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A COMPARATIVE ANALYSIS OF PRIMATE SUBCHONDRAL DENSITY OF THE FEMORAL HEAD

SEAN SIBURN
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Reviewed and approved* by the following:

Timothy Ryan
Associate Professor
Honors Advisor

Timothy Ryan
Associate Professor
Thesis Supervisor

Nina Jablonski
Evan Pugh Professor
Faculty Reader

* Signatures are on file in the Schreyer Honors College.

ABSTRACT

Obligate bipedalism is a unique feature of humans that results in the femoral head being loaded in a very specific manner in comparison to other primate taxa. The objective of this comparative analysis was to quantify the density variation of subchondral cortical bone in the proximal femur to look at how bipedalism loads the lower limbs differently than other forms of locomotor behavioral routines. High-resolution CT scans were collected from the femur of humans, chimpanzees, and orangutans. Subchondral articular bone was isolated from non-articular bone, and using a centroid probe analysis, continuous apparent density patterns were calculated and displayed using false color mapping. The results of the comparative analysis of the femoral head show that humans display very concentrated patterning within superior regions, orangutans show equal patterning within both superior and inferior regions, and chimpanzees show highly variant patterning of superior and inferior regions somewhere in between the previous taxa. This observation among all three taxa affirms the importance of body weight on the loading patterns of subchondral bone density within the superior portion of the femoral head for primates Subchondral bone provides a broad insight into the loading patterns that the proximal femur undergoes during varied locomotor behaviors, which can be further and more precisely examined in future studies that analyze trabecular architecture below the cortex and the influence of cortical thickness on cortical density.

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Chapter 1

Introduction

Locomotor behavior and the applied loads produced during the activity of motion are crucial factors that determine the structure and form of an primate's musculoskeletal system (Müller-Gerbl et al., December 1992). Because bone density can be measured as a determinant of compressive strength and loading, scientists can undergo comparative studies of primates to propose a structure-to-function relationship between the apparent density of subchondral bone and the effects of locomotor behavior variation on compressive patterns observed due to loading (Patel et al., October 2008).

The density of a bone is a major determinant of the compressive strength of the musculoskeletal system (Keller, September 1994). The degree of density is quantified through the amount of mineral deposited at the articulating surface and the porosity displayed by the subchondral bone (Keller, September 1994). The compressive strength of the subchondral bone can exhibit the habitual compressive loading regime of a limb because it acts as the direct source of force transmission across a joint (Radin et al., April 1970). Joint surfaces that align in congruent fashion can be used to estimate a species' behavioral locomotive pattern due to the transmission of the loading force through the structure of the limb (Müller-Gerbl et al., December 1992). Although there are various behavioral locomotive regimes displayed across primate taxa, sampling the quantitative properties of subchondral bone density can be extremely valuable to scientists studying the structure-to-function relationship of locomotion across various species (Lieberman et al., September 2003).

It has been hypothesized that trabecular bone is an integral factor within the musculoskeletal system of primates due to the premise that it dynamically responds to applied loads throughout the growth of an organism (Ryan et al., July 2002). Trabecular bone can be thought of as a dense, interconnected maze of bone rods and plates that vary among its three-dimensional structure throughout the body (Ryan et al., July 2002). The porous architecture of trabecular bone makes for an excellent structure for load transfer (Huiskes et al., June 2000). This success can be attributed to the suitable strength and stiffness of the trabecular bone matrix, which is also extremely lightweight due to its porous composition (Huiskes et al., June 2000).

Wolff's law states that the bone of a healthy, non-diseased individual will adapt to the loading conditions under which it is placed (Turner, January 1992). For example, if the loading stress on a particular bone increases, Wolff's law predicts that the bone will remodel over time to become stronger in order to resist the increased strain (Prendergast and Taylor, August 1994). The inverse is predicted as well; if the loading stress on a particular bone decreases, the bone will be resorbed due to the metabolically expensive cost to maintaining the musculoskeletal system (Prendergast and Taylor, August 1994). The internal structure of trabecular bone, which aligns with the principal stress direction, has been hypothesized to undergo the initial adaptive changes due to the presence or absence of a loading stress (Turner, January 1992). Secondary changes to the external cortical portion of the bone will then follow, becoming thicker or thinner in response to the individual's exposure to strain (Turner, January 1992).

The objective of this comparative study is to quantify the three-dimensional structure of the femoral head trabecular bone in a sample of three extant primate species: *Homo sapiens*, *Pan troglodytes*, and *Pongo pygmaeus* (Ryan et al., July 2002). *Homo sapiens* engage in obligate bipedalism, *Pan troglodytes* engage in natural quadrupedalism and arboreal climbing, and *Pan* *pygmaeus* engage mainly in arborealism (Fleagle, 2013 Print). These unique lifestyle patterns of locomotion should in theory affect the development of the density of subchondral bone within the femoral head (Carlson et al., June 2006). Extraction of trabecular bone from standardized regions of density within the femoral head will help to relate patterns of both inter- and intraspecific variation to locomotor behavioral variations among these three species (Ryan et al., July 2002).

Chapter 2

Materials and Methods

(a) Sample

Skeletal specimens were obtained from the Norris Farm #36 skeletal collection at The Pennsylvania State University (University Park, PA), the American Museum of Natural History (New York), and the National Museum of Natural History (Washington D.C.). All of the specimens used were adult males with no recorded pathologic conditions. Individuals that displayed signs of trauma, pathology, or advanced age were excluded from the analysis. One femur was scanned from each individual based upon accessibility, state, and quality. Femurs from the left and right sides were used , depending on preservation. There are three groups within the compared sample and the locomotor behaviors encompass obligate bipedalism (*Homo sapiens*), obligate arborealism (*Pongo pygmaeus*), and quadrupedalism and arboreal climbing (*Pan troglodytes*). Sex data were available for all individuals in the sample and only males were selected and pooled for analysis. Males were selected due to the greater proportion of available male specimens and to avoid the potentially confounding variables of increased calcium demands on the female skeleton throughout various stages of life history.

(b) Image Data Collection and Processing

All bones were scanned on high-resolution x-ray microcomputed tomography (microCT) scanner at the Center for Quantitative X-Ray Imaging at the Pennsylvania State University at University Park. In order to collect transverse slices, each bone specimen was positioned in florist foam and placed in the scanner. Serial cross-sectional scans began in the shaft region and extended proximally to cover the entire femoral head. All high resolution CT scans were collected with energy settings of 180 kV and 0.11 mA or 150 kV and 0.2 mA, ranging between 2400 and 4800 views. The voxel sizes ranged between 0.006 and 0.057 mm depending on the size of the bone specimen. In order to preserve the specimen, destructive sampling was not employed. All images were reconstructed from the scans as 16-bit TIFF greyscale images with a 1024x1024 pixel matrix.

The femoral microCT image data were loaded into Avizo 8.0.1, a computer software program used for 3-D data visualization and analysis. Within Avizo, a processing step known as "dual thresholding" was used to separate the cortical and trabecular regions of the femoral head. In this procedure, cortical and trabecular bone regions were separated using the duel threshold algorithm (Buie et al., 2007). This step was necessary to isolate only the cortical bone of the subchondral articular surface. The dual threshold algorithm uses two thresholds and a series of dilation and erosion steps to define the internal and external surfaces of the cortical bone (Shaw and Ryan, 2014). The routine results in an image mask that is then multiplied by the original data, resulting in a new data set of only the cortical bone compartment.

Following the extraction of the isolated cortical bone regions of each bone specimen, these data were used to construct a 3-D triangulated isosurface representation of the femoral head, as can be seen in Figure 1.

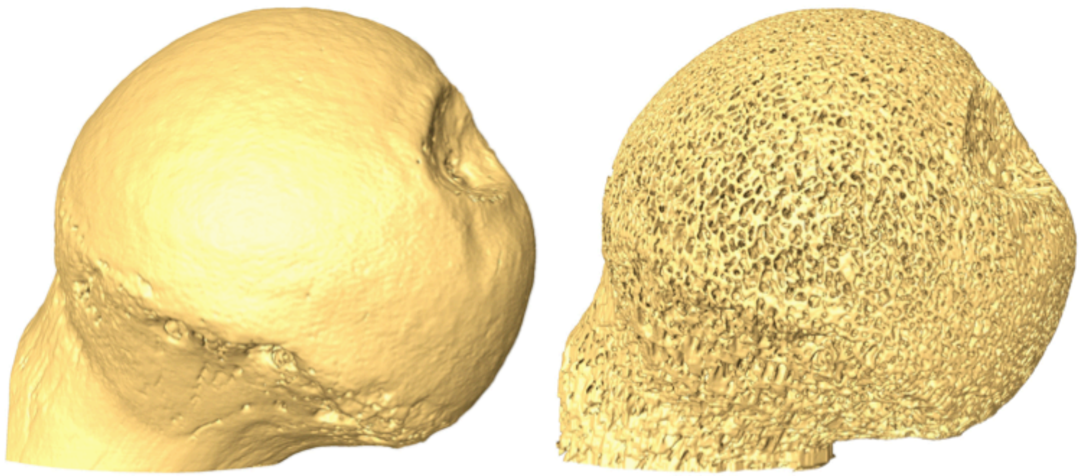


Figure 1: Dual Threshold Result – Isolated Cortical and Trabecular Bone of the Human Femoral Head

The articular surface was then extracted as a one voxel-thick surface cap by manually tracing the boundaries of the articular surface. The resulting dataset was a triangulated isosurface or 3-D point cloud of the femoral articular surface (surface shell). In order to analyze density variation across the femoral head, the isolated cortical bone was subdivided into an inferior and superior region to test the hypotheses of apparent density distribution across the femoral head. The head was divided using common landmarks associated with the taxa sample. Slices were fit to the midpoint of the landmarks and the original data set was individually cropped and saved to isolate the superior and inferior portions of the femoral head.

The subchondral bone density distributions on the inferior and superior articular surfaces were compared using a specialized code running in Avizo called "centroid probe". The purpose of the "centroid probe" is to map the variation in CT grayscale values across a curved surface, like the femoral head. It is similar to a 2-D projection of gray values as used in Patel and Carlson (2006) and Polk et al. (2008), but operates on complex 3-D surfaces, like most joints. The program works by first finding the centroid of the articular surface shell. Linear probes are then directed from the centroid to each point on the articular surface shell, traversing the isolated cortical bone dataset. Each probe logs the gray values along it's path and then finds the highest gray value, which corresponds to the densest voxel in the subchondral bone dataset. The product of the "centroid probe" routine is a density map of pixels that displays the variation in maximum densities within the inferior/superior isolated cortical bone data set. In this way, it is similar to the maximum intensity projection used in Patel and Carlson (2006) and Polk et al. (2008).

(c) Statistical Analyses

The maximum voxel values for the superior and inferior portions of the femoral head were exported from Avizo. These values were then normalized on a scale of 0-100 based upon the minimum and maximum non-zero values in each dataset. The equation used is as follows:

$$\text{normalized} = \frac{(\text{value} \times 100)}{(\text{maximum} - \text{minimum})}$$

The highest 0.1% of normalized values was removed from each dataset because these were usually a small proportion of the data with very high density values that unreasonably skewed the distributions. The data were compiled for both the superior and inferior regions of the femoral head for each individual as 10 bin histograms. The highest bin was compared both within individual superior and inferior values as well as between individuals of different and the same taxa. A repeated measure ANOVA test was run to conduct a statistical analysis of both the within-species and between-species variability.

Chapter 3

Results

The subchondral bone density patterns in the femoral head of three sample taxa used in this analysis were compared qualitatively and quantitatively. The quantitatively determined proportion of the halved femoral head regions (superior and inferior) that fell within the top 10% of normalized density values were utilized to assess the proportion of density within the subchondral bone of the femoral head. All density values in this densest bin for the sample taxa can be found in Table 1.

Intragroup variability is seen among the sample taxa to varying extents for the location and patterns of high apparent density areas within the femoral head. When observing the data for the sample, the most substantial observation within the qualitative analysis of the data can be seen among the orangutans (*Pongo pygmaeus*). This taxon shows a uniform patterning of high apparent density across the femoral head. The human (*Homo sapiens*) and chimpanzee (*Pan troglodytes*) data show variation within the sample, with the majority of the individuals showing high apparent superior density. However, one outlier shows high apparent inferior density within the femoral head for these two taxa.

For humans, three individuals show higher apparent density in the superior femoral head (819983, 819994, and 820647) and one individual shows high apparent density inferiorly (819977), as can be seen in Table 1. In previous studies, the typical trend seen among human samples is a greater proportion of denser subchondral bone within the superior femoral head due to the locomotor loading regimes of bipedal walking (Rydell, 1965**)**. Specimen 820647 shows the most polarizing ratio of superior density dominance, reflecting almost 32% of the highest apparent density of subchondral bone within the superior femoral head. This observation reflects the consistent loading of the superior femoral head during bipedal locomotion. The remaining human specimens do not show as high a proportion of apparent density subchondral bone.

For orangutans, all of the individuals within the sample show high apparent density of subchondral bone across the entire femoral head (49855, 49859, 49962, and 49967), as can be seen in Table 1. It can be postulated that the typical predicted trend seen among orangutan samples is an equalized proportion of dense subchondral bone within both the superior and inferior halves of the femoral head due to the constant, diverse joint forces that traverse the hip joint during arboreal climbing and bridging (Campbell et al., 2007). For the majority of the sample, there is a significant percentage of high apparent density within the femoral head. The proportion of the femoral head wth density values falling in the top 10% of values ranges from 71-74% of the total amount of articular surface voxels (49962, 49859, and 49967 respectively). Simply put, orangutans have extremely dense superior regions of their femoral head and more uniformly dense femoral heads in general in comparison to human taxa.

The chimpanzee (*Pan troglodytes*) data display variation similar to that of humans, showing three individuals with higher apparent density within the superior portion of the head (51202, 51377, and 51381), as can be seen in Table 1. One individual has higher apparent density within the inferior portion of the femoral head for patterning of subchondral bone (51379). Chimpanzees engage in a wide range of locomotor activities including quadrupedal "knuckle-walking", arboreal climbing, and even rudimentary bipedalism (Martin, 1990). Two of the individuals show extremely high levels of superior subchondral bone density, ranging from 46-79% (51381 and 51377 respectively) of total superior surface area. However, the other two individuals show extremely low patterning of high apparent density within the superior portion of the femoral head, thus resulting in a major statistical variance within the sample.

The high apparent subchondral bone density patterns of chimpanzees lie within the range of human and orangutan density, with humans encompassing the lower proportion of femoral head density and orangutans showing the highest density values, as can be seen in Figure 2. A statistical analysis was run to test between-species variability and within-species variability. For between-species variability, the analysis concludes that the three primate taxa are significantly different from each other. For within-species variability, the portion of the analyzed femoral head – either superior or inferior – is a significant factor when it comes to predicting density within the femur due to loading forces. Superior regions of the femoral head are significantly different than inferior regions within an individual. A boxplot analysis of the compared taxa data can be seen in Figure 2.

Taxa	Sample Number	Superior	Inferior
Homo sapiens	819977	0.009898277	0.0453
	819983	0.08240638	0.0366
	819994	0.1104968	0.0602
	820647	0.3258036	0.1280251
Pongo pygmaeus	49855	0.3899031	0.3266287
	49859	0.7347037	0.584951
	49962	0.7153622	0.4073138
	49967	0.7438521	0.5811394
Pan troglodytes	51202	0.01528676	0.0009955685
	51377	0.7922995	0.648316
	51379	0.07271235	0.2515616
	51381	0.4649856	0.2566648

Table 1: Proportion of the Halved Femoral Head within the Top 10% of Density Values

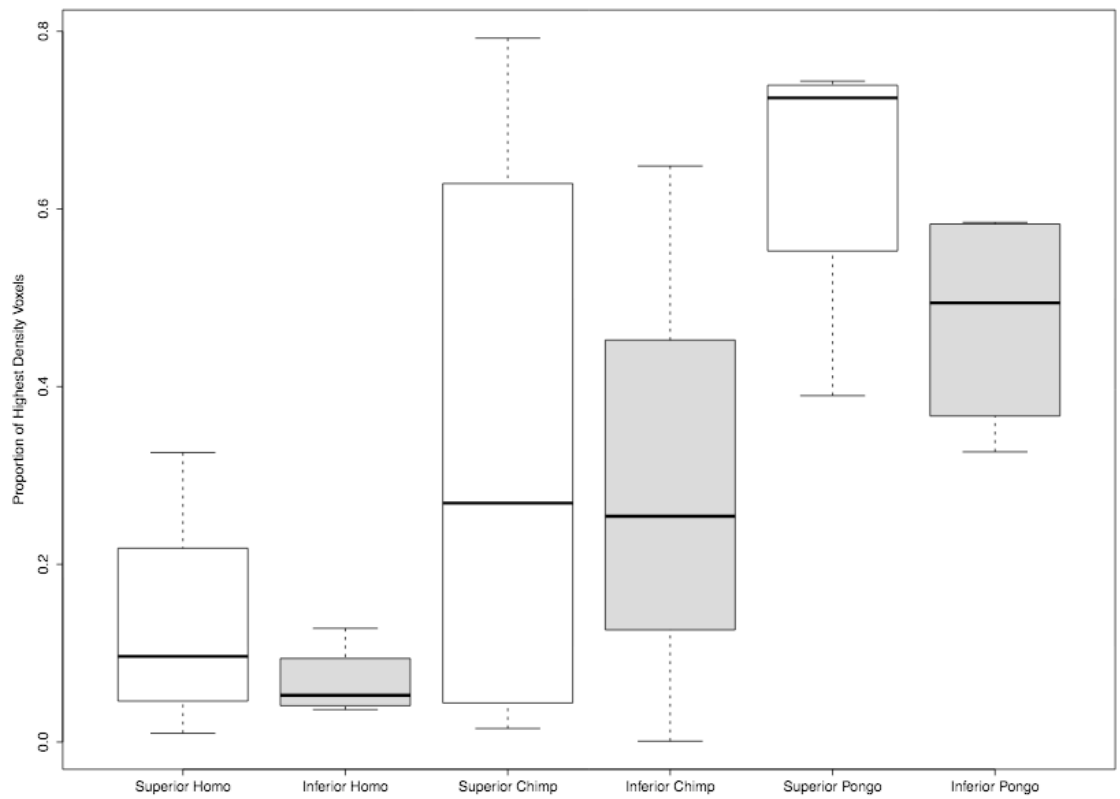


Figure 2: Box Plot of Significance for Femoral Density Difference Among Three Primate Taxa

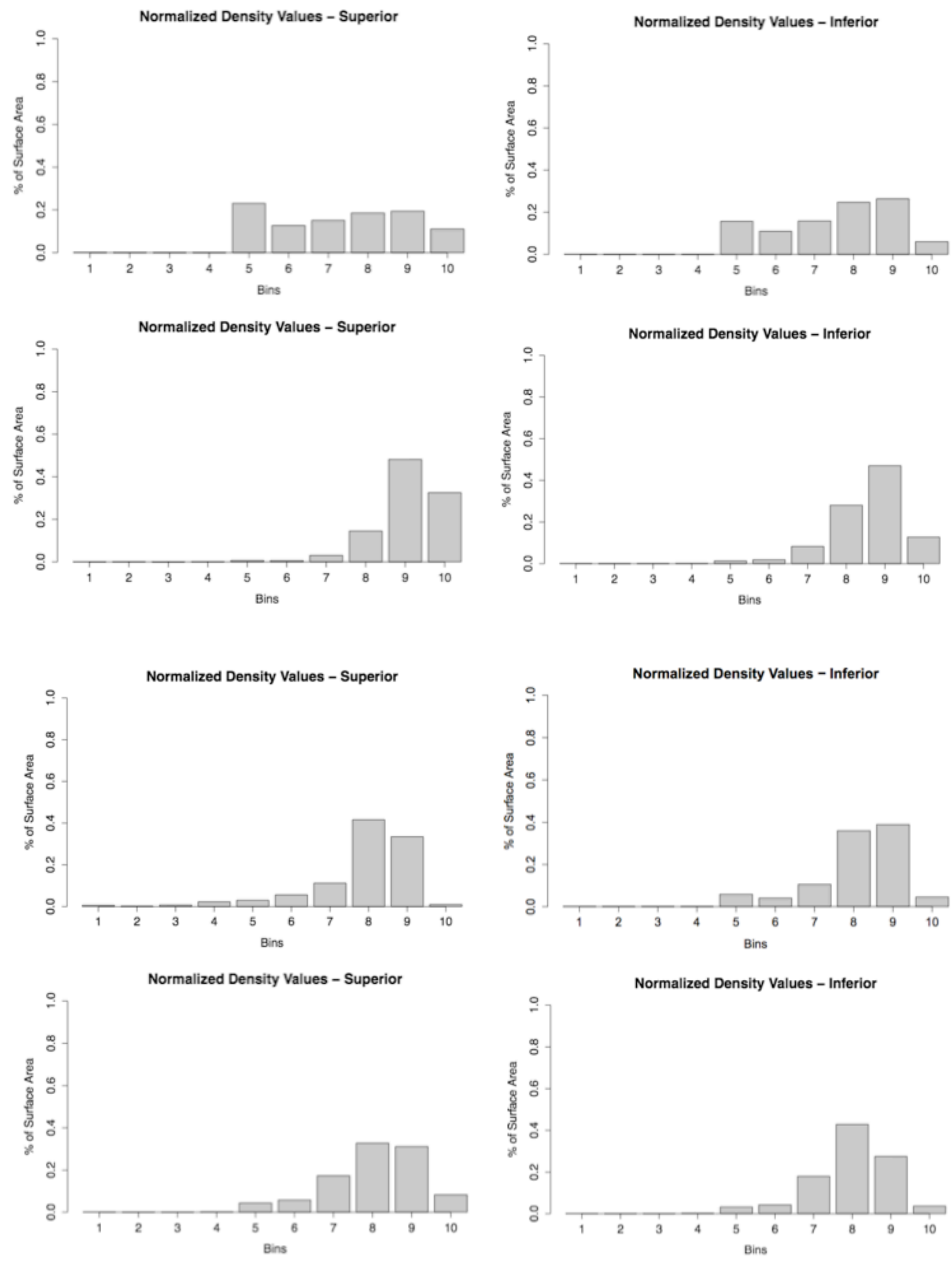


Figure 3: Histograms of Normalized Human Subchondral Density Values: (a) 819977, (b) 819983, (c) 819994, and (d) 820647

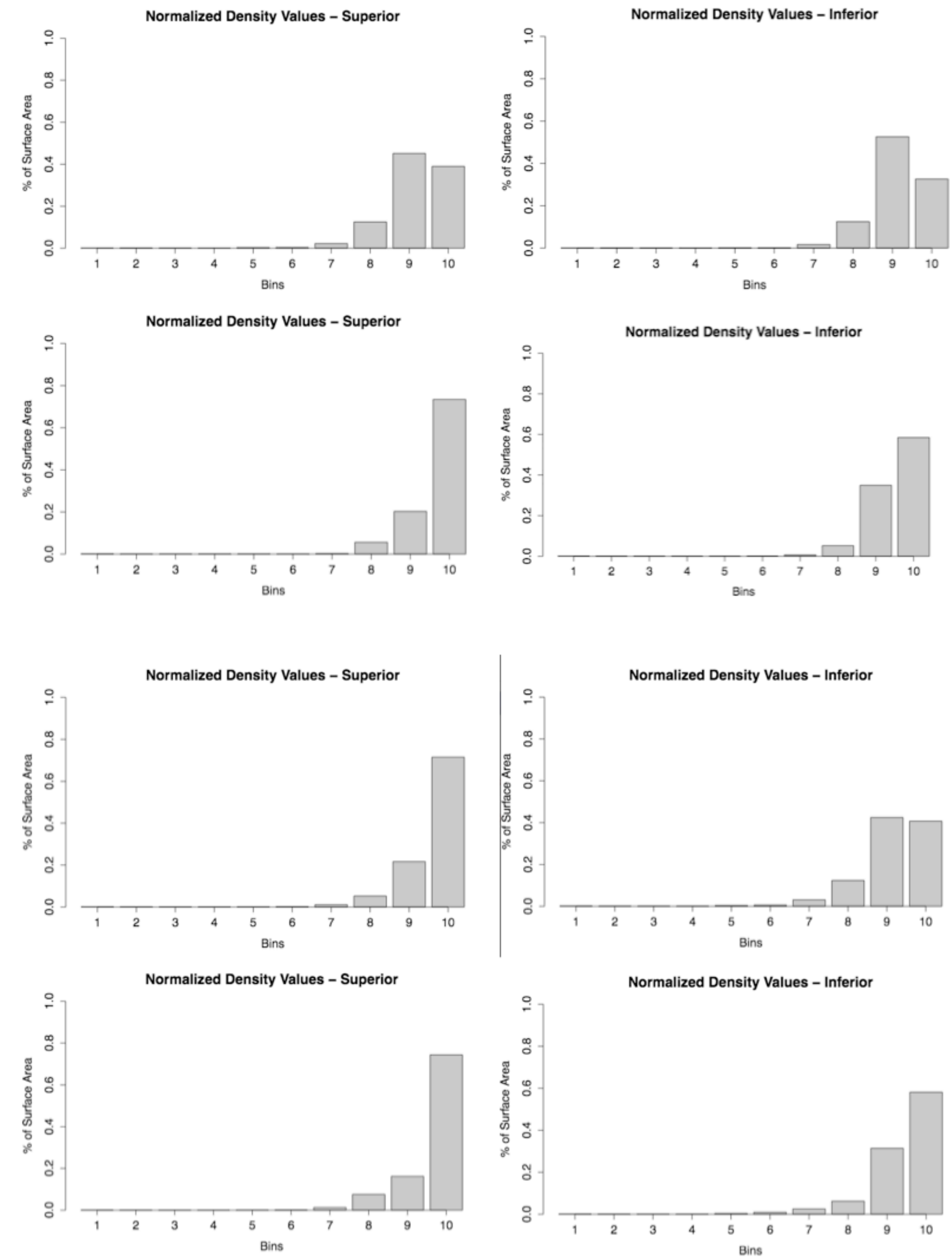


Figure 4: Histograms of Normalized Orangutan Subchondral Density Values: (a) 49855, (b) 49859, (c) 49962, and (d) 49967

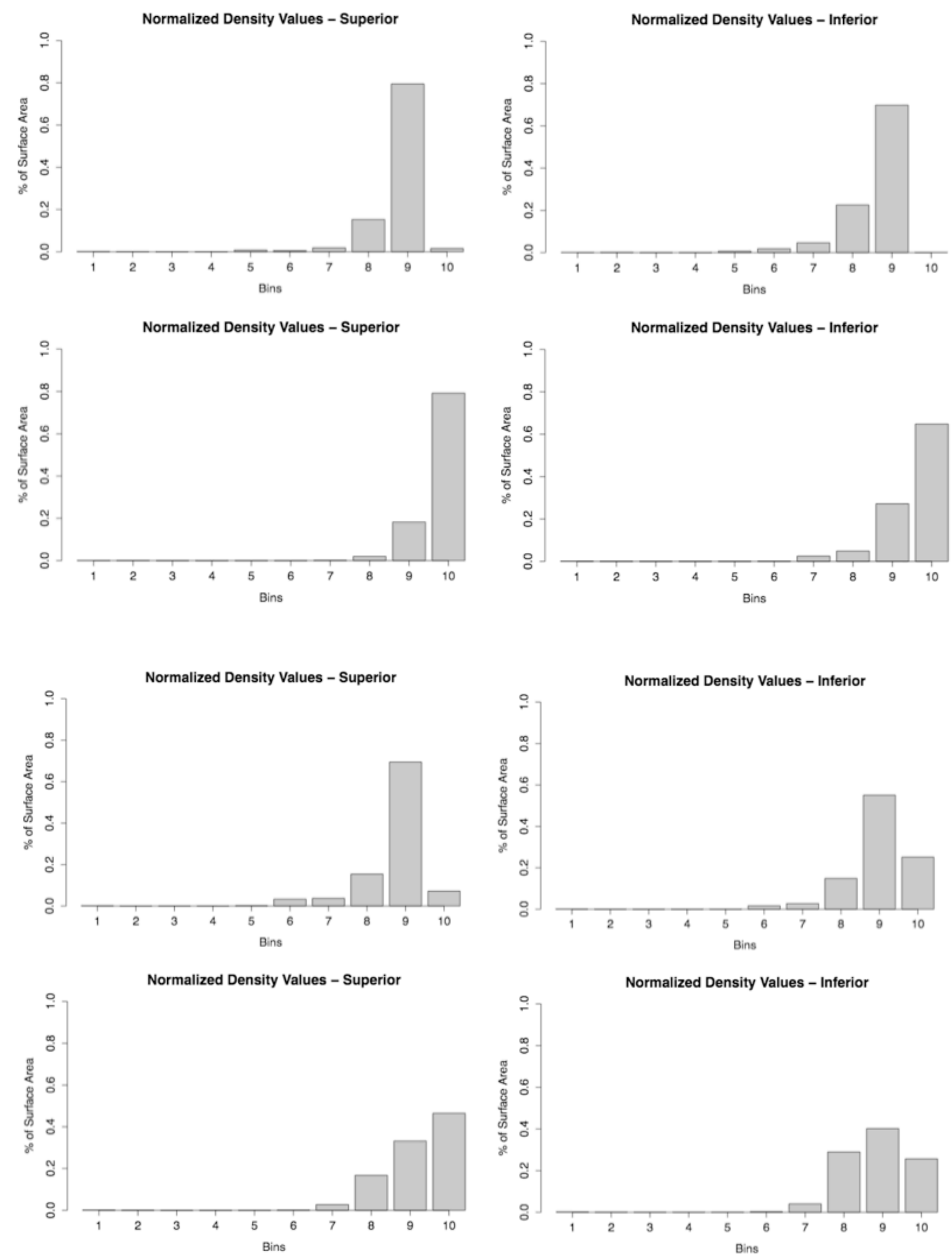


Figure 5: Histograms of Normalized Chimpanzee Subchondral Density Values: (a) 51202, (b) 51377, (c) 51379, and (d) 51381

Chapter 4

Discussions

Patterns from apparent subchondral bone density differentiate humans, orangutans, and chimpanzees upon comparison of the proximal femoral head. The specific loading regimes produced during habitual bipedalism leave a functional signature within the material properties of subchondral cortical bone of the proximal femur. For humans, the subchondral bone of the superior femoral head shows higher regions of density than the inferior portion due to this interaction. Simply put, habitual loading is thought to increase the density of subchondral bone within load-bearing regions of the musculoskeletal system.

The original hypothesis proposed for this analysis predicted that humans would show definitive patterning of high apparent density within the superior portion of the femoral head that articulates with the lunate surface of the acetabulum during the locomotor loading regimes of habitual bipedalism. The lowest relative apparent densities would thus be located where the proximal femur articulates the least with the acetabulum, and therefore is loaded less frequently, during walking. Bipedal locomotion produces very high, concentrated, and stereotypical patterns of loading at the hip joint and the other joints of the lower limb. This patterning goes hand-in-hand with the concept of "Wolff's law," which predicts that bone will remodel over time to become stronger in order to resist increased stress. The superior portion of the femoral head directly articulates with the cartilage of the acetabulum, resulting in the weight of the upper body directly interacting with the superior portion of the femoral head. By contrast, arboreal apes, such as orangutans engage in a more diverse set of locomotor postures and therefore load their femoral head in a more equalized manner between the superior and inferior portions of the head due to the hip joint's greater area of rotation. Chimpanzees engage in both the locomotor loading patterns of habitual quadrupedalism and arborealism, and would thus be predicted to show patterning of femoral head apparent subchondral bone density between the values of humans and orangutans.

As predicted, areas of high apparent density are most extensive in the superior region of the proximal femoral head that articulates with the acetabulum during loading. However, some observed patterns with the human and chimpanzee sample data did not match the prediction put forward by the study hypothesis. For example, some human and chimpanzee individuals displayed higher apparent inferior density dominance rather than superior. Orangutans and chimpanzees also show patterning of extremely dense cortical bone, which strongly affects the mapping of subchondral bone density within the analysis. Based upon these findings, it can be concluded that apparent density patterns of primate taxa do not solely reflect locomotive forces, but may also be influenced by various other physiological and environmental stimuli. Additional factors such as body size, age, sex, diet, hormones, and bone mineral metabolism (e.g. Vitamin D or calcium levels) levels may influence the apparent density of the proximal femur and can potentially alter patterns of relative high apparent density within bones (Patel and Carlson, 2006).

Upon running a statistical analysis, it was determined that between-species variability is a significant factor when it comes to determining the proportions of superior and inferior bin 10 voxel quantities for density. This statistical analysis of differences in density patterns between the superior and inferior head supports the idea that the three primate taxa within the comparison are significantly different. It was also determined that for within-species variability, the femoral head – either superior or inferior – is a significant factor when it comes to determining the proportions of superior and inferior bin 10 voxel quantities for density. Simply, the superior regions within the femoral head are significantly more dense than the inferior regions within individuals. Superior region density is greater than that of inferior region density, which rejects the null hypothesis.

(a) *Homo sapiens* Hip Joint

The three-dimensional structure of the trabecular bone within the femur is well documented for humans (Wolff, J., 1892). Trabecular bone acts as a support network of connective tissue that takes the form of a cancellous matrix of porous bone ((Ryan, T.M. & Ketcham, R.A., 2002; Ryan, T.M. & van Rietbergen, B. 2005; Shaw, C.N. & Ryan, T.M., 2012). Trabecular bone growth reflects the stress pattern that a bone experiences due to loading; regions of maximum trabaeculae density will coincide with regions of maximum stress within a bone (Ryan, T.M. & Krovitz, G.E., 2006). Within the human proximal femur, there are both tensile and compressive forces present that correspond to the path that locomotor force takes through bone (Nordin & Frankel, 2001). For the interest of this analysis, only the principal compressive and principal tensile trabecular patterning were taken into consideration due to their large impact on the femoral head.

The principal compressive trabeculae extend vertically from the medial cortex of the superior femoral head into the femoral neck (Figure 1). Pelvic trabeculae extend from the lower portion of the auricular surface on the ilium in an arch that aligns with the superior surface of the acetabulum. The pelvic trabeculae fall in line with the vertical supporting bundle of the principal compressive trabeculae, which subsequently transmits the main compressive forces of loading through the femoral head and neck (Aiello and Dean, 1990). In simple terms, the loading force travels through the pelvis and moves through the superior region of the femoral head. The result is regions of dense trabeculae and subchondral bone within the superior portion of the femoral head. Figures 1 and 2 depict the trabecular patterning for humans.

The principal tensile trabeculae extends from the lateral cortex of the inferior femoral head below the fovea. Pelvic trabeculae extend from the superior portion of the auricular surface on the ilium to the inferior surface of the acetabulum. The pelvic trabeculae once again fall in line with the arcuate bundle, which extends from the lower portion of the femoral head to the lateral side of the femur below the greater trochanter (Aiello and Dean, 1990). This stretch of trabecular bone counteracts the shearing stress that the femoral head and neck experience (Aiello and Dean, 1990). Due to the main compressive forces traveling through the superior portion of the human femoral head, there is not as high a ratio of high density patterning of trabecular and subchondral bone within the inferior femoral head. Figures 6 and 7 depict the trabecular patterning for humans.

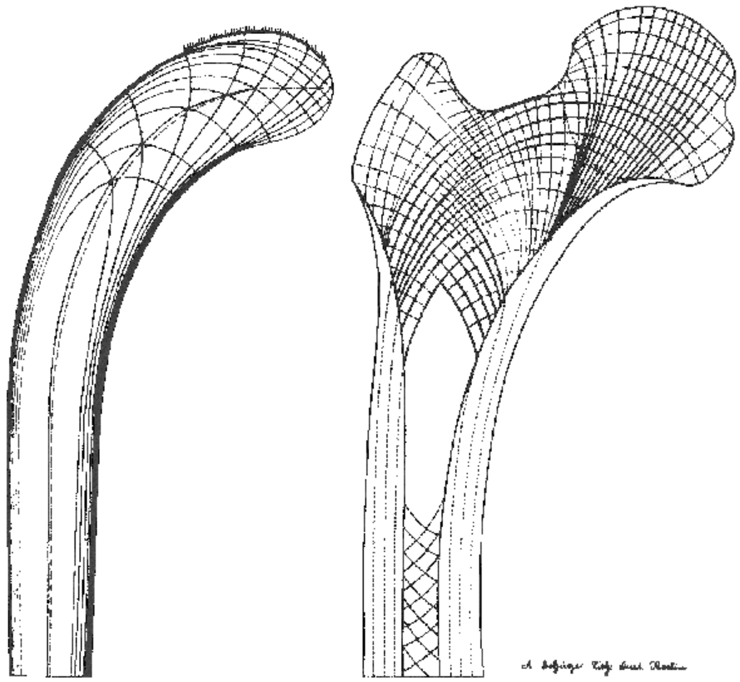


Figure 6: Trabecular Patterning of the Human Femur (Wolff J., 1892)

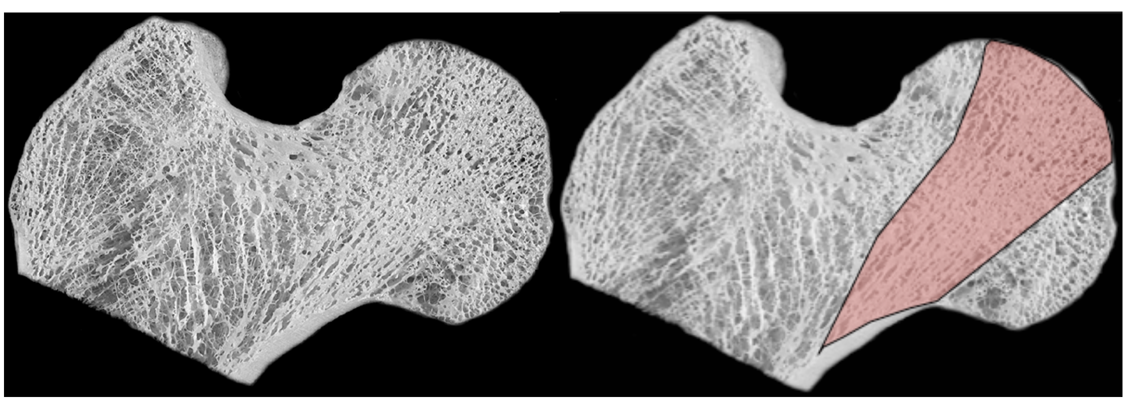
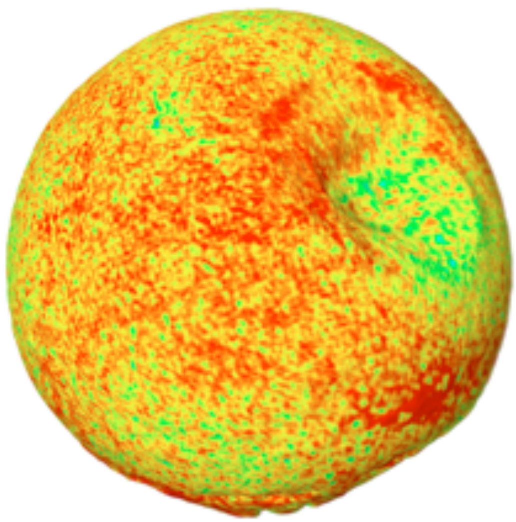


Figure 7: Compressive Trabeculae Patterning within a Cropped Human Femoral Head (Nordin & Frankel, 2001)

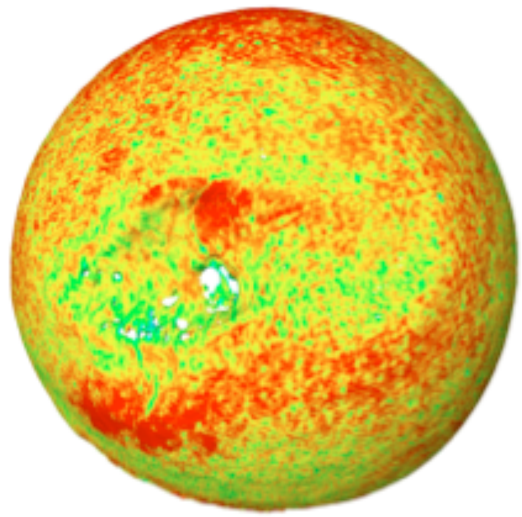
The bicondylar angle found in the femur of humans and our common hominin ancestors within the fossil record suggests an evolutionary increase in metabolic efficiency through the development of bipedal walking (Conroy & Pontzer). The bicondylar angle bows medially, placing the feet closer to the midline of the body, thus concentrating the body's center of mass during the stance phase (Conroy & Pontzer). This development decreases energy expenditure by minimizing the vertical and horizontal movements of the human body center of mass. The degree of the bicondylar angle distinguishes human and ape femora. The medial bowing of the femoral angle also shifts the position of the femoral head within the acetabulum, aligning a greater proportion of the superior region of the femoral head to interact directly with the body weight forces that traverse the hip joint. This upright posture and reliance on two limbs rather than four during walking places a great load on the hip and lower limbs. The result of this greater proportion of stereotypical locomotor behavior (i.e. humans walk and run on the ground) can be postulated to result in higher forces within the superior femoral head. The result would be greater amount of trabecular bone and high apparent density for subchondral bone.

Upon analysis of the human data, three of the individuals show superior density dominance (819983, 819994, and 820647), as was predicted by the hypothesis, and one individual shows inferior density dominance (819977). Three-dimensional surfaces were generated via Avizo and a density map was projected onto the surfaces of the femoral heads to create visualizations in order to qualitatively analyze the heads for density clusters, as can be seen in Figure 8. The density map is standardized on a common color scale (i.e. RGB). Clusters of red show the regions with the highest apparent subchondral bone density and lighter colors, ranging to green or light blue, show regions with lower apparent subchondral bone density.

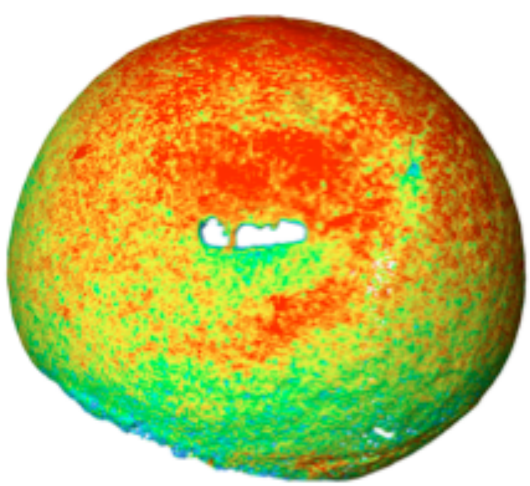
H. sapiens 819977



H. sapiens 819983



H. sapiens 819994



H. sapiens 820647

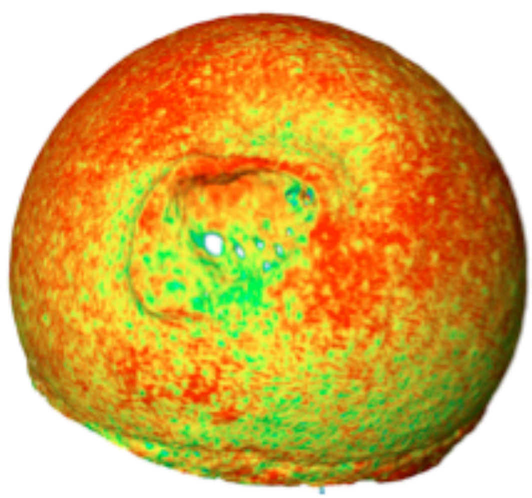


Figure 8: Projected Subchondral Density Mapping of the Human Femur

The results show striking red clusters of high apparent density subchondral bone concentrated within the superior portion of the femoral head. Clusters of green that depict regions of lower apparent density are mainly localized to the inferior portions of the femoral head. The exception is the outlier sample 819977 which displays a greater proportion of high apparent density within the inferior regions as opposed to the superior region of the femoral head. Radiating projections of density extend from the superior region to the inferior region of the head, creating clockwise and counterclockwise circular patterning around the fovea capitis. This patterning may be the result of the loading response of the subchondral bone as the femoral head rotates within the load-bearing process of locomotion. In relation to hip mobility, the distribution of the articular surface of the acetabulum relates to the loading pattern of the individual, with the expansion growth of the lunate surface reflecting frequent strain response to high loading (MacLatchy, 1996). The maximum area of the lunate surface reflects the amount of coverage the acetabulum allows for femoral head rotation. The cranial lunate surface has been found to provide greater femoral coverage than that of dorsal regions in humans, and thus would produce denser regions of subchondral bone (MacLatchy, 1996). A potential branch of this study would be match for density patterning on the femoral head and the lunate surface.

(b) *Pongo pygmaeus* Hip Joint

Orangutans are extremely unusual in that they are by far the heaviest primarily arboreal primate (i.e. full grown males weigh in excess of 70 kg, whereas sexually dimorphic females typically fall within the mid-30 kg) (Martin, 1990). Orangutans typically spend the duration of their lives within the arboreal canopies, with only solitary males sporadically patrolling the terrestrial landscape to seek out mating opportunities. Orangutans move on the ground using the support of their arms for stabilizing, with the outer margins of their hands acting as the point of contact with the surface (i.e. fist-walking) (Martin, 1990). In strong contrast to the stability of the terrestrial environment, arboreal canopies are characterized by discontinuous substrates of travel routes (Garber, 2007). Tree branches are oriented at various angles to the ground and become smaller and less stable as elevation from the forest floor increases. Primates that spend significant time traveling within an arboreal environment are burdened with the challenge of maintaining balance as tree branches bend, sway, and potentially break under body weight.

Arboreal primates have evolutionarily adapted to these unstable conditions by distributing their body mass over four support limbs, lowering the body center of gravity nearer to the support limbs, utilizing flexed and abducted limb postures, and engaging in suspensory below-branch postures to maintain stability (Garber, 2007). Body mass is an extremely important factor when it comes to position behavior of locomotion within arboreal environments. Within an unpredictable environment comes an unpredictable loading patterning of the femoral head for arboreal primate locomotion. Vertical climbing and leaping, suspensory below-branch swinging, and above-branch locomotion are all encompassed within the loading regimes of orangutans. Orangutans often load their femoral heads in tension when they are suspending some or all of their body weight from their feet (Martin, 1990). Orangutans do not possess a fovea on their femoral heads because they lack the transverse acetabular ligament (or round ligament) that is seen in other primate taxa. As a result, orangutans can move their femora around with a greater range of motion that most other primates, which results in a great range of loading on the femoral head. It can thus be postulated that orangutan high apparent density should be equally spread across the femoral head to adapt to the random occurrences of movement throughout arboreal environments, but with slightly higher concentrated regions of high density within the superior femoral head to encompass high body weight.

Upon analysis of the orangutan data, all of the individuals show superior density dominance (49855, 49859, 49962, and 49967). Three-dimensional surfaces were generated via Avizo and a density map was projected onto the surfaces of the femoral heads to create visualizations in order to qualitatively analyze the heads for density clusters, as can be seen in Figure 9. The density map is standardized on a common light scale (i.e. RGB). Clusters of red show the regions with the highest apparent subchondral bone density and lighter colors, ranging to green or light blue, show regions with lower apparent subchondral bone density.

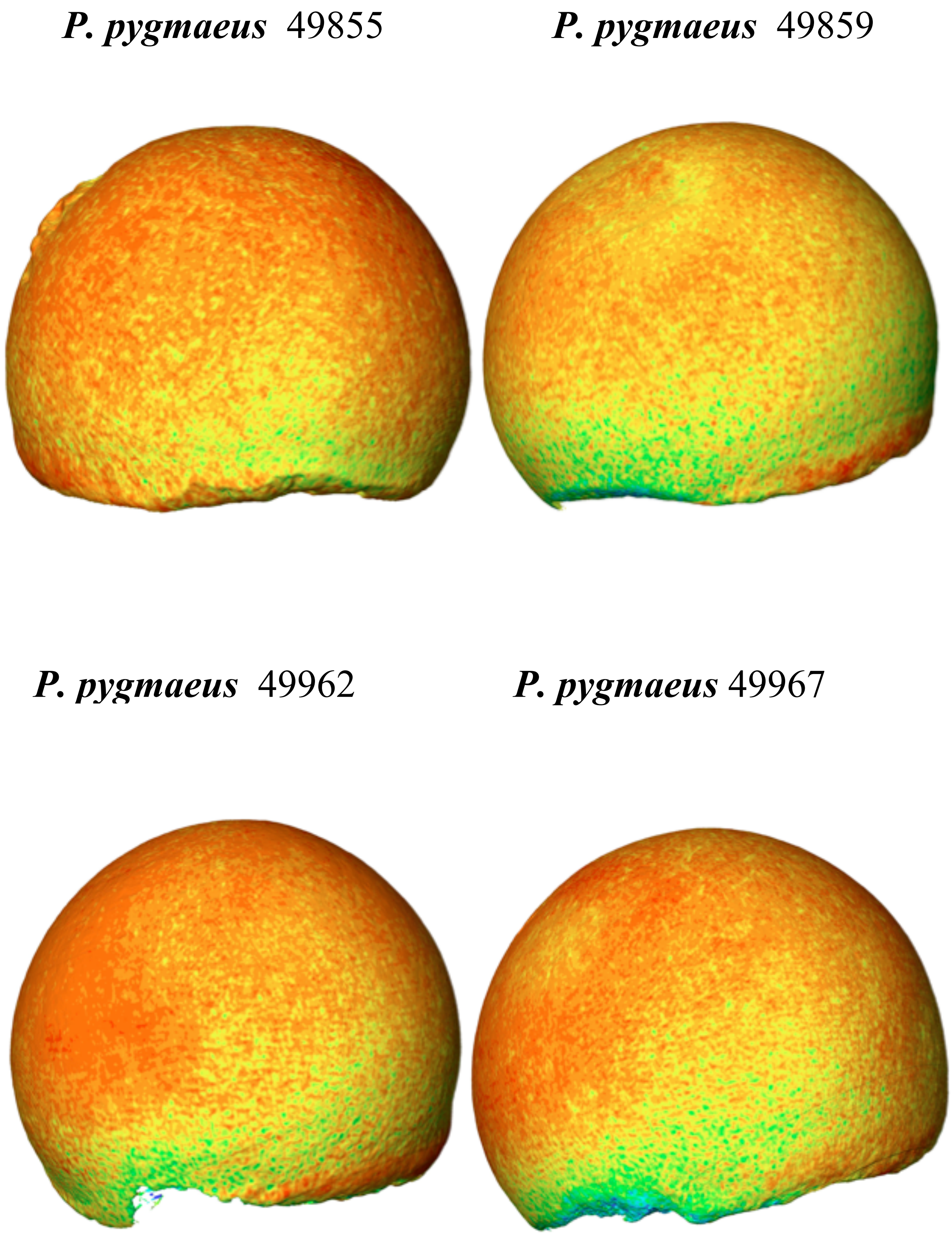


Figure 9: Projected Subchondral Density Mapping of the Orangutan Femur

The results show striking red clusters of high apparent density subchondral bone concentrated within the majority of the femoral head, most notably entirely encompassing the superior portion of the head as well as most of the upper localizations of the inferior regions. Clusters of green that depict lower regions of apparent density are mainly localized to the lower inferior portions of the femoral head. This patterning affirms the hypothesis of randomized distribution of high apparent density of subchondral bone due to the unpredictable loading of orangutans within their arboreal environments. Because orangutans undergo a wide variety of locomotive patterns (i.e. vertical climbing and leaping, suspensory below-branch swinging, above-branch walking, etc.) throughout the course of single day, a great range of loading transfers across the hip joint and into the femoral head. The four individuals within this study all employ a relatively equalized distribution of high apparent subchondral bone density within their density map visualizations, which can predict that these individuals underwent multiple forms of locomotive behavior throughout the course of life. The observed orthograde and pronograde behaviors seen utilized by orangutans also suggests variations of femoral loading during both stance and locomotive phases.

(c) *Pan troglodytes* Hip Joint

Chimpanzees are extremely diverse when it comes to their methods of employed locomotion within natural environments. Chimpanzees typically engage in quadrupedalism, spending the duration of their lives both on the terrestrial landscape and within arboreal canopies. This inherent use of quadrupedalism is reflected in the anatomical feature of having longer arms than legs. As a result, chimpanzees use the support of their arms for stabilization, with the margins of the knuckles acting as the point of contact with the surface (i.e. knuckle-walking) (Martin, 1990). During quadrupedal locomotion, the maximum force of compressive loads typically occurs near the mid-support of the stance phase (Polk, 2001). It can be predicted that the apparent density distribution of the proximal femoral head should display unique configurations of trabecular bone density at mid-support, assuming that individual body weight influences bone growth when compressive forces cross joint surfaces (Carlson and Patel, 2006). It should be noted that chimpanzees are also capable of employing bipedal locomotion similar to humans. However, chimpanzee bipedalism is not obligate or habitual and chimpanzees typically only use this mode of locomotion if objects need to be carried with the use of the hands.

Chimpanzees spend an equal amount of time within arboreal settings. As previously stated, in contrast to the regular stability of terrestrial landscapes, arboreal canopies are characterized by discontinuous substrates of travel routes (Garber, 2007). The random orientation of tree branches, as well as the thinning and decrease of branch stability as elevation within the canopy increases, results in unstable paths of travel within arboreal settings. Primates that spend significant time traveling within an arboreal environment are burdened with the challenge of maintaining balance as tree branches bend, sway, and potentially break under body weight. Arboreal primates have evolutionarily adapted to these unstable conditions by distributing their body mass over four support limbs, lowering the body center of gravity nearer to the support limbs, utilizing flexed and abducted limb postures, and engaging in suspensory below-branch postures to maintain stability (Garber, 2007). It should be noted that chimps rarely engage in tension loading of the femoral head, as seen within orangutans, when suspending some or all of their body weight from the feet (Martin, 1990). Chimpanzees rarely engage in such postures and only do so when they are within the juvenile age range. Body mass is an extremely important factor when it comes to positional behavior and locomotion within arboreal environments. Unpredictable environments result in unpredictable loading patterning of the femoral head for arboreal primates. It can thus be postulated that chimpanzees that spend a high portion of life within an arboreal setting will show high apparent density spread across the femoral head to adapt to the random occurrences of movement throughout arboreal environments.

Upon analysis of the chimpanzee subchondral bone data, three of the individuals display superior density dominance (51202, 51377, and 51381), as was predicted by the experimental, and one individual shows inferior density dominance (51379). Three-dimensional surfaces were generated via Avizo and a density map was projected onto the surfaces of the femoral heads to create visualizations in order to qualitatively analyze the heads for density clusters, as can be seen in Figure 10. The density map is standardized on a common color scale (i.e. RGB). Clusters of red show the regions with the highest apparent subchondral bone density and lighter colors, ranging to green or light blue, show regions with lower apparent subchondral bone density.

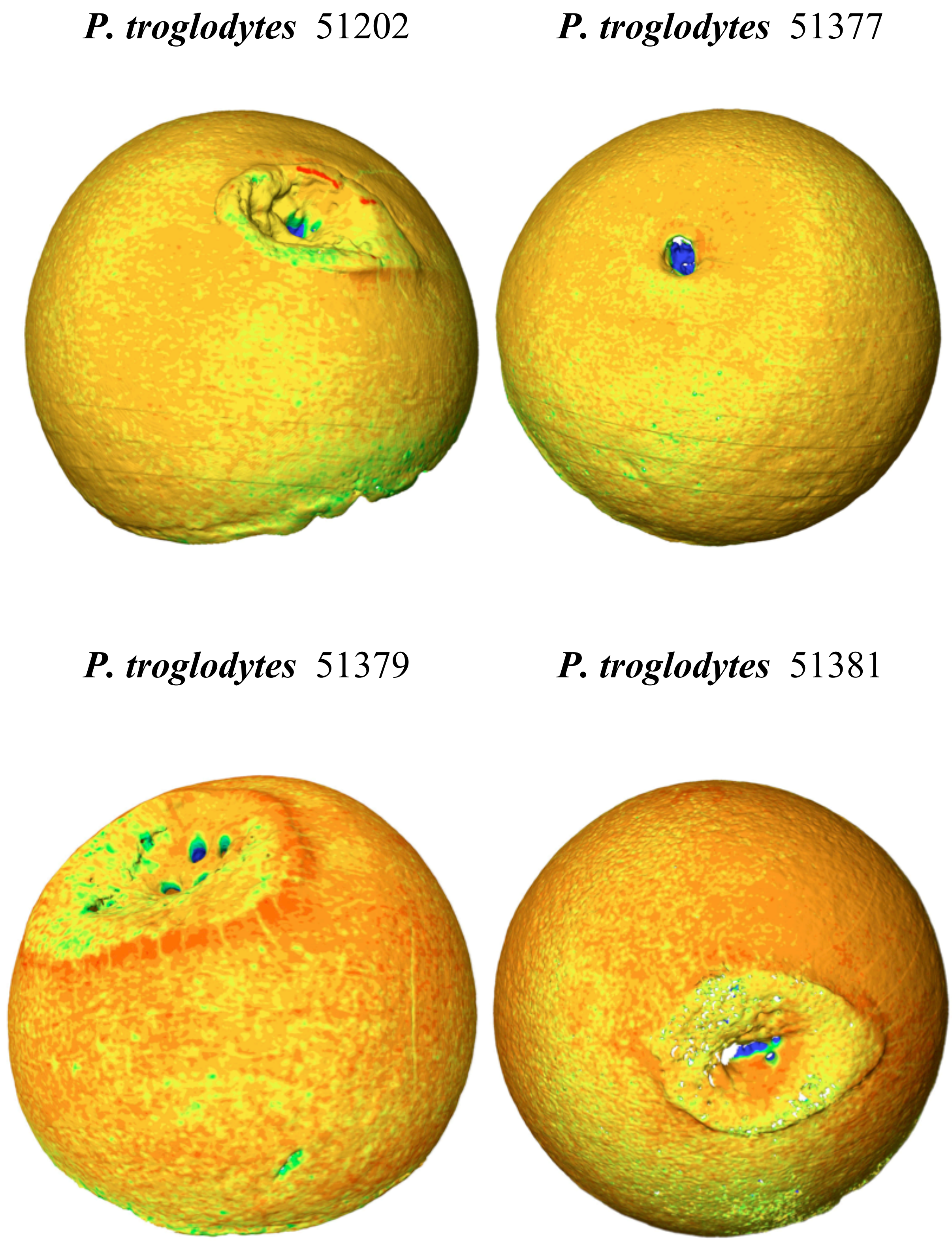


Figure 10: Projected Subchondral Density Mapping of the Chimpanzee Femur

The results show orange clusters of high apparent density subchondral bone concentrated within the majority of the femoral head, most notably entirely encompassing the superior portion of the head as well as most of the upper localizations of the inferior regions. Clusters of green and yellow that depict the lower regions of apparent density are mainly localized to the lower inferior portions of the femoral head, which is very similar to the patterning observed in the orangutan taxa. This patterning supports the hypothesis of randomized distribution of high apparent density of subchondral bone due to the unpredictable loading of chimpanzees within their arboreal environments. The four individuals within this study all employ a relatively equalized distribution of high apparent subchondral bone density within their density map visualizations, which may suggest that these individuals lived an active arboreal lifestyle as well as engaged in terrestrial quadrupedalism.

There is an extreme amount of variation within the top 10% of density values for the inferior and superior portions of the femoral head within chimpanzees for this sample. Because chimpanzees are known to engage in a wide variety of locomotor behaviors (i.g. terrestrial quadrupedalism, climbing, and bipedal walking) throughout the course of single day, a range of orientations transfer across the hip joint and into the femoral head. The prevalence of specific loading forces (i.e. quadrupedalism versus climbing) will differ to varying degrees from individual to individual. Some populations of chimpanzees are much more prone to engage in one form of locomotion over another due to extenuating environmental factors like predation, access to food, and deforestation. For this sample, three of the four individuals show a prevalence of high apparent subchondral bone density in the superior portion of the femoral head, which mimics the patterns seen within both humans and orangutans. This observation among all three taxa affirms the importance of body weight on the loading patterns of high apparent subchondral bone within the superior portion of the femoral head for primates.

Chapter 5

Conclusions

The objective of this comparative analysis was to quantify the density variation of subchondral cortical bone in the proximal femur to look at how bipedalism is reflected in the cortical bone of the lower limbs differently than other forms of behavioral locomotor routines. The results of the comparative femoral head analysis show that humans display very concentrated patterning within superior regions and little concentration in lower regions, orangutans show equal patterning within both superior and inferior regions, and chimpanzees show highly variant patterning of superior and inferior regions somewhere in between the other taxa. These data allow the null hypothesis to be rejected in support of the alternative, which states that there is a significant difference in the way that bipedal locomotor loads are distributed on the femoral head in comparison to other forms of locomotion used by primates, such as quadrupedalism and arborealism.

There is also evidence that suggests that there is a significant difference in the loading of the superior and inferior regions of the femoral head within individuals. All three investigated primate taxa do in fact show higher percentages of apparent density within the superior region of the femoral head. This observation demonstrates the importance of body weight as a crucial factor on loading patterns. Higher density within superior regions can be explained with the help of Wolff's law, which predicts that the bone will remodel over time to become stronger in order to resist the increased strain (Wolff, 1892; Prendergast and Taylor, 1994). Locomotor behavioral loading is influenced by body weight of the individual species.

A possible anatomical confounding factor of the data includes the observation that humans and chimpanzees share the more primitive morphology of possessing a transverse acetabular ligament (i.e. round ligament), which orangutans do not possess. This can be clearly seen within the 3-D visualization created by Avizo. Both humans and chimpanzees possess a fovea capitis on the femoral head, to which the round ligament inserts from its point of origin at the labrum of the acetabulum (Nordin & Frankel, 2001). This ligament limits the amount of rotation that the femoral head has within the acetabulum, preventing any overarching movements or displacement of bone from the hip joint. Orangutans, which lack a round ligament, have a much greater range of free motion within the hip joint. This evolutionarily derived trait, which developed from the more primitive trait of possessing a round ligament, has allowed the orangutan to specialize almost entirely to live an arboreal lifestyle. The extreme range of flexibility and evenly-distributed femoral head subchondral bone apparent density would not be possible if orangutans had this ligament.

There are several other natural factors that influence the relative amounts of organic materials and water content of bone. Diet has a major impact on the structure of the musculoskeletal system. Mineral imbalances or vitamin deficiencies can potentially erode or build up the densities of bone. High or low levels of calcium can significantly impact bone structure. Osteoporosis is one of the leading diseases that affects women within the United States. High levels of calcium in the blood leads to decreased activity of osteoclasts and lower bone resorption in humans. On the other hand, low levels of calcium in the blood leads to increased activity of osteoclasts and high bone resorption in humans. Good sources of calcium within diets include dairy products, green leafy vegetables (i.e. broccoli, kale, and collards), and nuts. Vitamin D also increases the absorption of calcium and phosphate within the intestinal track. This results in raised levels of calcium within blood plasma and lower bone resorption rates.

Subchondral bone provides a broad insight into the loading patterns that the proximal femur undergoes during varied locomotor behaviors. This analysis can be further and more precisely examined in the future by analyzing trabecular architecture below the cortex and the influence of cortical thickness on cortical density. By observing the interior response of bone to the stress of loading, scientists can continue to move forward to grow in understanding on how bipedal locomotion affects the rate of growth for lower limb bones. Extending this analysis to other primate taxa can help researchers grow in understanding of bone loading and help piece together the mystery as to how modern humans developed habitual terrestrial bipedalism.

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ACADEMIC VITA

Sean Siburn
710 Warren Street, Westfield, NJ, 07090
seansiburn@gmail.com

Objective

Passionate, enthusiastic student candidate seeking admission to medical school for future work in international global relief and assistance, a desire realized through urban volunteer efforts.

Education

Pennsylvania State University – Schreyer Honors College **2011-Present**

Undergraduate Program in Biological Anthropology

Experience

Primate Functional Morphology Laboratory – Research Assistant **2012-Present**

- Research oriented study of the evolution of human and primate locomotion.
- Assist with data collection and sampling of bone specimens; program virtual models of bone reconstruction; operate CT scanner used to collect bone slices for virtual image sequencing.

OrthoMedic, LLC – Office Support Staff **2010-Present**

- Medical sales company specializing in orthopedic products.
- Assist with inventory control and maintenance; deliver products and instruments to territory (New York, New Jersey, Pennsylvania, and Delaware) hospitals and/or surgery centers.

Mediplex Surgery Center – JFK Medical Center **Summer 2014**

- Adult volunteer interacting with same-day surgery patients.
- Assist with patient transport to and from operating room; offer food and drink to patient in post-operative setting; console both patients and family members after surgery; shadow practicing physicians

Leadership

SHOtime Team Leader **2012/2013**

- Faculty/administration nominated position. Head Chair of Finale committee (2012) and Move-In/Arrival (2013) for SHOtime freshman orientation for the Schreyer Honors College.
- Provide guidance and assistant to incoming freshmen and/or transfer student students within the Schreyer Honors College.

Scholar Assistant – Schreyer Honors College **2011-Present**

- Faculty/administration nominated position.
- Liaison between the Schreyer Honors College faculty/administration and SHC students, prospective students, and parents. Participate in all-school sponsored events, recruitment, and publicity.

Theta Chi Fraternity – Secretary **2012-Present**

- Brotherhood nominated/elected position.
- Secretary liaison between the brotherhood, active alumni, and the National Chapter. Take minutes during Chapter Meetings, register and orient new members, and communicate with National Chapter.

Theta Chi Fraternity – Pledge Marshal **Fall 2014**

- Brotherhood nominated/elected position.
- Pledge Marshal liaison between the active/alumni brotherhood and the newly joined associate members; orient and educate associate members into men who truly embody the morals of Theta Chi Fraternity.

Honors

Order of Omega National Greek Honor Society **2012-Present**

- Honor society that recognizes fraternity men and women who have attained a high standard of leadership within inter-fraternity activities.

Mortar Board National Honor Society **2013-Present**

- National leadership honor society that recognizes aspiring seniors for their scholarship, leadership, character, and service within the Penn State community.