differences in the medians of the activity groups per sex by total BMI standardized BMD and shoulder BMI standardized BMD. Results of this analysis will be presented in the following chapter.

CHAPTER FIVE

Results of the Pilot Study

A DEXA scanner was used to measure the BMD of the upper arm, the area that serves as both attachment and origin points of some active muscle groups used in climbing in a modern human sample. It was expected that individuals who practice frequent recreational rock climbing would have higher values of total body BMD and shoulder BMD when compared to individuals who do not climb for recreation. This would effectively overturn the null hypothesis, that there is no significant difference in BMI standardized BMD and BMI standardized shoulder BMD among rock climbing, active, and non-active groups, regardless of sex. Additionally, this study aims to provide a deeper understanding of the relationship between rock climbing and BMD, and more generally highlight relationships between frequencies of activity related to specific muscle groups and BMD on a whole.

The data analysis showcased general trends in the population means between the six previously defined activity per sex categories. On average the rock climbing individuals across sex showed an increased total BMI standardized BMD, as well as an increased shoulder region BMI standardized BMD. This would imply that the initial predictions - significant differences in activity group BMI standardized BMD regardless of sex – cannot be rejected. This chapter will discuss the descriptive statistics and observed trends in the sample used in the pilot study, as well as the results of the statistical analyses used to test the null hypotheses.

Descriptive Statistics

Table 5.1 and *5.2* describe the sample. The sample (n=32) was divided by sex and then activity group where the 32 total participants were first divided by sex (Females n=17, Males n=15), and then by activity group (rock climbers n=13, active n=6, non-active n=13). Sex and activity groups were joined to create one categorical variable that accounts for two quantitative variables, creating the six categories that were used through out the rest of the analysis. The six categories are, Female Rock climbers, FR n=6, Male Rock climbers, MR n=7, Female Active, FA n=3, Male Active, MA n=3, Female Non-active, FN n=8, and Male Non-active, MN n=5. These six described qualitative variable categories were used throughout the rest of the analysis as the standardized variable.

Table 5.1 presents the descriptive statistics, including the number of individuals, means, standard deviations, minimums and maximum values for each category listed. The mean age of the total sample population was 25.44 years old with a range from 19-35 years old. The mean height and weight of the total sample population was 171.4 cm and 67.33 kg with ranges from 142.2-190 cm and 47.08-94.6kg. Total body fat and shoulder body fat were nearly identical (roughly 2% difference in the means where total body fat was 25.98% and shoulder region body fat was 27.39%), indicating that there is a relationship between an individual's percent total body fat and the same individuals percent of fat in the shoulder regions. The total population mean BMI standardized BMD was 5.12 (with a range of 2.74-6.28) and the total population mean shoulder BMI standardized BMD was 4.38 (with a range of 2.04-5.38). (It is important to remember that BMI standardized BMD is a unitless measure because the units used to describe BMD and BMI cancel out when creating the ratio, refer back to the Methods chapter of this thesis for a full description of this measurement.)

Table 5.1. Descriptive statistics for the total sample.

Variable	N	Mean	SD	Minimum	Maximum
Age	32	25.44	4.06	19	35
Sex					
Male	15	N/A	N/A	N/A	N/A
Female	17	N/A	N/A	N/A	N/A
Activity Group					
Rock climbers					
Active	13	N/A	N/A	N/A	N/A
Non-active	6	N/A	N/A	N/A	N/A
	13	N/A	N/A	N/A	N/A
Height	32	171.4	10.44	142.2	190.5
Weight	32	67.33	12.07	47.08	94.60
Total % Body Fat	32	25.98	8.91	13.40	48.10
Shoulder % Body Fat	32	27.39	12.01	11.60	52.40
Total BMD/BMI	32	5.12	0.74	2.74	6.28
Shoulder BMD/BMI	32	4.38	0.69	2.04	5.38

*N/A represents where a value could not be calculated because the category is a number of individuals rather than a measurement.

Table 5.2 provides the description of the sample that was used for the full statistical analysis of relationships among activity groups. It shows the means for each variable including, mean age, mean height, mean weight, mean total percent body fat, mean percent body fat of the shoulder regions, mean BMI, mean total BMD/BMI, and mean shoulder region BMD/BMI, within each activity group with respect to sex. Based on sample means, it was found that rock climbers, of both sexes, expressed higher mean total BMI standardized BMD when compared to active and non-active groups. Secondly, it was found that rock climbers, of both sexes, expressed higher mean shoulder BMI standardized BMD when compared to the active and non-active groups. Both observations support a rejection of the original null hypotheses.

Non-active individuals were on average older, taller, possessed a higher percent body fat both overall and in the shoulder region, and had an increased BMI when compared to active and rock climbing individuals based on group means. However, active individuals possessed the highest average body weight, followed by rock climbing individuals, making non-active individuals the lightest group of participants. Additionally, the rock climbing sample had a significantly lower percent body fat within the shoulder regions compared to both active and non-active groups, which could support the expectation that the shoulder musculature are continuously engaged when rock climbing as opposed to other activities due to the high muscle/low fat ratio.

Table 5.2. Description of Sample. Mean values for each qualitative category used in the study analysis.

Fitness	Sex	Number of Individuals	Mean Age	Mean Height	Mean Weight	Mean Total % BF	Mean %SF	Mean BMI	Mean total BMD/BMI	Mean Shoulder BMD/BMI
Non-active	Female	8	26.4	167.7	63.8	34.9	39.9	22.7	5.1	4.1
	Male	5	28.6	176.8	68.3	20.9	19.9	21.9	5.2	4.4
	Total	13	27.2	171.2	65.5	29.5	32.2	22.4	4.4	4.2
Active										
	Female	3	28	151.9	63.3	35.5	40.7	28.1	4.1	3.1
	Male	3	25	178.5	80.5	21.8	21.2	25.3	4.7	4.3
	Total	6	26.5	165.2	71.9	28.7	31.0	26.7	4.4	3.7
Rock Climber	Female	6	23.7	167.1	58.0	26.5	27.6	20.7	5.6	4.5
	Male	7	22.7	181.0	74.8	16.7	15.2	22.9	5.3	4.9
	Total	13	23.2	175.6	67.1	21.2	20.9	21.9	5.5	4.7
Total Means	Female	17	25.7	164.7	61.7	32.0	35.7	23.0	5.1	4.1
	Male	15	25.2	179.1	73.8	19.1	18.0	23.0	5.1	4.6
	Total	32	25.4	171.4	67.3	26.0	27.4	23.0	5.1	4.3

The trend previously discussed in BMI standardized BMD is demonstrated for the overall sample population for total body BMD per BMI in *Figure 5.1*. *Figure 5.1* shows that on a total body scale BMI standardized BMD is greatest among the rock climbing group and least among the active group, therefore rejecting the primary null hypothesis. Secondly the trend for shoulder region BMI standardized BMD can be visualized in *Figure 5.2*. *Figure 5.2* shows that rock climbers have an increased BMI standardized BMD at the shoulder region when compared to non-active and active groups, therefore rejecting the secondary null hypothesis. Interestingly, the active groups possess the lowest BMD out of all groups for both sexes. Further statistical analyses were completed to determine the significance of the trends present.

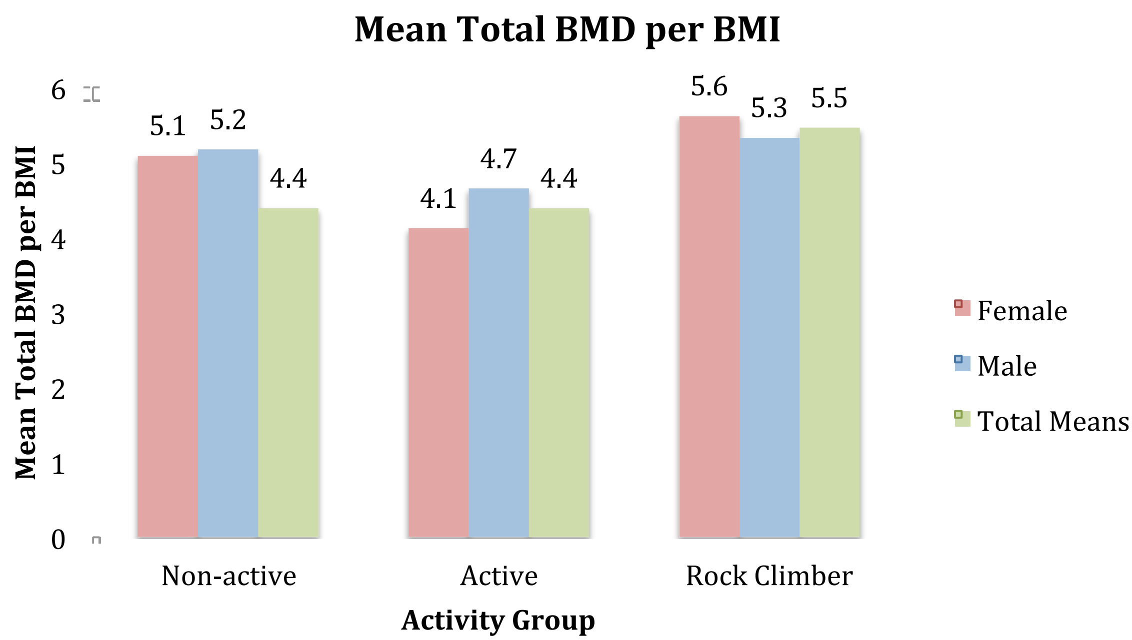

Figure 5.1. Bar graph of mean total BMD by activity group and sex – BMI standardized. This bar graph shows that rock climbers on average have an increased BMI standardized total body BMD when compared to active and non-active groups.

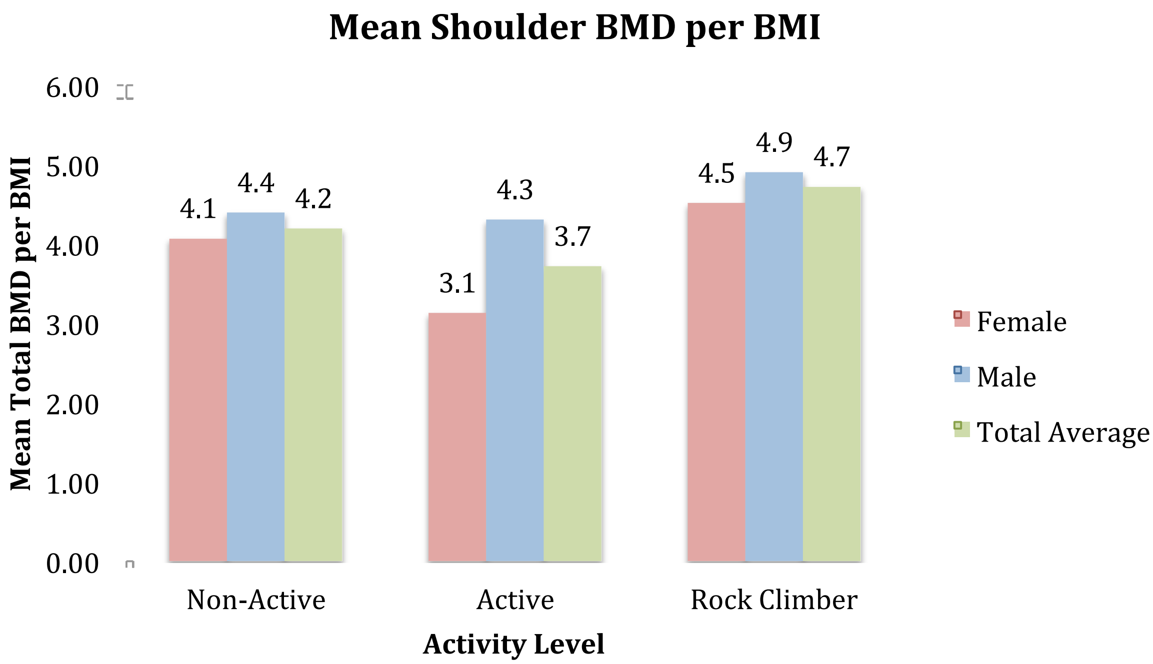

Figure 5.2. Bar graph of mean shoulder BMD by activity group and sex – BMI standardized. This bar graph shows that rock climbers on average have an increased BMI standardized shoulder region BMD when compared to active and non-active groups.

Multiple regression analysis

A multiple regression analysis (MRA) was completed to organize variables based on how much each variable contributes to BMD. It was found that only bone mineral content (BMC, p-value <0.001) and region area (p-value < 0.001) were statistically significant factors influencing BMD values. This was to be expected because BMC and region area are the two measurements that make up BMD (grams BMC per region area in cm^2).

Based on MRA, and after removing BMC and region area, the most significant contributing variables for total body BMD were total body fat, sex (male), and weight, indicating that they are the variables that best predicted total BMD. Due to variable significance and the research questions, primary variables including sex, and activity level were chosen rather than the best predicted variables derived from the MRA. The same process for MRA on shoulder region BMD was followed, resulting in the same primary variables, total body fat, sex (male), and weight. Due to the research questions presented in this thesis, *fitness* coded as 3 general categories (non-active, active, and rock climbing) was chosen as a primary qualitative variable and needed to be considered in all further analyses. Therefore, even though the MRA deemed *fitness* was a non-significant predictor of shoulder BMD, it was still used as a primary variable because of the hypotheses and predictions. The lackluster results of the MRA could indicate that the fitness measure was poorly estimated and that none of the target variables are strongly related to BMD. Aside for learning that more analysis could better categorize the fitness measure in regards to an MRA, the MRA itself was not used. While the process of MRA is important the chosen variables for the following analysis of variance were chosen in order to answer the proposed hypothesis and research questions and are not a reflection of the MRA itself, because as previously stated, the MRA only identified variables not directly questioned in the original hypotheses and predictions.

Analysis of Variance

An analysis of variance test was used to determine the statistical significances between the means of BMI standardized total body and shoulder region BMDs, amongst activity groups with respect to sex. Due to a small sample size and a non=normal sample distribution a Kruskal-Wallis one-way analysis of variance was used to establish statistical differences between groups. Through the Kruskal-Wallis, statistical significance is determined if the p-value is low ($p \leq 0.05$), indicating that the two groups are significantly different from one another. In contrast if the p-value is high ($p \geq 0.05$), then the two groups are not significantly different from one another.

The first sets of analyses were performed on BMI standardized total body BMD in order to established differences in total body BMD between activity groups across sex. It was found that at the $p \leq 0.05$ significance level, there is a statistical difference in BMI standardized BMD between rock climbers and active groups for both sexes. At the $p \leq 0.10$ significance level, there is a statistical difference in total BMD (BMI standardized) between female active and female non-active groups. *Table 5*.3 shows the results of the Kruskal-Wallis test for total body BMI standardized BMD. A single asterisk represents a p-value < 0.10 highlighting a trend towards significant, and a double asterisk represents a statistically significant p-value <0.05. In general total body BMD (BMI standardized) is approaching significance between all groups, indicating that there is a trend in overall BMD related to activity level.

Table 5.3. Kruskal-Wallis for total body BMI standardizes BMD between male and female activity groups.

Independent variable	**Dependent variable**	**P-value**
1. Female Active	Female Rock Climbers	0.0201**
2. Female Active	Female Non-Active	0.1521*
3. Female Non-Active	Female Rock Climbers	0.1962
4. Male Active	Male Rock Climbers	0.0527**
5. Male Active	Male Non-Active	0.2967
6. Male Non-Active	Make Rock Climbers	0.6847

Key: ** Represents p-value < 0.05; * Represents p-value < 0.1

The second set of analyses was performed on BMI standardized shoulder region BMD in order to establish differences in the effects of climbing specific musculature on the bony morphology of the shoulder. Six paired Kruskal-Wallis one-way analysis of variance tests were performed across activity level for both sexes to ascertain differences among the six activity-by-sex groups. In general it was found that the climbers maintained an increased median BMD of the shoulders when compared to non-climbers. Specifically, at the $p \leq 0.05$ significance level, there is a statistical difference in BMI standardized shoulder region BMD between female rock climbing and female active groups. Additionally, at the $p \leq 0.1$ significance level, there is a statistical difference in BMI standardized shoulder region BMD amongst all activity groups across both sexes, except for between active and non-active males. *Table 5.4* provides a description of the Kruskal-Wallis values for shoulder region BMI standardized BMD. A single asterisk represents a p-value < 0.1 and a double asterisk represents a statistically significant p-value < 0.05.

Table 5.4. Kruskal-Wallis for shoulder region BMI standardized BMD between male and female activity groups.

Independent variable	Dependent variable	P-value
1. Female Active	Female Rock Climbers	0.0201**
2. Female Active	Female Non-Active	0.1025*
3. Female Non-Active	Female Rock Climbers	0.0932*
4. Male Active	Male Rock Climbers	0.0674*
5. Male Active	Male Non-Active	0.6547
6. Male Non-Active	Make Rock Climbers	0.0881*

Key: ** Represents p-value < 0.05; * Represents p-value < 0.1

The results of the statistical analyses weakly reject the H_{0A}; that, there is no significance difference in BMI standardized BMD among rock climbing, active, and non-active groups, regardless of sex. This is because it was shown that at the 0.05 confidence level that only two pairs of activity groups were statistically significant from one another, female rock climbers versus female active individuals, and male rock climbers versus male active individuals. Being that only two of the six paired groups showed statistical significance, H_{0A} can be rejected for the rock climbing versus active groups for both sexes. Likewise, H_{1A}, that there is a significant difference in BMI standardized BMD among rock climbing, active, and non-active groups, regardless of sex, cannot be rejected at 0.10, but does indeed show a trend in the direction predicted.

Breaking H_{0A} and H_{1A} into the six specific paired tests does, however, show the trends seen in the descriptive statistics. It was seen that the mean total body BMI standardized BMD for rock climbers was highest across all activity groups, regardless of sex, with the active sample possessing the lowest average total body BMI standardized BMD. This trend corresponds with the significance test and proves that the only statistically significant paired test is between the rock climbing and active samples, regardless of sex; an expected result. Additionally when comparing the female active to the female non-active sample the p-value is approaching significance at the 0.10 confidence level, again highlighting a trend in the data towards significant sample differences.

The results are similar for H_{0B}. Due to statistical analyses H_{0B}; there is no significant difference in BMI standardized shoulder BMD among rock climbing, active, and non-active groups, regardless of sex, can be weakly rejected. It was shown at the 0.05 confidence level that only one paired test, female rock climbers versus female active individuals, was statistically significant. Therefore, it can be argued that H_{0B} should be weakly rejected as a majority of the pairing was found to be statistically insignificant at the 0.05 confidence level. However the result does correlate with the trends seen in the samples mean shoulder BMI standardized BMD distribution, where the highest shoulder BMI standardized BMD was found among the rock climbing groups and the lowest mean shoulder BMI standardized BMD was found among the active groups, regardless of sex. This indicates that H_{1B}; changes in BMI standardized shoulder

BMD can be partially attributed to habitual shoulder specific activities in males and females, should not be rejected.

Breaking H_{0B} and H_{1B} into the six specific paired tests does illustrate the patterns seen within the data in regards to the shoulder region. Tests show that all six pairings, except for male active versus male non-active, are statistically significantly different at the 0.1 confidence level. These results speak to the trends seen within the descriptive data and demonstrate that the sample is approaching significance at the 0.05 levels between all activity groups regardless of sex. This trend indicates that H_{0B} can be generally rejected at the 0.1 significance level; stating that, BMI standardized shoulder BMD can be partially attributed to habitual shoulder specific activities in males and females. Furthermore, this analysis describes a trend in both overall BMD and shoulder BMD values, where rock climbers possess denser bones compared to active and non-active individuals.

Chapter Five Summary

Chapter five summarized the results of the present pilot study. It is evident that that there is a general trend towards a higher BMI standardized BMD for both the whole body and the shoulder region, among rick climbers. MRA displayed a significant relationship between BMC, region area, and BMD for both whole body and shoulder regions. MRA analysis was not used for any other variable analysis or statistical significance. Significance testing via Kruskal-Wallis one-way analysis of variance of BMI standardized total body BMD showed significant differences between female active and female rock climbers as well as between male active and male rock climbers at the $p \leq 0.05$ level. Additionally, Kruskal-Wallis one-way analysis of variance for BMI standardized shoulder region BMD showed significant differences between female active and female rock climbing groups at the $p \leq 0.05$ levels. The results presented here allow rejection of both of the original null hypotheses.

CHAPTER SIX

Discussion

The results of this study indicate that there is a potential use for using modern human proxies as comparisons for modeling and understanding both modern human and early hominin climbing adaptations. This pilot study developed a new approach to examining how rock climbing affects bone remodeling at the shoulder in modern humans. This research was intended to provide a reliable proxy for understanding the effects that climbing had on analogous anatomy in hominins, namely the shoulder. It has been well documented that bone responds to its physical environment and that activity is a primary driver of bony deposition and resorption (Kirchner et al. 1995, Nichols et al. 1994, Whalen and Carter 1988, Sylvester et al. 2006, Havill et al. 2007, Haapasalo et al. 1998, Forwood 2008, Barak et al. 2011, Ruff et al. 2006, Gross et al. 2010). Additional factors contributing to overall bone formation (e.g., diet, sex, age, growth and development) are also well researched (Havill et al. 2007, Haapasalo et al. 1998, Forwood 2008, Kirchner et al. 1995) but were not specifically addressed in this study due to time constraints. Sex, age, general health and activity patterns for each participant was obtained from the survey given at the beginning of the pilot study. Descriptive statistics on these characteristics were addressed but no significance was found among them, nor were they specifically discussed in the results. General descriptive characteristics such as these were collected in order to define the sample and eliminate confounding variables. More specifically it was identified that none of the descriptive characteristics associated with the individuals in the sample, aside from sex, aided in predicting shoulder BMD.

The sample included participants between the ages of 18 and 35 years old in order to exclude the influence of growth and development on bone as well as any effects of menopausal or other degradational factors of bone loss. It should be noted that some of the younger male participants could have some growth factors that impacted the study. For example it has been shown that the clavicle is one of the last bones to complete formation at around 21 years old, especially in males, and has been previously reported as a reliable age identifier in bioarchaeology (Walker and Lovejoy 1985). This factor may have influenced the results of some of the male sample; however, due to the mean age of 26 years old it is unlikely that the development of the clavicle in some individuals affected the results on a whole. Additionally, the age range used in this study is a representation of the environment where it was conducted, a university campus.

This study aimed for an equal sex sample, where sexes were analyzed independently to avoid sex-based biases on activity patterns or BMD. Dietary intake was largely ignored due to time restrictions for the study. Additionally, as stated in the previous results chapter, due to the relatively small sample size (n=32) there were limitations to how the results are interpreted and the overall strength of the predictions described. The remainder of this discussion will present interpretations of 1) the study results, 2) the use of modern humans as analogues to early hominin climbing adaptations, 3) why rock climbers were chosen as a sample population, 4) the choice of using the DEXA scanner, and 5) an in depth look at the shoulder as the region of interest.

Study Interpretations

Stemming from interest in australopithecine climbing morphologies, the pilot study presented in this thesis aimed to better understand the effects of modern human rock climbing on bone deposition and resorption within the shoulder, specifically at the deltoid tuberosity on the proximal humeral shaft. Due to the anatomy of the shoulder girdle remaining relatively unchanged through time and because modern humans are still highly capable vertical climbers, examining climbing behavior though modern joint morphology was possible. It was predicted that modern human joint morphology could be used as a proxy for understanding past hominin climbing behavior. The degree and extent of morphological change due to climbing behavior was measured in bone density. Bone density was used to indicate a change in activity level, specifically with regards to rock climbers. The hope was that behavioral categories would be reflected in the sample and that a difference between habitual climbers and non-climbers would show. The expectations in differences between sub samples (particularly between sexes and activity grades), was then used to assess predictions for boney responses to climbing in past hominins. Generally this study aimed to provide further analyses and a new view on how functional morphology is looked at in both modern humans and as a window to past behavior.

The study examined 32 individuals, male and female, between the ages of 18 and 35 years old, who ranged on an activity scale from non-active individuals, to active individuals, and rock climbing individuals. Participants were categorized into their sex and activity groups based on a self-assessment survey on physical activity and rock climbing behaviors, resulting in six different categorical variables. Each group was tested for significant differences in total body BMD as well as shoulder region BMD, where all BMD variables were first standardized per individual by using the individual's BMI. The preliminary null hypothesis (H_{0A}) was that there is no significant difference in BMI standardized BMD among rock climbing, active, and non-active groups, regardless of sex. If H_{0A} could be overturned then the secondary hypothesis (H_{0B}), that there is no significant difference in BMI standardized shoulder BMD among rock climbing, active, and non-active groups, regardless of sex, would be addressed.

It was found that the sample weakly rejects the null hypothesis for both the preliminary and secondary hypotheses, indicating that there is a significant difference, albeit small, between activity groups in BMI standardized BMD for both total body and shoulder region measurements regardless of sex. As stated in Chapter 5, when the hypotheses are broken into the six pairs of specific tests used in the data analysis the results become more clear. It was shown that female active and female rock climbing group comparisons are the most statistically significant out of the whole sample for total body BMD. For the shoulder region, all of the categorical pairings are significant at the α=0.1 level, except when the male active participants are compared to the male non-active participants. This supports the interpretation that rock climbing encourages a bony response in the shoulder region to support muscle development, producing a quantitatively more dense shoulder region. Interestingly, it appears that activity patterns produce more of an impact on BMD in women compared to men. This implies that women who do not participate in physical activity have substantially lower BMD compared to women who do participate in physical activity. In contrast males who do not participate in physical activity have lower BMDs than males who do participate in physical activity, but not significantly lower. This is possibly related to a hormonal interaction in females due to the estrogen/calcium interactions within bone deposition and resorption that happens at menopause (VanPutte et al. 2014). However this is unlikely because the age restrictions placed on the sample were placed in part to eliminate the possibility of menopause in the female participants.

Modern Humans as Analogues

This thesis utilized modern human anatomy and locomotor behavior as analogues to past hominin anatomy and locomotor behavior. This is not a controversial technique, however it does beg questions about the use of modern humans as proxies for at least two different genera of hominins, i.e., early *Homo* and *Australopithecus*. When compared to early hominins, modern humans are more linearly built, are typically taller, and heavier, and have larger brains (Larsen and Repcheck 2008). Modern humans have also lost some of the morphologies that indicate habitual use of trees – elongated fingers and toes, and more ape-like limb proportions (Ward 2013, Larson 2013, Harmon 2013). In addition, environmental reconstructions suggest that australopithecines lived in at least partially wooded environments and relied on trees for resource acquisition (Potts 1998, Behrensmeyer and Reed 2013, Stern and Susman 1983, Stern 2000, McHenry and Berger 1998). In attempting to better understand how australopithicines might have used trees in resource acquisition, research designs that rely on proxy species, like related extant animals of similar diets, body sizes and from similar environments are used for insight into past behavior (Behrensmeyer and Reed 2013). However, modern humans are none of these characteristics. Modern humans are much larger than early hominins, require a diet that is vastly different, and with the exception of very few remote cultures, humans no longer live in environments that resemble the early hominin landscape. With all that said, it is difficult to assess why modern humans are good analogues for examining past behavior. Humans have roughly tripled in size since Australopithecus however our anatomy and the way we move through varying substrates, in regards to forests and rock walls, can be argued to be very similar (see Larson 2013 in The Paleobiology of *Australopithecus*). This thesis focused on the use of anatomical similarities in the morphology of bone, particularly at the shoulder, to address behavior. It was stated in Chapter 2 that the anatomy of the shoulder girdle has remained relatively unchanged through time and that because of this it is a good region for comparisons between modern humans and early hominins.

Of course this is not a foolproof science, and there are obvious challenges that present themselves while making assumptions about past behaviors based on present ones. First and foremost it is only a prediction. Using any modern proxy only works because of the working assumption that past behaviors must have been similar to modern ones based on fossil similarities seen in modern samples. For example we know that early hominins were bipedal because they possess similar identifiable skeletal markers described on modern human femora that are biomechanically linked to aiding in bipedal movements (Ward 2013, Crompton et al. 2008, Crompton et al. 2010), not because there has been an instance of observing australopithecine locomotion. When considering australopithecines, neither chimpanzees nor modern humans are great analogues. Chimpanzees are poor analogues due to variances in size, diet, and habitat, however it can also be argued that those differences are less so than the differences between modern humans and early hominins. As previously stated, modern humans are poor analogues because they do not interact with the same environmental influences that early hominins did, they possess different diets and are much larger. However, there is also no other animal alive today that is more similar to an australopithecine than a chimpanzee or a modern human. This study did not have access to chimpanzees; so modern humans were used as the default analogy, and it is argued that similarities in anatomy further support this decision.

As reviewed in chapter three of this thesis it is understood that arboreal locomotion was a factor in the early hominin locomotor pattern, due to environmental reconstruction and morphological characteristic present in the fossil record (Sylvester 2006, Crompton et al. 2012). The uses of modern humans as proxies' allows for the examination of climbing behavior on shoulder morphology with the hope of better understanding how form and function are related. This is further supported due to the remarkable similarities in shoulder morphology across time

(Ward 2013, Larson 2013). This factor made the shoulder girdle a good choice of examination because in both modern humans and early hominins the shoulder is organized to allow equal amounts of flexibility and stability (Freeman and Herron 1998, Sylvester 2006), qualities necessary for suspensory and vertical climbing locomotion, as previously reviewed in this thesis. Because it is not confidentially known how early hominins locomoted through an arboreal environment, future research should include varying locomotor patterns of non-human primates, in order to provide a more holistic view the effects of climbing on bone.

In the study presented here on shoulder density, it would be ill-advised to assume that the increased BMD in the shoulder regions of rock climbers is strictly due to the rock climbing behavior. Further comparisons across other arboreal, suspensory, and vertical climbing behaviors need to be analyzed in order to gain a better assessment of how the types of activity effects shoulder morphology. Again it is important to keep in mind that the sample size used in this study was small, and that any week or null results could be greatly affected by increasing the sample size. It is argued that an increased sample size would illuminate the significant differences between the sub-groups and allow for more in depth statistical analyses. Additionally a study comparing other taxa to modern human anatomy is necessary to better understand if modern humans are in fact the best proxy for this type of analysis.

Ultimately this research aims to develop another tool for better understanding early hominin vertical climbing behavior based on a modern proxy, rock climbing behavior and morphology. The goal of using a modern proxy is to set up a framework, or a set of expectations, about the fossil record that can be quantitatively tested in a modern sample so that the results can be further applied to the fossils themselves. This process provides a window into testable assumptions about the past, due to similarities in hominin and modern human anatomy.

Through application and understanding of how modern human analogues respond to the biomechanical pressures of climbing, it is possible to gain a greater understanding of the morphologies seen in the fossil record. Additionally any result found on a modern sample could be used as a basis of reference for tests within the fossil record itself. This would create a modern comparison anchored in bony morphology and supported by anatomy.

Why rock climbers?

This thesis focuses on modern human rock climbers as a proxy for early hominin climbing behavior, begging the question: why rock climbers? Rock climbing, especially bouldering, utilizes core muscle groups that are an integrated part of the relatively primitive suspensory shoulder girdle, a synapomorphy of the hominoids. Muscles such as the supra- and infraspinatous, subscapularis, teres minor, deltoids, latissimus dorsi, pectoralis major and minor, trapezius, and coracobrachalias, act as critical abductors and adductors necessary for suspensory movements. When comparing human bouldering to gibbon brachiation and suspension, for example, there are some stark similarities in the shoulder movements.

One prominent example can be seen when rock climbers execute dynamic movements (dynos) while bouldering. A dynamic movement is defined as a large leap or swing where the arms must catch all or most of the climbers body weight with the arms and hands on a hand-hold (Preuit personal communication 2014, Long 2010). In a dynamic movement, the legs act as the propulsive force, the back and abdominals must flex to increase stability in the body's core, while the arms swing above the head due to the flexibility of the shoulder joints, lastly the hands and forearms must produce great gripping strength upon contact with the rock or wall. Upon completion of a successful dyno all of the body weight remains suspended from the shoulders, arms, and fingers. Additionally, while bouldering, the arms typically remain in the adducted position, near shoulder height or above or near the head; another similarity to most suspensory apes while they locomote in trees. This allows for increased muscle strength (Sylvester et al. 2006, Pruit personal communication 2014), as well as supports the joints of the shoulder girdle to prevent joint shear and displacement. Once again, the hominin shoulder is built for stability while providing the flexibility necessary to support hyper abduction of the glenohumeral joint as well as tensile hanging forces (Sylvester 2006, Veeger and van der Helm 2007).

Lastly, rock climbers' posses a culture within their sport. It seems that they spend most of their time recreationally training for such skills as the dyno, making them the ideal group of modern humans to study shoulder morphology related to climbing behavior. It is assumed that the amount of time spent recreationally rock climbing is long enough to potentially modify the joint and bones of the shoulder region. It is understood that bone can remodel in six to eight week increments depending on the intensity and frequency of the activity (Wallace et al. 2012, VanPutte et al. 2014). With this principle in mind is it assumed that rock climbers who spend roughly six consecutive weeks rock climbing will impact the morphology of their bones. Additionally, studying rock climbing during childhood and adolescence could potentially provide greater information about how the shoulder responds to continuous tensile forces during growth (Haapasalo et al. 1998, Wu 2004).

This study was able to show that recreational rock climbing has a positive effect on bone deposition, leading to an increase of BMD. A next logical consideration to this study would be to examine the exact lengths of time spent climbing and see if there are any relationships to the participant's BMD. This would show what level of intensity and frequency is necessary for bone to respond to the activity, answering the question – what is long enough or habitual enough to promote bone deposition while climbing?

Activities such as rock climbing could allow for greater bone formation due to increased stress causing the joint to more closely resemble other climbing primates. A future examination of climbing on non-human primates BMD in relation to their climbing behavior would provide additional comparisons important to understanding the duration necessary for climbing to impact bone remodeling. A chimp sample, for example, would provide excellent information about the morphologic differences terrestrial quadrupedalism and suspensory locomotion have on shoulder morphology. Further examination onto the direct stressors involved in climbing and their impact on bony morphology needs to be completed. This would include quantifying muscle forces activated during climbing and to what degree of activation is necessary to complete the activity. In particular isolating which muscles of the shoulder complex are utilized most while vertical climbing compared to while suspending or brachiating would provide insight into where the bones would be likely to first remodel, based on muscular origin and insertion sites. All in all, modern human rock climbers provide researchers a window into how climbing impacts bony morphology and are a good analogue to studying aspects of past climbing behaviors.

Why use a DEXA?

It is important to reflect on why a DEXA scanner was chosen to analyze density rather than observational robustness. Robusticity is often a characteristic used to describe how large and defined a feature on the bone is or when comparing the exterior appearance of different individuals to one another (Ruff et al.1993, Shackelford 2003). While robust and gracile are useful terminology for obtaining a general description of the sample, they are still observational qualifiers, and these qualitative results can vary from researcher to researcher due to observational bias. For example, the differences between a “3” and a “4” on a robusticity scale may be so minimal that either score could be interpreted as a correct assessment of the feature at hand. When comparing two similarly robust individuals this observational bias can become a problem. Conversely, calculating density is a quantitative measurement resulting in a numeric value that can be ranked from lowest to highest, creating a much less biased measurement for which individuals are larger versus which are smaller.

Using a DEXA scanner also allowed the analysis of modern humans by giving a safe and non-invasive method for collecting bone measurements on living individuals. It would have been nearly impossible to assess humeral robusticity or density on a living individual without removing the flesh, a process that by definition would have been neither safe nor non-invasive. Hence, DEXA results provide a new way to assess living bone for research purposes without the use of radiographs, MRI machines, or CT scanners. DEXA also allowed for the creation of a region of interest. The region of interest was created around the should girdle using known bony landmarks to aid in its creation. Unfortunately it is difficult to create a region from a whole body DEXA scan due to the low resolution of specific areas. Due to variance in individual size and the image resolution it was nearly challenging to make each individuals regions identical. However because of the method used it is considered that the regions are comparable to one another and slight error due to region outlines is forgiven.

Furthermore, DEXA measurements are trusted to have less than 1% error in precision for total body BMD and roughly 6% error in precision for regional measurements, and all measurements are comparable to other visualization methods (Mazess et al. 2009). It would be interesting to assess the precision of these techniques by comparing the DEXA measurements against a cortical thickness measurement retrieved from a CT scan or radiograph of the same individual. This may also help to further understand the relationships between cortical thickness and bone density on a more holistic scale, and possibly increase understanding on bone remodeling. Additionally it would also better allow the use of this thesis's data in the study of fossilized remains, such as the hominin record.

Region of interest

This study focused on the shoulder region of modern humans and the effects of rock climbing on bone remodeling. It was assumed that any type of vertical climbing, including rock climbing, utilizes an extreme amount of shoulder musculature, and therefore the shoulder region may be a good location to look for differences in bony morphology between climbing and non-climbing activity groups. Previous studies on region specific BMD analysis have shown that particular activities can have various effects regionally on BMD (Nichols et al. 1994, Sylvester et al. 2006). For example, over a 27-week training session, gymnasts show an increased total BMD, as well as regional increases within the lumbar spine and proximal femur (Nichols et al. 1994), indicating the effects of the training session on the gymnast's BMD. A more directly related example is the finding of Sylvester and colleagues, which stated that rock climbing promotes osteological changes in the hands and fingers (Sylvester et al. 2006). Using radiographs Sylvester and colleagues calculated medullary cavity width, cross-sectional area, total width, and second moment of area on the hands for each participant (Sylvester et al. 2006). Their findings show that recreational rock climbers on average have an increased cross-sectional area and a decreased medullary cavity width when compared to non-climbers (Sylvester et al. 2006). This result indicates that rock climbing promotes the subperiosteal deposition of bone in the hands and fingers of rock climbers (Sylvester et al. 2006), and directly supports the preliminary results of this thesis's pilot study.

Both of these studies agree with this pilot study in that specific activity promotes increased bone deposition in regions that are specific to the activity itself. For instance, gymnastics is a high impact sport causing repetitive and high-energy compressive forces through the lumbar spine and the proximal femur; therefore, it would be expected to see bone respond to the forces active on these regions. The same concept can be thought of for rock climber's hands, where there are intensive tension forces acting on the hand bones in rock climbers in order to grip the wall. In this study the same principle is applied to forces acting on the deltoid tuberosity within the shoulder region, and it is assumed that the tension forces created by the deltoid muscle on the proximal humerus will evoke bone remodeling, creating a stronger muscle attachment site for the deltoid muscle.

Given the nature of the present results it can be argued that the shoulder region may not have been the most ideal location to examine variances in BMD across rock climbing activity groups, though the non-robust results could also be due to poor sample size. Regardless of sample size, the shoulder girdle is an important region to look at for behavioral indicators in the fossil record because it has remained relatively unchanged trough time and can therefore be compared to modern arboreal traits in hominoids, where in contrast the hands vary across all hominoids. Suspensory hominoids are known for their long upper limb proportions including lengthened and curved phalanges (Larson and Repcheck 2008). Knuckle-walkers have modified suspensory phalanges that include a groove for the tendons that flex them allowing greater support for weight bearing (Fleagle et al. 2013). Modern humans have short upper limb proportions and short phalanges relative to our ape cousins, where our australopithecine ancestors appear to have some what intermediate digital length compared to modern humans and modern suspensory hominoids (Ward 2013, Larson 2013, Richmond et al. 2001, Green and Alemseged 2012). This highly variable morphology makes comparisons between modern humans and our ancestors more challenging because the researcher would have to consider a more representative sample that includes all types of hand morphology, where as the shoulder region provides a more consistent morphology across time. Lastly, the forearm and elbow joint may show a stronger morphologic signal compared to the shoulder because it serves as the origins of hand and finger flexors, muscles necessary in successful climbing. Examining the morphology of the elbow using the methods described in this thesis may aid in more comprehensive survey of the effects of rock climbing on modern anatomy.

Chapter Six Summary

This thesis was concerned with measuring and understanding any differences in shoulder region BMDs of rock climbers versus active and non-active individuals, in hopes to better understand the effects of modern human climbing on shoulder morphology. It is assumed that having a better understanding on modern morphology and how it relates to behavior allows researchers to better apply behaviors onto past hominins because of the related morphologies found on the fossils. With this in mind, it is then argued that the more we know about how climbing effects modern morphology, the better informed we can be about similar behaviors in the past.

The method of data collection used here required bone to not be completely mineralized and therefore cannot be used on fossil hominin remains themselves. However, previous research supports a strong correlation between bone density and cortical bone thickness, a measurement that can be obtained from fossils, and hence giving researchers a new tool to examine fossils with. Additionally, with further investigation it is this researcher’s belief that markers on modern human bones such as deltoid tuberosity robusticity as part of the proximal humerus’s density can be attributed to climbing. This in turn presents a new characteristic that can be attributed to the suite of features that are looked for on fossil specimens as indications of climbing behavior. Looking for new features that correspond with specific climbing behaviors is important when trying to distinguish when and to what extent climbing behaviors were an important part of the early locomotor pattern.

This chapter provided an overview of the previously discussed pilot study's goals, hypotheses and results. Chapter six aimed to clarify why modern humans are a good analogue for studying past fossil behavior, and reflected on how this study can inform the fossil record and provide a new set of tools and concepts for studying and understanding hominin behavior. It reviewed the impact of rock climbing on the body and why modern human rock climbers are sufficient analogues for implying behavior from the fossil record. The importance of using quantitative over qualitative data when describing bony morphology was addressed, with special consideration placed on why the DEXA scanner was chosen. Chapter six addressed questions pertaining to why the shoulder was chosen as a region of interest and why the deltoid and shoulder morphology are critical to this research and to further understanding of the fossil record. The last chapter of this thesis will provide a brief over view of the whole project and its implications on future research.

CHAPTER SEVEN

Conclusion

This thesis focused on human climbing adaptations as a proxy for understanding how climbing behavior affects bone deposition and resorbtion. It is well known that bone responds to the functional environment and that patterned behaviors can leave bony identifiers linking the bones back to the behavior (Goodship and Cunningham 2001, Ruff et al. 2006). It is also well understood that early hominins lived in an environment that was strongly dependent on resource acquisition among the trees (Potts 1998, Behrensmeyer and Reed 2013). Using these principles it was thought that there is likely to be a range of bony landmarks that could aid in identifying the amount of time early hominins spent in an arboreal landscape, and that these markers could be quantified. This study focused on examining the impact that rock climbing has on a living human sample with regards to BMD.

This pilot study assessed the relationship between individuals who actively rock climb and their BMD, for both the whole body and specifically at the shoulder region. The primary prediction was that rock climbing individuals would possess an increased total body BMI standardized BMD, as well as increased shoulder region BMI standardized BMD when compared to active and non-active individuals regardless of sex. A sample of 32 individuals (females n=17; males n=15) ranging from rock climbers to active individuals and non-active individuals were selected. Participants were asked to complete a self-assessment survey on their general health and activity levels, a push up test, body measurements and a standardized DEXA scan. The participants were categorized into groups based on activity level and rock climbing abilities; from there the categorized groups were analyzed for statistical significance between and among them.

The primary null hypothesis stated that there is no significant difference in BMI standardized bone mineral density (BMD) among rock climbing, active, and non-active groups, regardless of sex. This hypothesis was over turned in that there was a weak significant difference in BMI standardized bone mineral density (BMD) among rock climbing, active, and non-active groups, regardless of sex. Although the signal was stronger in the female sample compared to the male sample. The secondary hypothesis stated that there is no significant difference in BMI standardized shoulder bone mineral density (BMD) among rock climbing, active, and non-active groups, regardless of sex. This hypothesis was also overturned in that there were weak significant differences in BMI standardized shoulder bone mineral density (BMD) among rock climbing, active, and non-active groups, regardless of sex. It was then further argued that this difference in BMI standardized shoulder BMD can be partially attributed to habitual shoulder specific activities in males and females, with some influence stemming from rock climbing. It was found that rock climbing has a positive effect on bone deposition at the proximal humerus and shoulder, creating increased density measurements of both the shoulder and whole body when compared to groups of both active and non-active individuals.

The results of this pilot study illuminated patterns among the sample that support the initial predictions. Rock climbers did have increased total body BMD as well as increased shoulder region BMD however these results were weakly statistically supported. The weak statistical significances indicate a sample population that is too small or not diverse enough in regards to activity level contrast. It is expected that an increased sample size would better illustrate the trends seen in this study, and potentially create stronger correlations within the sample. Additionally, exploration into the mechanics of how modern human rock climbers vertically climb would provide a deeper understanding and analysis of contemporary climbing ability, movements, and forces exerted, and could allow comparisons to other primate climbing studies. This type of analysis could then further aid to the current research on morphologies related to climbing and arboreal locomotion. (See Yamazaki et al. 1984, Bertram et al. 1999, DeSilva 2009, Hanna et al. 2008, Hirasaki et al. 2000, and Isler 2005 as a selection of past research on hominin and modern human climbing.)

Future directions

One of the main concerns with examining BMD with the intentions of applying it onto the hominin fossil record is that fossils do not have bone density because they are entirely mineralized. With that said, it is understood that in adult humans, BMD increases with the deposition of bone, and subsequently increases the cortical thickness of the shaft (Sylvester et al. 2006, Wallace et al. 2012, Beamer et al. 2002, Gosman et al. 2013, Tingart et al. 2003). It has been shown that cortical thickness is a reliable predictor of BMD of the proximal humerus (Tingart et al. 2003). This implies that a transition from a modern human proxy using BMD to establishing behavioral activity relationships, and then inferring similar behavioral patterns from fossils cortical thicknesses is not terribly farfetched. Additionally, it opens the door for other types of data collection and analysis on living modern humans without endangering them. Using living modern humans allows for true behavior data collection, in this case climbing behavior was observed and collected via a survey. Observation and survey data were critical to processing how climbing was assessed and scored for activity category placement in this thesis and in future research the survey data should be more deeply analyzed and attention would be focused on scaling rock climbers for duration, frequency, and difficulty before looking at statistical significances across BMD. It has already been shown that rock climbing causes morphological and physiological changes in the human body (Sylvester et al. 2006, Sheel 2004, Watts 2004). It is therefore believed that further research of this thesis's type could provide a much deeper understanding of how each factor of habitual rock climbing, i.e. frequency, duration, or difficulty, effect bone deposition.

The next step to further this research is to increase the study's sample size and more strictly identify activity categories, because it has been assumed that a larger, more equally and normally distributed sample size may strengthen the significance of the results. It would also be important to include rock climbers who are more extreme in their activity levels. Perhaps a comparison of professional rock climbers against non-active individuals would provide the most striking statistics, however this is just conjecture. Additionally, cortical thickness data at the region of interest, proximal humerus and deltoid tuberosity, would be taken as a comparison analysis against the shoulder region BMD data in order to support the literature (Sylvester et al. 2006, Tingart et al. 2003) on the relationship between BMD and cortical thickness, as well as its relationship to rock climbing . This process would necessitate further data collection methods such as MRIs or CT scans, as DEXA scanning does not show cortical thickness. If positive correlations between BMD and cortical thickness at the proximal humerus and deltoid tuberosity are present, then it could be inferred with confidence that cortical thickness at a muscle attachment could be used as an indicator to assume regular use of that muscle. It could then be extrapolated that the subject depended on an activity or locomotor pattern that relied on the particular muscle's function. This supporting evidence is critically important when examining fossil evidence for habitual vertical climbing behaviors, because it gives a quantitative assessment to a presumed behavior or adaptation.

In future research it would be important to consider the deltoid muscle and other muscles that have a similar insertion point on the proximal humerus. The muscles of the shoulder girdle are all activated while climbing, and therefore are important to consider when relating the present study to the hominin fossil record in attempts to infer climbing behaviors. Future research correlating BMD measurements at specific locations to cortical thickness would help to clarify the use of BMD in future research and would help to gain understanding about hominin functional morphology. This preliminary research highlights the utility of drawing analogies from BMD patterns of a modern human sample and, with further research, these conclusions may provide insight into early hominin anatomy and morphologies related to climbing behavior.

This thesis aimed to evoke interest in additional data collection strategies for future research projects using modern humans as proxies and proved that DEXA may be a powerful data collection tool on living participants due to its safety, conservative time requirement and commitment necessary for participants. Additionally, it asked questions related to early hominin climbing behavior and attempted to use modern rock climbing as an analogue due to similarities in anatomy, morphology and related vertical climbing behavior between the groups. It brings to question ideas about modern human movement and behavior that may be considered deviant from the norm. Rock climbing is not a common locomotor practice in most modern humans; however, there is a habitual practice to the culture of rock climbing that makes it synonymous to early hominin climbing behavior.

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APPENDIX 1

Survey ID:AF_

Bone Mineral Density in Habitual Climbers: an analogue for early hominins?

Age:
Sex:

<u>Part 1: Health and Wellness</u>

1. Do you take any prescription drugs? (Please circle.) Yes No
   a. If yes, please briefly explain.

2. Do you take any non-prescription drugs, including performance enhancers or diminishers?

   Yes No

   a. If yes, please briefly explain.

3. Have you ever been diagnosed with joint problems, osteoporosis or other diseases or conditions associated with bone loss?

   Yes No

   a. If yes, please briefly explain.

<u>FOR FEMALES ONLY</u>
Males Please Continue at <u>Part 2: Climbing Skills</u>.

1. Are you currently pregnant? Yes No

2. Have you reached a phase of menopause? Yes No

   a. If yes, which stage? (Please circle one.)

   Perimenopause Natural Menopause Postmenopause

Part 2: Climbing Skills

1. Do you consider yourself a frequent recreational rock climber? Yes
   No

   If NO skip to question #2.

   If Yes,

   i) Do you climb outdoors or indoors? (Please circle.)

   Outdoor Indoor Both

Please indicate what level of climb you typically complete for outdoor or indoor rock climbing or both.

   ii) What level of climb do you complete on average?

   (a) Outside:

   (b) Inside:

   iii) What is the hardest level that you have completed?

   (a) Outside:

   (b) Inside:

   iv) How long ago did you complete the hardest level of climb?

   v) If you participate in both outdoor and indoor climbing, do you notice a difference in the difficulty between the two? Is indoor climbing harder or easier than outdoor climbing? Why?

2. Do you participate in any other recreational vertical climbing including but not limited to: rock climbing, bouldering, tree climbing, rope climbing, etc.? (Please circle.)
   If NO, Please Skip To PART 3.

   Yes No

a. If yes, what type?

b. If yes, how often?

i. Please circle the number of days per week, on average, you climb.

1	2	3	4	5	6	7

ii. Please circle the number of hours per week, on average, you climb.

1-3	4-6	7-9	10-12	13-15	16-19	≥20

c. If yes, how would you classify your skill level? (Please circle.)

1	2	3	4	5
Beginner		Intermediate		Advanced

3. If yes, on average, how difficult is the vertical climbing you participate in?

1	2	3	4	5
Easy				Very difficult

4. How fatigued did you feel immediately after completing an average climb?

1	2	3	4	5
No Fatigue				Extreme Fatigue

5. What muscles or region of your body would you say you use the most during an average climb?

6. What regions of your body or muscles are most fatigued after an average climb? Which were the least fatigued?

7. In your opinion how often to you think you use those same muscles (indicated in questions 4 and 5) in your daily life? How do you use them; during what types of activities?

Part 3: Other Physical Activity

1. Do you participate in any other physical activity that uses the arm and shoulder? (Please Circle.)
   If no, please skip to Question#2

   Yes No

   a. If yes, what?
      i. Examples: baseball, basketball, boxing, weightlifting, tennis, swimming, wrestling, competitive arm wrestling, gymnastics, etc.

   b. If yes, how often?
      i. Please circle the number if days per week you participate in this activity.

1 2 3 4 5 6 7

      ii. Please circle the number of hours per week, on average, you participate in this activity.

1-3 4-6 7-9 10-12 13-15 16-19 ≥20

   c. If yes, what arm muscles or parts of your arm do you feel are being used most during the activity?

2. Do you participate in any other form of physical activity? (Please circle.)

   Yes No

a. If yes, please describe or list.

i. Examples: cross training, running, cycling, endurance training, track and field, golfing, swimming, etc.

b. If yes, how often?

i. Please circle the number if days per week you participate in the above specified activity(s).

1	2	3	4	5	6	7

ii. Please circle the number of hours per week, on average, you participate in the above specified activity(s).

1-3	4-6	7-9	10-12	13-15	16-19	≥20

3. Do you have a past and or childhood that included large amounts of physical activity? This would include competitive childhood sport, employment that required extreme physical ability, lifting, or any other strenuous activity? (Please circle.)

Yes No

a. If yes, please describe or list.

For Researcher Use Only

Anthropometry Measures:

1) Height

2) Weight

3) Upper arm length (cm)

4) Arm circumference (cm)

Push-Up Test:

ID_Num	Consent	RockClimbers	SEX	AGE	HEIGHT.(cm)	WEIGHT.(kg)	R_UAL.(cm)	R_AC.(cm)
AF_01	Y	N	F	29	166	94.6	35	32
AF_02	Y	N	F	28	172	64.1	34	26
AF_03	Y	N	M	28	179	70.6	35	27
AF_04	Y	N	M	34	168.5	64.8	30	30
AF_05	Y	N	M	23	171	55.6	34	27
AF_06	Y	N	F	35	166.1	60.8	34	28
AF_07	Y	N	F	23	147.32	47.08	29	25.5
AF_08	Y	N	M	24	187.45	65.4	37	26
AF_09	Y	Y	F	26	165.1	60.96	34	28
AF_10	Y	Y	M	26	180.34	70.13	36	31
AF_11	Y	Y	F	24	169	56.4	34	24.5
AF_12	Y	Y	F	28	178.5	72.8	38	31
AF_13	Y	N	M	26	178	89.8	38	36
AF_14	Y	Y	M	25	172	76	36	32
AF_15	Y	N	F	23	162	64.3	34	28.5
AF_16	Y	Y	M	23	181.5	78.8	39	30.5
AF_17	Y	N	F	27	162.5	50	34	25
AF_18	Y	N	M	24	177.5	77.2	36	34
AF_19	Y	N	F	26	171.5	61	36	28
AF_20	Y	Y	M	21	180	71.8	37	31
AF_21	Y	N	M	25	180	74.4	36	30
AF_22	Y	N	F	20	172.5	61.5	35	25
AF_23	Y	Y	F	24	162.5	50.1	31	24
AF_24	Y	N	F	27	166	54.4	33	26
AF_25	Y	N	F	31	169	60.2	34	26
AF_26	Y	Y	M	24	177.04	76.07	37	31
AF_27	Y	Y	M	19	190.5	78.93	40	32
AF_28	Y	Y	M	21	185.42	71.76	38	31
AF_29	Y	Y	F	20	167.64	48.72	36	23
AF_30	Y	Y	F	20	160.02	59.19	33	28
AF_31	Y	N	F	26	142.24	82.1	34	30
AF_32	Y	N	M	34	177.8	85	37	33

L_UAL.(cm)	L_AC.(cm)	%BF_TOT	BMD_TOT.(g/cm2)	BMC_TOT.(g)	Area_TOT.(cm2)	%BF_R_A
36	32	48.1	1.169	2477.8	2119.49	50.6
34	26	41.6	1.094	2123.04	1939.89	52.3
35	27	23.4	1.09	2529.01	2322.12	24.6
30	30	24.3	1.07	1979.57	1848.56	23.5
34	27	19.6	1.09	2051.78	1890.39	16
34	28	28.9	1.117	2238.02	2002.83	29.4
29	25.5	37.2	0.987	1607.16	1627.51	39.6
37	26	13.8	1.133	2591.41	2287.19	12.2
34	28	24.8	1.23	2319.35	1885.4	27.4
36	31	15.9	1.107	2510.35	2267.24	14.1
34	24.5	31.5	1.071	2130.69	1989.78	30.2
38	31	30.8	1.219	2796.46	2294.1	29
38	36	25.5	1.208	2826.35	2339	25
36	32	18.2	1.393	3111.68	2233.85	17.8
34	28.5	32.9	1.149	2188.51	1904.97	35.2
39	30.5	13.4	1.174	2840.79	2418.82	12.2
34	25	26.1	1.128	2004.17	1776.8	28.1
36	34	15.3	1.211	2799.16	2310.99	14.8
36	28	31.9	1.161	2304.91	1984.79	41.4
37	31	14.7	1.225	2758.98	2252.66	11.1
36	30	24.7	1.092	2533.07	2319.05	22.6
35	25	36.4	1.057	2016.5	1906.89	44
31	24	28.2	1.081	1912.23	1769.12	29.4
33	26	27.1	1.151	2271.16	1973.28	25.7
34	26	34.9	1.064	2123.82	1995.92	38.5
37	31	24.4	1.181	2664.36	2256.88	21.4
40	32	16.7	1.234	2898.13	2348.98	14.4
38	31	13.6	1.218	2918.92	2396.56	11.2
36	23	19.3	1.087	1988.54	1829.75	19.8
33	28	24.3	1.258	2314.6	1840.12	21.9
34	30	40.3	1.111	2130.18	1917.64	51.5
37	33	23.4	1.179	2799.6	2374.69	22.5

BMD_R_A.(g/cm2)	BMC_R_A.(g)	Area_R_A.(cm2)	%BF_L_A.	BMD_L_A.(g/cm2)	BMC_L_A.(g)
1.002	83.02	82.89	52	0.964	78.82
0.854	66.78	78.29	52.5	0.789	60.53
0.97	81.75	84.43	25.3	0.88	86.74
0.86	62.87	73.3	24.2	0.85	60.39
0.92	79.12	85.96	16.2	0.91	77.22
0.843	62.14	73.68	30.3	0.844	62.8
0.783	50.21	64.09	43	0.74	46.57
0.929	78.47	84.43	11.6	0.914	85.6
0.923	69.82	75.6	30.3	0.95	78.4
1.08	90.32	83.66	15.1	1.046	95.09
0.868	65.98	75.98	33.5	0.857	59.51
1.071	106.05	99.01	32.5	1.033	101.46
1.138	105.7	92.87	26.3	1.103	102.85
1.201	122.18	101.7	19	1.189	119.53
0.899	79.39	88.26	36.8	0.905	70.51
1.062	119.83	112.82	12.2	1.044	121.75
1.003	80.86	80.59	29	0.953	79.77
1.18	127.66	108.22	15	1.099	117.29
0.83	79.35	95.56	40.5	0.868	82.24
1.167	120.89	103.61	12	1.156	119.78
1.023	111.47	108.99	23.9	0.956	103.09
0.861	67.1	77.9	45.2	0.819	65.37
0.857	69.39	80.97	31.4	0.825	67.09
0.922	76.4	82.89	26.4	0.916	77.67
0.914	83.81	91.72	40.2	0.862	80.02
1.13	126.68	112.06	23.8	1.101	112.36
1.114	135.48	121.65	15.9	1.12	137.93
1.116	131.07	117.43	12.3	1.131	130.67
0.833	67.12	80.59	21.5	0.825	67.13
1.112	95.61	85.96	24.8	1.052	90.83
0.819	81.12	99.01	50.4	0.84	80.95
1.153	122.62	106.3	23.2	1.168	128.6

Area_L_A.(cm2)	%BF_N_A	BMD_N_A.(g/cm2)	BMC_N_A.(g)	Area_N_A.(cm2)	PUSH_UP.(15sec)
81.74	51.3	0.983	161.83	164.63	4
76.75	52.4	0.822	127.4	155.04	2
98.63	24.9	0.92	168.5	183.05	16
71.38	23.9	0.85	123.25	144.68	18
85.19	16.1	0.91	156.34	171.16	16
74.45	29.8	0.843	124.94	148.13	0
62.94	41.3	0.762	96.78	127.02	14
93.64	11.9	0.921	164.06	178.06	19
82.51	28.8	0.937	148.22	158.11	11
90.95	14.6	1.062	185.41	174.61	14
69.46	31.8	0.863	125.49	145.44	3
98.24	30.6	1.052	207.51	197.25	12
93.25	25.6	1.12	208.55	186.12	28
100.54	18.4	1.195	241.72	202.24	23
77.9	36	0.902	149.9	166.17	13
116.66	12.2	1.053	241.59	229.49	9
83.66	28.5	0.978	160.62	164.25	12
106.68	14.9	1.14	244.95	214.9	18
94.79	41	0.849	161.59	190.34	11
103.61	11.6	1.161	240.67	207.23	20
107.84	23.2	0.99	214.56	216.82	18
79.82	44.6	0.84	132.47	157.72	2
81.36	30.4	0.841	136.48	162.33	14
84.81	26	0.919	154.06	167.7	9
92.87	39.3	0.888	163.83	184.59	10
102.08	22.6	1.116	239.04	214.14	22
123.19	15.2	1.117	273.41	244.84	19
115.51	11.8	1.124	261.74	232.94	17
81.36	20.7	0.829	134.24	161.95	13
86.35	23.3	1.082	186.44	172.31	19
96.32	50.9	0.83	162.06	195.33	5
110.14	22.9	1.161	251.22	216.44	19