POSITIONAL AND MORPHOLOGICAL DEVELOPMENT OF WILD CHIMPANZEES, *PAN TROGLODYTES*

by

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DEDICATION

Thank you Mom and Dad for the moral support at every step of this journey!

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CHAPTER I

Introduction

The goal of this thesis is to document the locomotor and anatomical development of chimpanzees from infancy through adulthood in order to understand the dynamic relationship between bone function and shape. During development, stress placed on bone through locomotor behaviors can cause significant response in bone strength and shape. This is especially true during development (Bouvier and Hylander, 1981; Bass et al., 2002; Lieberman et al., 2003; Pontzer et al., 2006). Finding epigenetic skeletal traits, those that are a product of environmental effects and not indicative of phylogeny (Lovejoy et al., 1999), will allow behavioral interpretation of fossil specimens. This is because the presence or absence of such a trait is primarily indicative of the manner in which that fossil specimen moved. This relationship between function and form is examined in chimpanzees because they are our closest living relatives and therefore their positional repertoire likely includes elements shared with our common ancestor. If epigenetic traits indicative of suspension, climbing, knuckle-walking, or quadrupedalism exist in chimpanzees, they could potentially be used to reconstruct the positional repertoire of fossil hominoids, including purported hominins. Therefore, this study has two main goals: 1) document the specifics of the locomotor and postural development of chimpanzees in the wild and 2) identify “plastic” anatomical features that are responsive to use.

I first present a detailed analysis of developmental changes in chimpanzee locomotion and posture in Chapter II. Frequency data from both focal follow and video footage form the basis for interpreting skeletal changes in the context of a developmentally driven and changing loading environment. Fieldwork for this project was conducted on wild chimpanzees at Ngogo, Kibale National Park, Uganda. I provide a cross-sectional analysis of locomotor and postural changes across a large number of individuals. One of the important consequences of this study is that it generates data that can used to make predictions about how behavioral transitions influence skeletal change. I test these predictions in subsequent chapters by investigating whether morphological features respond to changes in loads experienced during the lifetime. To do so, I examine metacarpal and long bone morphology in differently aged wild-caught chimpanzee skeletons from museum collections. In Chapter III, I investigate the degree of variability in third metacarpal curvature and distal ridge formation with regard to changes in knuckle-walking behavior over the course of development. Chapter IV examines changes in cross-sectional geometric properties of the humerus and femur in relation to degree of suspensory and terrestrial behaviors during development.

Loading and patterns of use influence the growth and development of bones, but the nature and sensitivity of this relationship is largely unknown. Finer-grained ontogenetic behavioral data such as that presented here in Chapter II, combined with complementary anatomical data in Chapters III and IV, provide a clearer understanding of this relationship and ultimately furnishes a means to reconstruct behavior from fossils.

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CHAPTER II

Locomotor and postural development of wild chimpanzees.

Introduction

Few data exist regarding developmental changes in the positional behavior of wild chimpanzees. Although observations have been made of how mature chimpanzees move in the wild (Hunt, 1992; Doran, 1993a, b; Doran and Hunt, 1994), only one study has examined the locomotion of immature chimpanzees (Doran, 1992; Doran, 1997). Results of this study suggested that infants moved in a suspensory fashion more often than did adults, while older individuals moved quadrupedally more frequently than did young chimpanzees (*ibid.*). Doran (1992) found that quadrupedalism was the predominant locomotor behavior starting at two years of age and that adult patterns of locomotion were reached at juvenility, a relatively early time insofar as it precedes epiphyseal fusion.

In this study, I build upon the pioneering work of Doran (1992) with a more detailed kinematic analysis to investigate weather the same trends exist when locomotor behavior is divided into more detailed categories. Specifically, I classify locomotion into 13 kinematically distinct categories with further subdivisions that correspond to the loading environment. In doing so, I follow other researchers, who have noted that conventional systems of categorizing locomotion in apes fail to recognize the “intermediate” forms of locomotion that occur between broad categories, such as exists between quadrupedal locomotion and bipedal walking (D’Août et al., 2004). Moreover, I consider the effects of individual variation on positional development by collecting and analyzing data from a large sample of individuals. Understanding the relationship between form and function requires an analysis of the entire positional repertoire, which includes both locomotion and posture. This study is the first to examine posture in addition to locomotion during development in wild chimpanzees.

Assessing chimpanzee developmental changes in both locomotion and posture will potentially illuminate how the loading environment subsequently changes as individuals age. This, in turn, has implications for determining whether changes in the loading environment coincide with morphological changes in chimpanzee skeletal features. Lovejoy and colleagues (Lovejoy et al., 2003) argued that, in the absence of fracture, bone shape changes in response to the strain environment are negligible in adults. However, other studies have found that stress placed on bone through habitual behaviors during early development can cause significant responses (Bouvier and Hylander, 1981; Bass et al., 2002; Lieberman et al., 2003; Pontzer et al., 2006). If plastic morphological features in chimpanzee skeletons indicative of suspensory or quadrupedal walking exist, they could potentially be used to reconstruct the degree of quadrupedalism in fossil hominoids, including purported hominins.

The purpose of this chapter is to document how chimpanzee positional behavior, which includes both locomotion and posture, changes over time. A goal is to understand the loading environment of joints and shafts of long bones from infancy through adulthood. Adult chimpanzees knuckle-walk ~90% of the time during travel (Doran, 1993; Doran and Hunt, 1994). During knuckle-walking, chimpanzees experience higher peak vertical forces on their hindlimbs compared with those on their forelimbs, in contrast with nonprimate mammals for whom the reverse is typical (Demes et al., 1994). Based on Doran's (1992, 1997) previous work and the fact that knuckle-walking is hindlimb driven, I hypothesize that infant chimpanzees predominantly use their forelimbs more than they use their hindlimbs in locomotion, and that the pattern of limb dominance changes with a trend towards increasing hindlimb usage in older chimpanzees. I hypothesize that this pattern of forelimb bias is also reflected in infant postural behavior. Previous work on humans suggests that these locomotor and postural shifts are likely to occur during key developmental periods (Burnett and Johnson, 1971).

Materials and methods

Data were collected on the locomotor and postural behavior of chimpanzees at Ngogo, Kibale National Park, Uganda, from February to August 2009. The Ngogo chimpanzee community contains approximately 160 individuals. Chimpanzees were divided into four age categories: infants (0.1 – 5 years old), juveniles (5.1 – 10 years old), adolescents (10.1 – 13 years old), and adults (> 20 years old). These age groupings are based off of known birth dates for individuals. Some adult birth dates are estimated but these individuals are all over 20 years of age. Age groupings are based off of chronological ages and not behavioral markers in order to facilitate morphological comparisons. For example, juvenility if often behaviorally marked by the birth of a subsequent sibling, however, intra- and inter-individual variation of inter-birth intervals leads to chronological variation in this occurrence. Juvenility usually begins by the fifth year of life, which was the chronological period used in this study (Plooij, 1984; Boesch and Boesch-Acherman, 2000). In order to examine developmental changes in detail, infants and juveniles were further broken down into multiple age categories. Since there is limited independent locomotion in the first year of a chimpanzee's life, year one and two were collapsed when breaking down infants into four categories (infant 1: 0.1 - 2 years, infant 2: 2.1 – 3 years;

infant 3: 3.1 – 4 years; infant 4: 4.1 – 5 years). Juveniles were also further divided into two age classes, younger and older juveniles (juvenile 1: 5.1 - 7.5; juvenile 2: 7.6 – 10; Table II.1). Morphological correlates of adolescence include female sexual swelling and male testes decent both of which usually occur by age 10 (Boesch and Boesch-Acherman, 2000). Therefore, 10 years marks the beginning of adolescence in this study. The onset of adulthood varies between sexes. For females, it begins when they are 13 – 15 years old and give birth for the first time (Goodall, 1986; Boesch and Boesch-Acherman, 2000; Nishida et al., 2003); for males, adulthood starts around 16 years of age after individuals attain physical and social maturity (*ibid*.). Adolescents selected for study were between 10 and 13 years old, and thus clearly subadult. In contrast, all adults were estimated to be at least 20 years old. Restricting analyses to these older individuals negated the potential problem of including chimpanzees that made early or late transitions to adulthood. Making a clear separation between adults and adolescents also made it more likely to discern developmental differences in locomotion between members of the two age classes.

Data were collected on 53 chimpanzees, including 20 infants, 11 juveniles, 11 adolescents, and 11 adults (Table II.1). Each individual was sampled for 5 one-hour-long observation sessions (Table II.1). The positional behavior of focal individuals was recorded every two minutes during instantaneous scan samples. Chimpanzee positional behavior was classified according to body parts that bear the individual’s weight, using categories defined in prior studies (Hunt et al., 1996; Thorpe and Crompton, 2006). These categorical modes were further subdivided into submodes following Thorpe and Crompton (2006; Table II.2). Modes are broad types of positional behavior, such as “vertical descent.” Submodes are kinematically distinct behaviors within a broader mode, such as “rump first extended elbow descent.” The locomotor context was also recorded and consisted of two main categories, play and travel. The category travel also included foraging. The percentage of time members of each age class spent in each mode and submode was calculated for both locomotion and posture. To ensure independence of postural scans, observations of consecutive postural modes made during a single focal observation session were collapsed. Observations of arboreal and terrestrial behaviors were combined in analyses because the goal of this study was to document how the overall loading environment changed as a function of age.

Because the positional mode data were not normally distributed, nonparametric statistical tests were employed in the analyses. A Kruskal-Wallis test was used to examine heterogeneity in positional modes among members of different age categories; post-hoc comparisons between treatments were made following the procedure outlined in Siegel and Castellen (1988). When only two categories were analyzed, e.g. the sexes, pairwise comparisons were conducted using the Mann-Whitney U test (*ibid.*). Levels of significance were set at $p < 0.05$.

Results

Locomotion

Age category differences

The amount of time chimpanzees spent moving varied as a function of age (Kruskal-Wallis Chi Square = 14.58, df = 3, $p = 0.002$; Figure II.1). Adult chimpanzees spent 16% of their time moving, which was significantly less compared to that shown by members of the three other age classes (post-hoc tests, $p < 0.05$ for all three comparisons; Figure II.1). Adolescents were also less active compared to infants (post-hoc test $p < 0.05$; Figure II.1). While adults were the least active age group, infants were the most active. Infants spent 28% of their time moving, an amount that was significantly more than individuals of any other age category (Figure II.1). Juveniles, adolescents, and adults primarily moved while traveling (96%, 97%, and 99% respectively). In contrast, infants traveled only 62% of the time they were moving. Infants spent 36% of their locomotor time playing; playing comprised a much smaller percentage of locomotion for members of the three other age categories (juvenile = 3%, adolescent = 2%, and adult <0.5%).

Overall, several robust age-specific trends emerged. First, there was significant heterogeneity among age classes in the tendencies to engage in torso-orthograde suspensory locomotion, vertical climbing, and quadrupedal walking (Kruskal – Wallis $p < 0.001$ for all three comparisons; Table II.2); torso-orthograde suspensory locomotion and vertical climbing decreased with age, while quadrupedal walking increased with age (Figure II.2, Table II.2). Post-hoc analyses revealed that infants engaged in quadrupedal walking significantly less than did individuals in the three other age groups ($p < 0.05$ for all three comparisons; Table II.3). While juveniles walked quadrupedally more than did infants, they still engaged in this locomotor mode significantly less than did adults and adolescents (post-hoc tests, $p < 0.05$ for both comparisons; Table II.3). The opposite relationship occurred with torso-orthograde suspensory locomotion (TOSL), with infants engaging in significantly more suspensory locomotion compared to individuals in the three other age groups (post-hoc tests, $p < 0.05$ for all three comparisons; Table II.3). Juveniles engaged in intermediate levels of TOSL with rates lower than infants but higher than adolescents and adults (post-hoc tests, $p < 0.05$ of both comparisons; Table II.3). Finally, infants and juveniles engaged in significantly higher rates of vertical climbing compared to adolescents and adults (post-hoc tests, $p < 0.05$ for all four comparisons).

There as also variability in the amount of time individuals of different age classes spent in bipedal locomotion, leaping, and quadrupedal running, although these did not vary systematically across age groups in the same manner as torso-orthograde suspensory locomotion, vertical climbing, and quadrupedal walking (Table II.2, Table II.3). There was significant heterogeneity in the amount of time chimpanzees moved bipedally (Kruskal-Wallis $p < 0.01$; Table II.2). Post-hoc comparisons revealed that infants moved bipedally significantly more than did individuals in the three other age classes ($p < 0.05$ for all three comparisons; Table II.3). There was also significant variability in the amount of time chimpanzees of different ages spent leaping (Kruskal-Wallis $p < 0.05$; Table II.2); post-hoc comparisons, however, failed to reveal significant differences between members of different age classes ($p > 0.05$ for all three comparisons; Table II.3). Quadrupedal running displayed significant variability among individuals of different ages (Kruskal-Wallis $p < 0.001$; Table II.2). Juveniles spent the most time moving in this fashion, and they did so significantly more than did infants, adolescents, and adults (post-hoc tests, $p < 0.05$ for all three comparisons; Table II.3).

The frequency of submodes within different locomotor modes also varied as a function of age. Rates of vertical descent did not vary between the different age groups but the way individuals descended did (Table II.2). Infants descended vertically 47.9% of the time in rump-first forelimbs only descent, headfirst scramble descent, or headfirst cascade. These three submodes only use the upper limbs or position the body head first, thus loading the upper arms more than vertical descent submodes where the legs descend first. Adolescents descended 77.2% of the time via submodes that were rump-first and predominantly load the lower limbs (excluding rump-first forelimb only descent) and adults engaged in these submodes 75% of the time they descended vertically (Table II.2). Juvenile movements were more variably distributed between upper limb and lower limb loading vertical descent submodes (Table II.2). Infants not only descended in submodes that loaded the upper limbs more than adults did, they were also more varied in how they chose to descend. Infants engaged in 9 submodes of vertical descent, compared to juveniles who displayed 8 submodes, adolescents who displayed 7, and adults who displayed 6 (Table II.2).

As reported above, bipedal locomotion varied significantly between infants and individuals in other age classes. While the submode bipedal hop and flexed bipedal walk are solely hindlimb loading, the rest of the submodes engage the upper limbs during bipedality to some extent. All age groups relied on upper arm loading and stabilization at least 90% of the time they engaged in bipedal locomotion (Table II.2). Similar to vertical descent, infants were more variable in how they moved bipedally compared to the other age classes; infants engaged in 5 submodes while juveniles engaged in 3 and adolescents and adults both engaged in 2 submodes (Table II.2). This increased variability in submode selection was also present in vertical climbing where infants and juveniles engaged in 6 different submodes while adolescents and adults engaged in 4 (Table II.2). Lastly, torso-orthograde suspension was also more variable for the two younger age classes with infants and juveniles engaging in 5 submodes and adolescents and adults engaging in 3 (Table II.2).

Changes in locomotion during infancy and juvenility

The largest change in locomotion occurred between infancy and juvenility, even after subdividing these age groups (Figure II.3). Infants and juveniles were divided into six age groups to examine changes in locomotion over time. Several changes became clear when doing so. Quadrupedal running, quadrupedal walking, and torso-orthograde suspensory movement differed significantly between age groups (Kruskal – Wallis $p < 0.01$ for all three comparisons). Both younger and older juveniles engaged in significantly more quadrupedal running and walking and less TOSL compared to all of the infant categories but not compared to one another (post-hoc test $p < 0.05$ for all 24 juvenile vs. infant comparisons; Figure II.3).

As infants aged they spent less time moving in a torso-orthograde suspensory fashion and more time walking quadrupedally (Figure II.3). The highest rates of torso-orthograde forelimb-suspension were reached by infants in category 2 who engaged in this behavior 51% of their locomotor time. The rate of TOSL dropped for individuals in the subsequent infant age category 3, with these individuals spending less time in this locomotor mode compared to infants in categories 2 and 4 (post-hoc tests $p < 0.05$ for both comparisons, Figure II.3). Infants in category 1 engaged in vertical climbing 39% of their locomotor time, which was at least 20% more than any other subadult age group (Figure II.3).

Infants in category 1 spent 6% of their locomotor time walking quadrupedally, which was significantly less compared to infants in categories 3 and 4 (27% and 21% respectively, $p < 0.05$ for both comparisons; Figure II.3). When only infants were examined, the largest difference in locomotor rates between age categories occurred between individuals in the two youngest categories and individuals in the two oldest categoreis for quadrupedal walking (Mann-Whitney $U = 23.000$, $z = -2.014$, $p = 0.046$; infant 1 and 2 vs. Infant 3 and 4).

One infant, Frida, was born during this study (February 2009), and her positional behavior was recorded at least once a week for the first 7 months of her life. She showed the first signs of independently moving her own body from one location to another at around 5 months of age. Prior to 5 months her positional behavior consisted entirely of sitting, lying, and clinging. Five hours of focal observations during the fifth, sixth, and seventh month of her life revealed she spent 5.5% of her time engaged in locomotion. The time she spent moving only consisted of the upper limb loading modes of vertically climbing, swaying, or moving with her forelimbs in an orthograde fashion (4.1%, 0.7%, and 0.7% respectively). When vertically climbing, she frequently engaged in the submode, bimanual pull-up, only loading her upper limbs.

Posture

Age category differences

Members of different age classes showed significant heterogeneity in the amount of time they spent clinging, in orthograde forelimb suspension, pronograde standing, sitting, and squatting (Kruskal – Wallis $p < 0.01$ for all five comparisons; Table II.4). Post hoc tests revealed that infants utilized all of these postural modes differently than older chimpanzees (Table II.5). While chimpanzees of all ages spent a considerable amount of time sitting, infants did so less often than individuals in the three other age classes (post-hoc tests $p < 0.05$ for all three comparisons; Tables II.4 and II.5). Infants also spent more time clinging and less time pronograde standing and squatting compared to individuals in the three older age groups (post-hoc tests $p < 0.05$ for all 12 tests; Table II.5). Infants spent more time in orthograde forelimb suspension compared to adolescents and adults (post-hoc tests $p < 0.05$ for both comparisons; Table II.5). Juveniles engaged in intermediate levels of orthograde forelimb suspenion, pronograde standing, sitting, and squatting compared to both younger infants and older adolescents and adults (Table II.4 and 5). Mirroring variation in locomotion, infants displayed more varied postures than older chimpanzees. Infants engaged in 4 modes that each comprised at least 10% of postural time. In contrast, juveniles spent a similar amount of time in 3 modes, while adolescents and adults did so in only two modes, sitting and laying.

Changes in posture during infancy and juvenility

While infants engaged in higher rates of orthograde forelimb suspension compared with older chimpanzees, infants of different ages did not differ among each other (KW Chi-Square = 2.211, df = 3, $p = 0.530$; Figure II.4).

Infants engaged in clinging ~15% of their postural time while chimpanzees in all other age classes spent under 2% of postural time clinging (Table II.4). Rates of clinging dropped off drastically when individuals attained juvenility, as they no longer breast-fed or traveled on their mothers; thus, we only compared clinging between infants of different ages. Infant 1 individuals engaged in clinging 28.4% of their postural time with rates decreasing as they aged (Infant 2 = 14.6%, Infant 3 = 13.3%, Infant 4 = 8.8%; Figure II.4). Infants of different ages showed significant heterogeneity in the amount of time they spent clinging (Kruskal-Wallis Chi-Square = 10.121, df = 3, $p = 0.018$; Figure II.4). Post hoc analyses revealed that Infant 1 individuals, i.e. those under two years of age, engaged in clinging significantly more than infants in the three older age categories (post-hoc tests $p < 0.05$ for all three comparisons; Figure II.4). Similarly, infant 2 individuals clung to their mothers more than did infants in the infant 4 category (post-hoc test, $p < 0.05$; Figure II.4).

Changes in sitting also occurred during infancy, with significant heterogeneity displayed among members of the four infant age categories (Kruskal-Wallis Chi-square = 9.38, df 3, $p < 0.05$; Figure II.4). Category 1 infants sat significantly less than did infant 3 and 4 individuals, while infant 2 individuals sat significantly less than infant 4 individuals (post-hoc tests, $p < 0.05$ for all three comparisons).

Clinging to their mothers while she was moving likely required more muscular effort compared to when the mother was still. Therefore, we examined infant clinging patterns when mothers traveled. There is a trend toward increased dorsal clinging as infants aged, but the amount of dorsal clinging across infant age categories was only marginally significant (Kruskal-Wallis Chi-Square = 7.38, df = 3, p = 0.06, Figure II.5). While infant 4 individuals never engaged in ventral pronograde locomotor behavior, likely due to size constraints of fitting under a mother while she is moving horizontally across a substrate, they did engage in ventral orthograde clinging at rates higher than infant 3 individuals. Reasons for this inverse trend for the oldest infant category are explored in the discussion.

Sex differences

At all stages of their lives, males and females did not differ in the amount of time they spent in any locomotor mode (Mann – Whitney U all comparisons $p > 0.05$). The amount of time adults spent standing in pronograde fashion was the only postural difference found between males and females (Mann – Whitney U = 3.00, z = -2.191, p = 0.030; Table II.4).

Discussion

Several milestones occur during chimpanzee locomotor development. The first is a shift around 5 months of age with the inception of independent locomotion, as inferred from opportunistic but systematic observations of one newborn. In the second year of life, individuals have the highest rates of suspensory behavior. As individuals grow older, they engage in less torso-orthograde suspensory and more quadrupedal locomotion. During juvenility, chimpanzees display a drastic decrease in clinging and torso-orthograde suspensory behavior, and pronounced increases in quadrupedal walking and running. At adolescence, individuals display a dramatic decrease in torso-orthograde suspensory locomotion and vertical climbing and an increase in quadrupedal walking. As individuals age, they engage in fewer locomotor modes and submodes, making the loading environment less variable with age.

Positional behavior of infants

Although there was only one opportunity to systematically observe a newborn's early positional behavior development, it was consistent with previous findings. Doran (1992) observed 2 infants, 0 – 6 months, and found that locomotion independent of mothers began at 5 months. Frida did not start to move independently until 5 months of age at which point she only engaged in upper arm loading behavior.

As hypothesized, infants frequently loaded their forelimbs while moving, e.g. using torso-orthograde suspensory locomotion. The loading environment changed during development as older individuals began to walk quadrupedally frequently, placing more weight on their hindlimbs in the process (Demes et al., 1994). Even in locomotor modes in which the loading environment was less clear, e.g. vertical descent, infants engaged in more upper limb loading submode behaviors, while adolescents and adults engaged in more frequent lower limb loading submode behaviors.

Compared with locomotion, postural behaviors often exert less pressure in terms of the loading environment because they involve mainly sitting and lying for most age classes (Table II.4). Infants displayed a greater range of postural behaviors than did older chimpanzees. They also spent considerable time utilizing postures that loaded their upper arms, such as clinging and orthograde forelimb suspension (Table II.4), further supporting the hypothesis that infants use their forelimbs more than older chimpanzees.

During travel, chimpanzees cover considerable distances and expend the greatest amount of daily energy on this activity (Leonard and Robertson, 1997). Since infants primarily travel long distances on their mothers, they are freed from the constraints of spending their locomotor time efficiently as they go from point A to point B. Because of this, they devote a large percentage of their locomotor time to play (36% compared to 3% for juveniles and even less for adolescents and adults). Expending locomotor energy on play rather than long distance travel allows infants to engage in a wide variety of locomotor modes and submodes, such as summersault, that are not as energetically efficient compared to quadrupedal walking, the primary mode of adult locomotor travel.

The transitions during infancy

Infancy is not a static period in terms of locomotion and posture. As infants age, they increase the amount of time moving quadrupedally and sitting and decrease the time moving in torso-orthograde suspensory fashion and clinging. Although clinging decreases as infants age, they still predominantly employ upper limb dominated positional behavior even after they reach 2 years and gain greater independence from their mothers. Doran (1992) found a shift in behavior between very young infants 0.5 yr – 2.0 years old and older infants over 2 years of age. With infants divided in this way, there was a decrease in climbing/scrambling and suspensory locomotion and an increase in quadrupedal locomotion in infants 2 years and older. In this study, I classified infants older than 2 years into three distinct age categories. Using this classification scheme, I was able to pinpoint the transitions toward increased quadrupedalism and decreased suspensory behavior after 3 years of age. In fact, infants between 2 and 3 years displayed the highest rates of TOSL for any age class. The largest shift in rates of infant quadrupedal walking, and therefore increased hindlimb dominated locomotion, occurred after individuals were 3 years of age. In a study on maternal investment, Hiraiwa-Hasegawa (1990) found that chimpanzee infants at the Mahale Mountains increased the amount of time they traveled when they were 3 years old, but that the amount of time they spent traveling independently did not exceed the time they were carried by their mothers until their fourth year of life. Ngogo infants also experienced a postural transition at 3 years old. Infants younger than 2 years spent most of their time clinging ventrally to their mothers. During the second year of life, chimpanzee infants spent an equal amount of time clinging ventrally and dorsally to their mothers. This changed when infants reached 3 years of age, with a shift toward dorsal clinging. This shift is significant because dorsal pronograde clinging may have limited loading impact since most of the infant's body weight is supported through his or her rear or stomach, thereby decreasing levels of upper arm loading compared to infants between 2 and 3 years old. It is important to note, methodological differences are possibly responsible for differences in the patterns of infant locomotor behavior reported here and in Doran's (1992) study. For example, differences in the number of infant age categories and locomotor modes and submodes make direct comparisons difficult.

Despite the aforementioned trends, I documented relatively few locomotor changes during infancy. This is in sharp contrast to Doran (1992) who found that quadrupedalism "dominated" the locomotor profile of chimpanzees by the age of 2 years. The lack of difference between infants found in this study is likely due to the high degree of individual variation that exists in infant positional behavior. This was especially noticeable in the degree of torso-orthograde suspensory locomotion between 3 - 4 and 4 -5 year old individuals. Shifts in locomotion during the first year of life may be attributable to differences in the rate at which the central nervous systems of individuals develop. Chimpanzees, like humans, develop over a prolonged period during which they depend on mothers who serve as their primary caregivers. Certain mother-infant interactions change reliably with infant development. For example, there is a dramatic decrease in nipple contact during the first six months of an infant's life (Plooij, 1984; Hiraiwa-Hasegawa, 1990). However, mothers vary in their personalities and how they handle infants. Goodall (1984, 1986) recognized that there are different types of chimpanzee mothers and hypothesized that mothers had the greatest impact on their offspring's development. Differences in how primate females handle their infants have been widely recognized in chimpanzees and Old World Monkeys; some mothers refuse to carry or remain in contact with their infants frequently, while others do so more often (Fairbanks, 1996; Maestripieri, 1999; DeLathouwer and Van Elsacker, 2004). While most human infants walk between 11 – 13 months of age, individuals vary in this regard, starting anywhere between 9 and 22 months (Variot and Gotcu, 1927). Some aspects of human maternal style have been found to correlate with the timing of walking in infants, with less attentive mothers having infants that walk sooner than more positive reinforcing mothers (Biringen et al., 1995). It is therefore likely that variation in chimpanzee maternal behavior may also influence the rates that infants engage in different locomotor modes.

Weaning conflict may also affect the rates and types of clinging. As infants age, they begin to spend more time clinging dorsally rather than ventrally, but older infants may revert to clinging ventrally as they attempt to prolong the period they breastfeed and negate weaning efforts by their mothers.

Juveniles

Despite moving entirely independently from their mothers, juveniles did not engage in quadrupedal locomotion as much as adolescents or adults. While previous research found a shift between the locomotor behavior of infants and juveniles and argued that the adult overall locomotor pattern was reached at juvenility (Doran, 1992), this study found juveniles represented an intermediate locomotor phase between infants and older chimpanzees. This research also shows that juveniles utilize more locomotor submodes than adolescents and adults, indicating that the way they move varies in degree as well as diversity. This underscores the gradual, rather than abrupt, transition that occurs during juvenility, which is an intermediate stage between the forelimb dominated and diverse behavior of infants and the hindlimb dominated and less variable behavior of adolescents and adults.

Sex differences

Prior studies of *Pan troglodytes verus* at the Taï National Park and *schweinfurthii* at the Mahale Mountains failed to document any sex differences in chimpanzee locomotion (Doran, 1993a; Doran and Hunt, 1994). In contrast, female *schweinfurthii* at the Gombe National Park displayed more quadrupedal locomotion and more climbing than did males (Doran and Hunt, 1994). My results conform to those from Taï and Mahale; sex differences in locomotion did not exist in the Ngogo chimpanzees. It is possible that sex differences would emerge in Ngogo chimpanzees if arboreal and terrestrial locomotion were analyzed separately, but this was not undertaken in this study since a picture of overall locomotor behavior was desired to determine the loading environment for each age class.

Taï chimpanzees exhibited sex differences in overall postural activity but post hoc tests comparing specific postural modes were not conducted so comparison with the present study is difficult (Doran, 1993b). Analyses of postural differences between male and female chimpanzees at Gombe and Mahale are not available. Only one postural mode, pronograde stand, exhibited a sex difference in the Ngogo chimpanzees. The lack of sex differences in positional behavior suggests that the changes in development documented in this study occur irrespective of sex and are not driven by males or females alone.

Between site comparisons

The results presented here can be compared with those derived from research on chimpanzees elsewhere. Positional behavior of adult chimpanzees has been studied at the Gombe and Mahale Mountains National Parks in Tanzania (both *schweinfurthii*), and at the Taï National Park, Ivory Coast (*verus*). Although chimpanzees at all four sites spend a similar amount of time moving, adult locomotor and postural behavior varies among sites.

Adult chimpanzees at Mahale and Gombe engaged in locomotor behavior ~18% of the time (Hunt, 1991a), similar to the level of locomotor activity found in adult Ngogo chimpanzees (17%). Chimpanzees at Mahale and Gombe traveled quadrupedally an average of 92% of the time they moved (Hunt 1991a, b), while adult chimpanzees at Taï moved quadrupedally ~86% of the time (Doran 1993a). In contrast, the Ngogo chimpanzees spent less time moving quadrupedally (76%, Table II.2). Data recorded at Ngogo are derived from both wet and dry seasons of 2009. Data from a 3-month pilot study conducted during the dry season of 2007 based on 130 hours of observation yielded similar results to the 2009 study, with adults engaging in quadrupedal locomotion 74% of their locomotor time. It is unclear why the Ngogo chimpanzees spend less time moving quadrupedally than do chimpanzees at other sites. Several possibilities exist, including but not limited to, differences in sample sizes, observational techniques, ecologies, and chimpanzee foraging strategies. Additional study will be required to investigate this issue. Despite the relatively low rates of adult quadrupedal locomotion at Ngogo, chimpanzees there nonetheless still display a pronounced shift toward this form of movement as they age. A similar shift is expected in the other populations where adult rates of quadrupedal locomotion are even higher.

Adult chimpanzees from Taï engaged in sitting or lying ~92% of their postural time. The frequency of these two postural modes at Ngogo was the same (92%), but this percentage decreases to ~77% when consecutive postural modes are deleted to negate the dependence of scans (Table II.4). Mahale and Gombe chimpanzees engaged in sitting or lying ~90% of their postural time after data were collapsed (Hunt, 1992). Ngogo chimpanzees are therefore more similar to Taï chimpanzees as they spend a smaller proportion of time in the dominant positional behaviors of sitting and lying. Like chimpanzees at Taï, the Ngogo chimpanzees engage in more diverse postural behaviors that are likely to exert greater load bearing forces.

Doran and Hunt (1994) found that locomotor differences between Taï and its eastern counterparts were related to degree of arboreality and argued that it was likely due to habitat differences. The postural differences that align Taï and Ngogo and the lower rates of quadrupedal locomotion in these two populations compared to Mahale and Gombe may also relate to differences in habitat structure. Taï is a lowland rainforest where many of the food trees are more than 30 meters high (Doran and Hunt, 1994). Similarly, Ngogo is also covered mostly by old-growth, evergreen forest (Struhsaker, 1997). In contrast, relatively few trees cover the landscapes at Gombe and Mahale. Small pockets of forest exist at Mahale (Nishida, 1990), and miombo woodland with trees of low stature can be found at both Gombe and Mahale.

Conclusion

Chimpanzees undergo several developmental transitions in positional behavior from infancy, through the juvenile, adolescent, and adult phases, with each transition leading to more quadrupedal walking and less torso-orthograde suspensory locomotion. Infants engage in the highest levels of upper limb loading locomotion and posture. The highest levels of torso-orthograde supsensory behavior occur in individuals 2 - 3 years of age. Juveniles (5 - 10 years) move independently from their mothers, no longer cling to their mothers, and walk and run quadrupedally significantly more than younger individuals. Individuals reach adult patterns of positional behavior at adolescence (~10 years of age). These changes in locomotion and posture mean that the skeleton is loaded in different, but predictable ways as chimpanzees mature. Overall, it can be inferred that infant chimpanzees primarily load their upper arms in locomotion and posture, juveniles are intermediate, and adolescents and adults primarily load their lower limbs during locomotor behavior.

Previous research had reported that chimpanzee adult locomotor behavior is achieved early in life with quadrupedalism dominating locomotion by 2 years of age and an adult repertoire achieved by juvenility, long before epiphyseal fusion (Doran, 1992). However, this study found that quadrupedal locomtion does not “dominate” the locomotor repertoire until adolescence and that the pattern of adult locomotor behavior is also not reached until adolescence, closer to the time of epiphyseal fusion. These findings question the assumption that adult patterns of locomotion primarily influence loading patterns in chimpanzees (Carlson et al.,

2006) and warrant further investigation of how developmental changes in morphological properties correlate with these developmental patterns of behavior to evaluate the relationship between form and function.

CHAPTER II TABLES

Table II.1 Sample size and sex breakdown for each age category.

Age Class	Subclass	Sample Size	Female	Male
Infant		**20**	**6**	**14**
	I1	4	2	2
	I2	5	0	5
	I3	5	2	3
	I4	6	2	4
Juvenile		**11**	**5**	**6**
	J1	6	3	3
	J2	5	2	3
Adolescent		**11**	**4**	**7**
Adult		**11**	**6**	**5**

Age classes were broken down as follows: infant 0 - 5 years, infant 1: 0.1 - 2 years, infant 2: 2.1 – 3 years; infant 3: 3.1 – 4 years; infant 4: 4.1 – 5 years, juvenile 5.1-10 years, juvenile 1: 5.1 - 7.5 years; juvenile 2: 7.6 - 10 years, adolescent 10.1 - 13 years, and adult 20+ years.

Table II.2 Percentage of locomotor time spent in each mode and submode for each age category.

	Infant	**Juvenile**	**Adolescent**	**Adult**	**P value**
MODE *SUBMODE*					
Bipedal	**6.0**	**2.7**	**0.8**	**2.6**	**0.004**
Bipedal hop	*0*	*9.1*	*0*	*0*	
Bipedal scramble	*12.2*	*0*	*0*	*0*	
Flexed bipedal walk	*8.2*	*0*	*0*	*0*	
Hand-assisted bipedal scramble	*57.2*	*63.6*	*66.7*	*27.3*	
Hand-assisted extended bipedal walk	*2*	*0*	*0*	*0*	
Hand-assisted flexed bipedal walk	*20.4*	*27.3*	*33.3*	*72.7*	
Bridge	**0.2**	**0.5**	**0.3**	**0.9**	**NS**
Drop	**2.9**	**3.2**	**0.8**	**1.2**	**NS**
Forelimb-hindlimb suspensory	**0.2**	**0.2**	**0**	**0**	**NS**
Leap	**1.1**	**0.5**	**1.3**	**0**	**0.039**
Quadrupedal run	**0.5**	**5.4**	**1.0**	**0.7**	**< 0.001**
Quadrupedal walk	**19.1**	**44.2**	**65.7**	**75.6**	**< 0.001**
Asymmetrical gait	*5.6*	*2.2*	*0.8*	*1.3*	
Irregular gait	*42.8*	*8.9*	*4.5*	*2.7*	
Symmetrical gait	*1.2*	*0*	*1.1*	*8.5*	
Unspecified	*58.6*	*77.7*	*92.9*	*86.7*	
Quadrupedal walk and run					**< 0.001**
Ride and sway	**1.3**	**2.5**	**2.8**	**1.2**	**NS**

Torso-orthograde suspensory					
	44.1	**20.1**	**12.5**	**7.7**	**< 0.001**
Arrested drop	*0.6*	*1.2*	*0*	*0*	
Forelimb swing	*38.9*	*54.9*	*54*	*54.9*	
Orthograde clamber	*9.5*	*20.7*	*12*	*12.1*	
Orthograde transfer	*4.5*	*15.9*	*34*	*33.3*	
Unimanual forelimb-twist	*46.5*	*7.3*	*0*	*0*	
Vertical climb	**18.9**	**13.8**	**9.5**	**3.7**	**< 0.001**
Bimanual pull-up	*10.8*	*1.8*	*0*	*0*	
Extended-elbow vertical climb	*4.4*	*7.2*	*2.6*	*6.3*	
Flexed-elbow vertical climb	*36.9*	*48.2*	*60.5*	*50*	
Unspecified	*2.5*	*8.9*	*10.5*	*6.3*	
Vertical climb forelimbs only	*0.6*	*1.8*	*0*	*0*	
Vertical scramble	*45.1*	*31.7*	*26.3*	*37.6*	
Vertical descent	**5.3**	**6.6**	**5.5**	**6.5**	**NS**
Fire pole slide	*4.5*	*7.4*	*13.6*	*0*	
Head first cascade	*2.3*	*0*	*13.6*	*0*	
Head first scramble descent	*25.1*	*14.8*	*4.5*	*3.6*	
Rump first cascade descent	*0*	*0*	*0*	*3.6*	
Rump first extended elbow descent	*20.5*	*11.1*	*13.6*	*3.6*	
Rump first forelimbs only descent	*20.5*	*14.8*	*4.5*	*21.4*	
Rump first scramble descent	*18*	*23.2*	*18.2*	*32.2*	
Rump first symmetrical descent	*4.5*	*18.5*	*31.8*	*35.6*	
Sideways vertical descent	*2.3*	*3.7*	*0*	*0*	
Unspecified	*2.3*	*7.6*	*0*	*0*	
Wrestle and somersault	**0.4**	**0.2**	**0**	**0**	**NS**

Kruskal-Wallis test was used to examine heterogeneity in locomotor modes among members of different age categories.
Modes and submodes from Hunt et al., 1996 and Thorpe and Crompton, 2006.
a. Locomotor submodes are included for modes if they comprise at least 5% of the locomotor repertoire of at least one age class. Gray highlight signifies the submode engaged in most frequently for that age class.

Table II.3 Significant differences in locomotor mode frequencies among age categories.

	Infant	**Juvenile**	**Adolescent**
Juvenile	**Bipedal walk**		
	Quadrupedal run		
	Quadrupedal walk		
	Torso-orthograde suspensory		
Adolescent	**Bipedal walk**		
		Quadrupedal run	
	Quadrupedal walk	**Quadrupedal walk**	
	Torso-orthograde suspensory	**Torso-orthograde suspensory**	
	Vertical climb	**Vertical climb**	
Adult	**Bipedal walk**		
		Quadrupedal run	
	Quadrupedal walk	**Quadrupedal walk**	
	Torso-orthograde suspensory	**Torso-orthograde suspensory**	
	Vertical climb	**Vertical climb**	**Vertical climb**

Results are significant at the $p < 0.05$ level. Post hoc comparisons between treatments were conducted using the inequality $| R_u - R_v | \geq z_{\alpha/k(k-1)} \sqrt{((N(N+1)/12) \times (1/n_u + 1/n_v))}$ (Siegel and Castellen, 1988).

Table II.4 Percentage of postural time spent in each mode and submode for each age category.

MODE *SUBMODE*	**Infant**	**Juvenile**	**Adolescent**	**Adult**	**P value**
Cling	**16.2/15.1**[a]	**1.1/1.7**	**0.6/1.5**	**0.2/0.6**	**< 0.001**
Forelimb-hindlimb suspension	**1.2/2.0**	**0.7/1.6**	**0.2/0.4**	**0.5/0.9**	**NS**
Hindlimb suspension	**0.1/0.1**	**0/0**	**0/0**	**0/0**	**NS**
Lie	**17.3/12.9**	**14.2/12.6**	**16.3/10.9**	**16.8/11.6**	**NS**
Orthograde forelimb suspension	**11.7/17.3**	**7.2/12.1**	**2.2/5.5**	**2.2/7.5**	**0.001**
Orthograde quadrupedal suspension	**0.7/1.1**	**0.7/1.8**	**1.2/3.1**	**0.5/1.3**	**NS**
Orthograde stand	**1.2/2.0**	**1.2/2.4**	**0.6/1.4**	**0.5/1.7**	**NS**
Pronograde bridge	**0/0**	**0/0**	**0.1/0.3**	**0/0**	**NS**
Pronograde stand	**1.5/2.9**	**2.6/5.5**	**2.7/7.5**	**2.4/8.0***	**0.008**
Pronograde suspension	**0.5/1.0**	**0.5/1.0**	**0.1/0.2**	**0/0**	**NS**
Sit[b]	**49.4/45.2**	**71.2/60.3**	**75.1/67.1**	**74.8/64.9**	**0.000**
Butt only	*82.3*	*86.5*	*82.2*	*84.9*	
Forelimb cling	*0.4*	*0*	*0.1*	*0*	
Forelimb compression	*0.2*	*0.1*	*0*	*0*	
Forelimb-hindlimb compression	*0.1*	*0*	*0*	*0*	
Forelimb-hindlimb suspend	*0.4*	*0.6*	*0.6*	*0.4*	
Forelimb-suspend	*11.7*	*10.3*	*9.6*	*5.8*	
Hindlimb cling	*0*	*0.1*	*0.1*	*0.1*	
Hindlimb compression	*0*	*0.1*	*0.5*	*0.7*	
Hindlimb Suspend	*0*	*0*	*0*	*0.1*	

Squat	*1.0*	*2.3*	*6.9*	*8.0*	
Squat	**0.4/0.3**	**0.5/1.0**	**1.0/2.2**	**2.2/3.5**	**0.000**

Kruskal-Wallis test was used to examine heterogeneity in postural modes among members of different age categories. Modes and submodes from Hunt et al., 1996 and Thorpe and Crompton, 2006.

a. Percentages of postural modes are given. The first number is for aggregated individuals and the second number is for aggregated individuals with duplicates collapsed. Statistical analysis are done are aggregated data with duplicates collapsed.

b. Postural submodes are included for the most prevalent mode sit. Gray highlight signifies the submode engaged in most frequently for that age class.

*The only significant difference in posture modes engaged in between the sexes within any of the age classes was pronograde stand (F=11% and M=5%; Mann-Whitney U = 3.00 z = -2.191, p = 0.030).

Table II.5 Significant differences in postural mode frequencies among age categories.

	Infant	**Juvenile**
Juvenile	**Cling**	
	Pronograde Stand	
	Sit	
	Squat	
Adolescent	**Cling**	
	Orthograde forelimb suspend	**Orthograde forelimb suspend**
	Pronograde Stand	
	Sit	**Sit**
	Squat	**Squat**
Adult	**Cling**	
	Orthograde forelimb suspend	**Orthograde forelimb suspend**
	Pronograde Stand	**Pronograde Stand**
	Sit	
	Squat	**Squat**

Results are significant at the $p < 0.05$ level. Post hoc comparisons between treatments were conducted using the inequality $| R_u – R_v | \geq z_{\alpha/k(k-1)} \sqrt{((N(N+1)/12) \times (1/n_u + 1/n_v))}$ (Siegel and Castellen, 1988).

CHAPTER II FIGURES

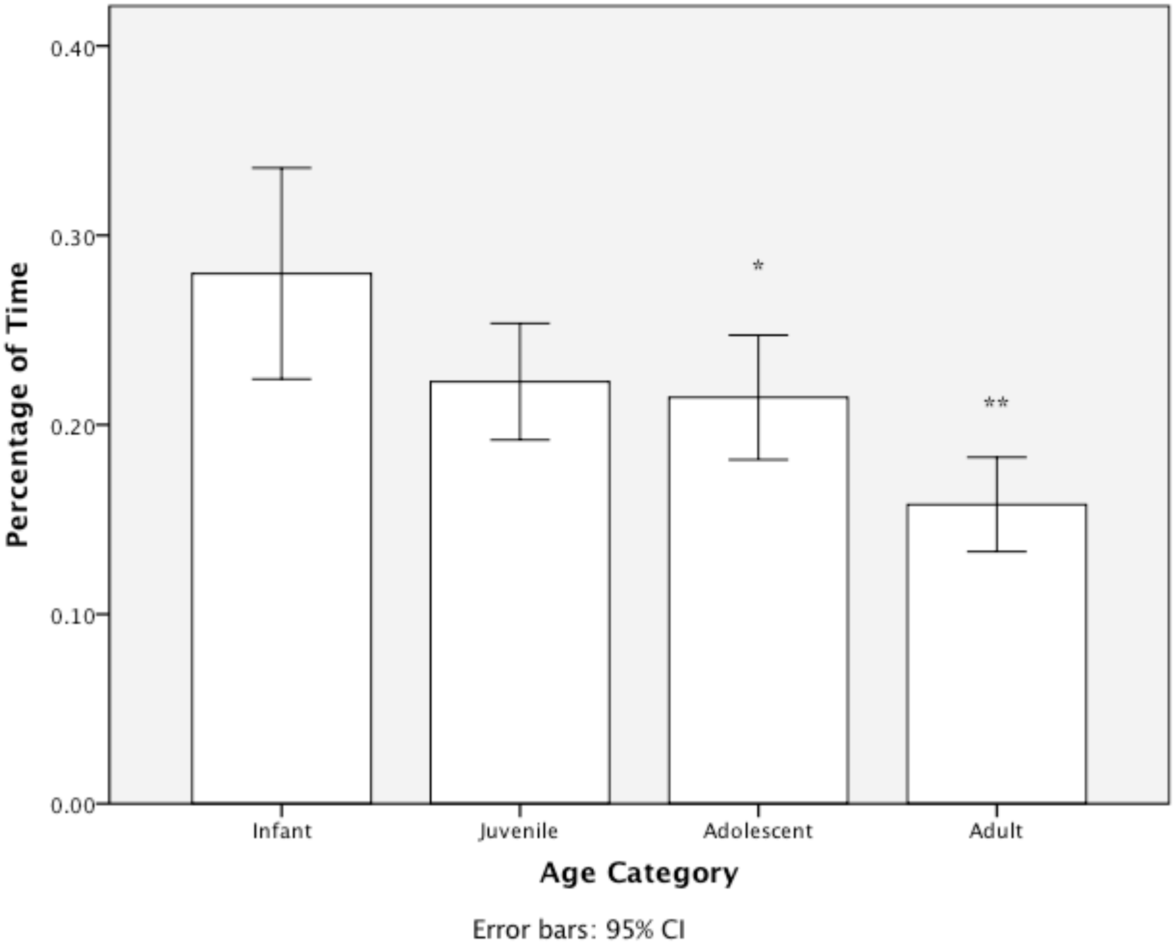

Figure II.1 Percentage of overall time spent in locomotion for each age category.

* Adolescents are significantly less active compared to infants at the $p < 0.05$ level.

** Adults are significantly less active compared to all three other age classes at the $p < 0.05$ level.

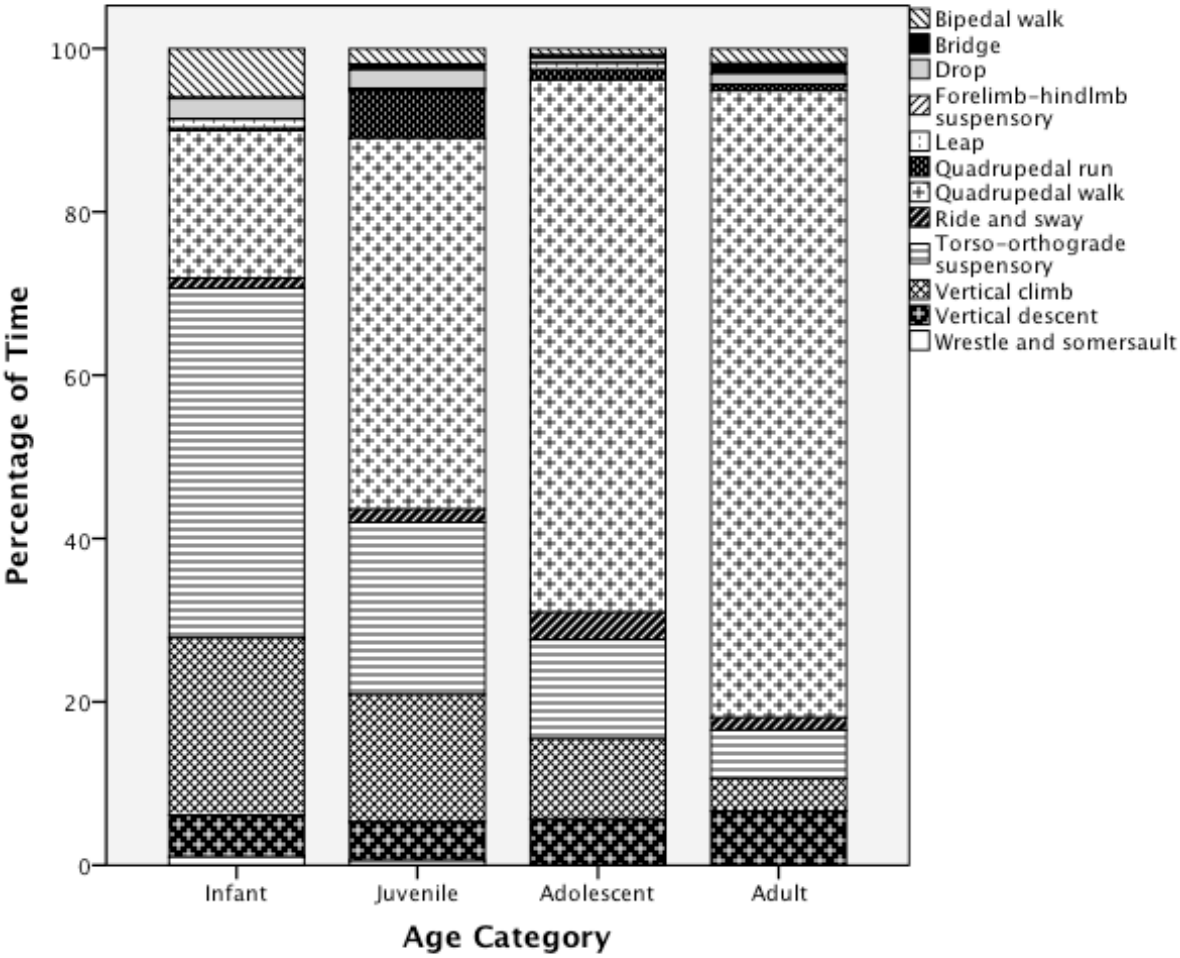

Figure II.2 Percentage of locomotor time spent in each mode for each age category of chimpanzee.

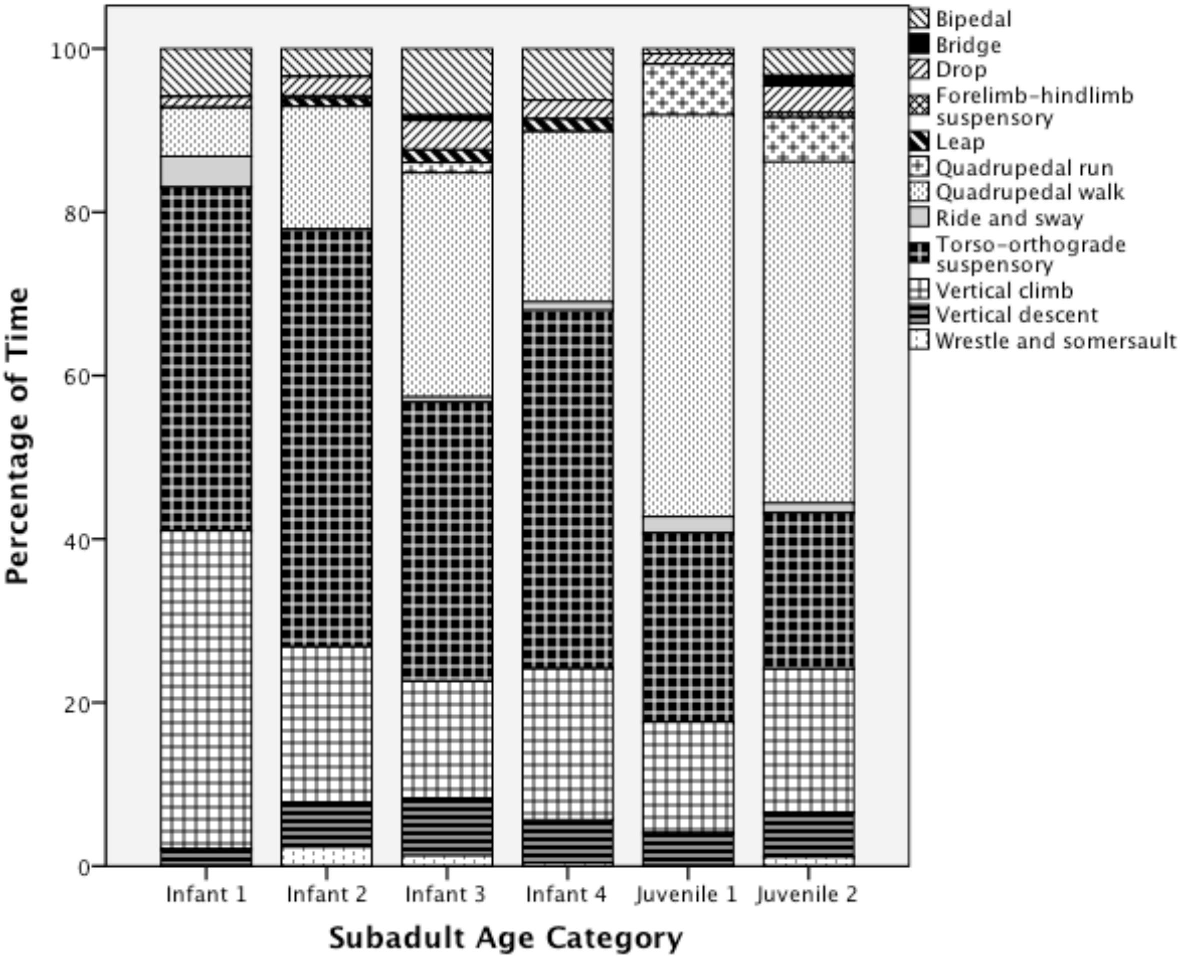

Figure II.3 Percentage of locomotor time spent in each mode for each age category of subadult.

a. Kruskal-Wallis revealed significant results for quadrupedal run, quadrupedal walk, torso-orthograde suspensory. Post Hoc significant results where $p < 0.05$; quadrupedal run I1 vs. J1, I1 vs. J2, I2 vs. J1, I2 vs. J2, I3 vs. J1, I3 vs. J2, I4 vs. J1, I4 vs. J2; quadrupedal walk I1 vs. I3, I1 vs I4, I1 vs. J1, I1 vs. J2, I2 vs. J1, I2 vs. J2, I3 vs. J1, I3 vs. J2, I4 vs. J1, I4 vs. J2; torso-orthograde suspensory I1 vs. J1, I1 vs. J2, I2 vs. I3, I2 vs. J1, I2 vs. J2, I3 vs. I4, I3 vs. J1, I3 vs. J2, I4 vs. J1, I4 vs. J2.

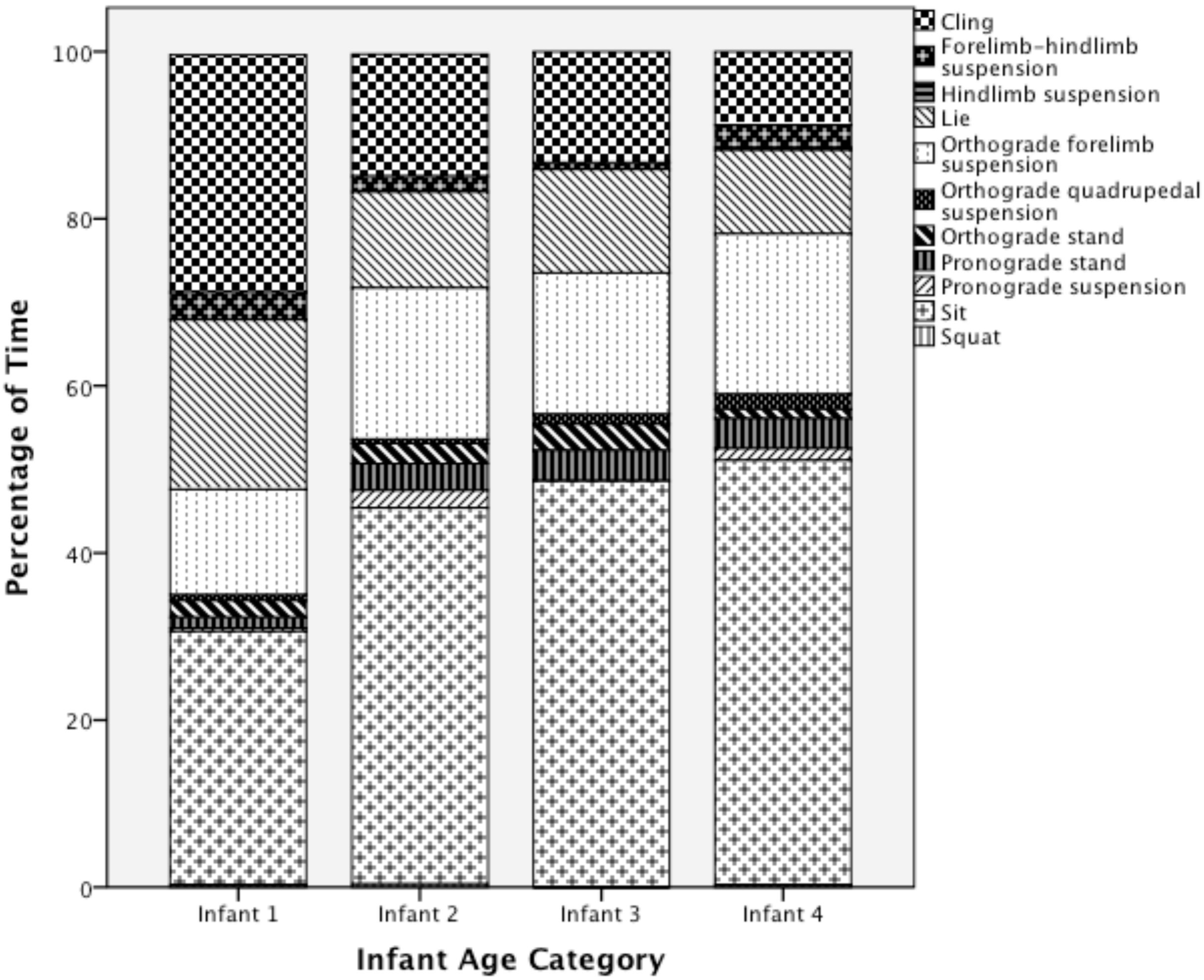

Figure II.4 Percentage of postural time spent in each mode for each age category of infant.

a. Kruskal-Wallis revealed significant results for cling and sit. Post hoc significant results where $p < 0.05$; cling I1 vs. I2, I1 vs. I3, I1 vs. I4, I2 vs. I4; sit I1 vs. I3, I1 vs. I4, I2 vs. I4.

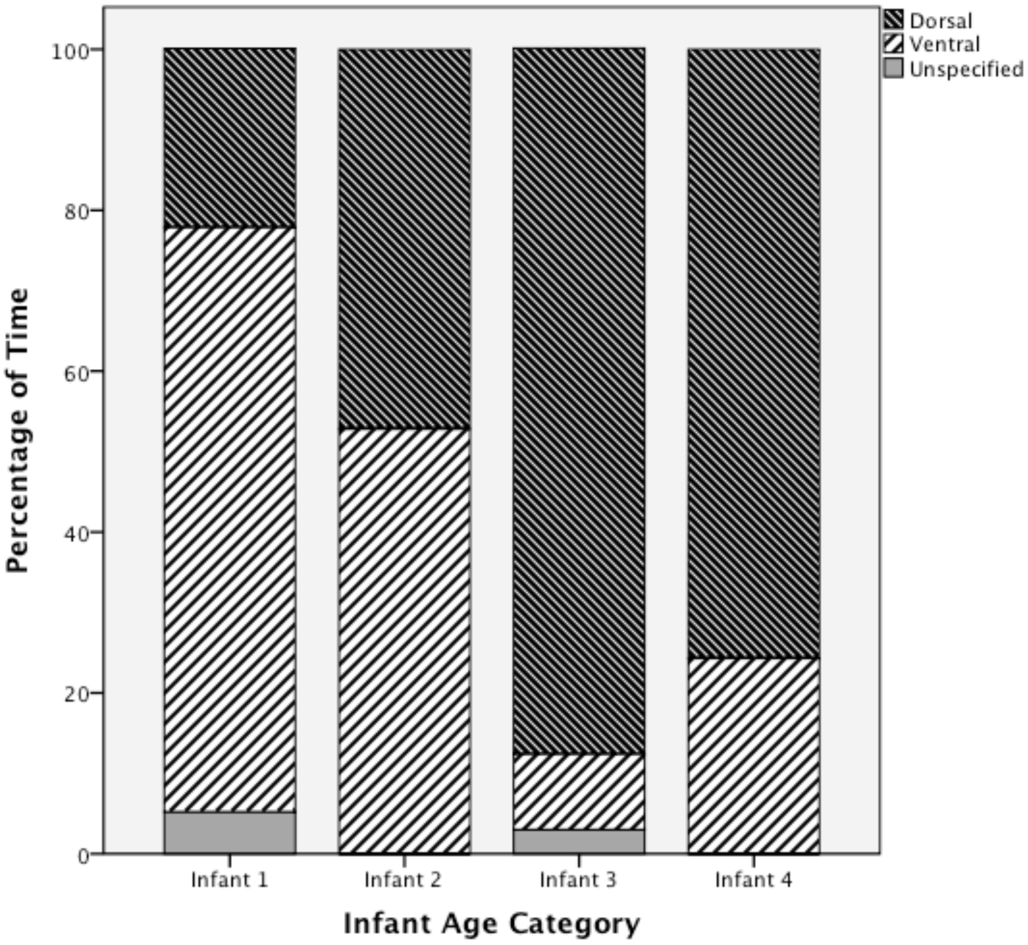

Figure II.5 Percentage of time spent clinging ventrally or dorsally during mother locomotion for each age category of infant.

a. Kruskal-Wallis revealed no significant results for cling ventrally or dorsally during maternal locomotion**.**

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Chapter III

Changes in metacarpal morphology during development are indicative of knuckle-walking in chimpanzees.

Introduction

Bipedality is a hallmark of humankind, and is currently used as the *sine qua non* to recognize our earliest human ancestors (Haile-Selassie, 2001; Pickford et al., 2002; Zollikofer et al., 2005; MacLatchy et al., 2010). Due to significant gaps in the fossil record, how our ancestors moved before they became bipedal is unknown. Three prominent hypotheses are currently debated: 1) early humans evolved from a chimpanzee-like, knuckle-walking ancestor that moved quadrupedally on the ground (Washburn, 1967; Richmond and Strait, 2000); 2) early humans evolved from an orangutan-like ancestor that moved upright using suspension and bipedality in the trees (Thorpe and Crompton, 2006; Thorpe et al., 2007; Crompton et al., 2010); and 3) early bipeds evolved from a *Proconsul*-like ancestor that walked on the palms of its hands (Lovejoy et al., 2009a; Lovejoy et al., 2009b; Lovejoy and McCollum, 2010). Testing these hypotheses depends on determining the skeletal correlates of locomotion. A suite of anatomical features of the wrist and hand (such as concavity and ridges in the capitate, hamate, and scaphoid) have been found to cluster in knuckle-walking chimpanzees and gorillas, but these features have been found to be variably present in individuals and are thus not entirely diagnostic of knuckle-walking (Richmond and Strait, 2000; Richmond et al., 2001; Kivell and Schmitt, 2009). One of the most promising regions to search for such knuckle-walking features is in the hand, especially the metacarpals, which are exposed to unusual and high stresses during this form of locomotion. This chapter aims to identify metacarpal features that are sensitive to the occurrence of knuckle-walking. I do this by tracking changes in knuckle-walking behavior and metacarpal bone morphology in tandem in chimpanzees who vary in age.

Chimpanzees are our closest living relatives and their behavioral repertoire likely shares elements with our ancestors. Bone changes shape in response to repeated locomotor activity but this modification primarily occurs before individuals reach maturity (Lieberman et al., 2003; Pontzer et al., 2006; Gosman and Ketcham, 2009). Subadult chimpanzees are ideal subjects for investigating how behavior influences bone because they display several locomotor transitions during development. This involves an overall shift from predominantly suspensory to predominantly quadrupedal locomotion (Chapter II). Infants spend nearly half (44%) of their locomotor time in forelimb suspension and less than a quarter (19%) of the time in quadrupedal locomotion. Juvenility is characterized by individuals traveling completely on their own and no longer on their mothers. At this point, suspensory behavior decreases dramatically and quadrupedal walking increases to make up half (50%) of their time spent moving (Table III.1). At adolescence, individuals again increase the amount of time they spend walking quadrupedally so that it becomes their primary means of locomotion (67%). The locomotor behavior of adolescents is similar to that of adults (Chapter II). Even when subadults are further subdivided into additional age categories, the largest change in quadrupedal walking still occurs at juvenility and adolescence (*ibid.*).

During quadrupedal walking, primates use their hands in different ways by placing their weight on their digits, fists, knuckles, palms, or both palms and digits while grasping (Tuttle, 1967; Schmitt, 1994; Patel and Wunderlich, 2010). Adult chimpanzees primarily knuckle-walk when moving quadrupedally, but it has been suggested that young infants go through a palmigrade phase prior to knuckle-walking (Doran, 1992). Testing this prediction has been difficult in the absence of any quantitative analysis of hand position during quadrupedal movement by chimpanzees during development. I hypothesize that the significant increase in quadrupedal walking that occurs when individuals reach juvenility and again when they attain adolescence will correspond with a significant increase in knuckle-walking by individuals.

Several anatomical regions are likely to be sensitive to the large changes in loading that accompany the introduction of new locomotor behaviors, such as knuckle-walking. For example, Richmond (1998) found that changes in phalanx shaft curvature during development correlated with the amount and the timing of the introduction of suspensory behavior in apes. It is thus likely that other hand elements, such as the metacarpals, will experience anatomical alterations with the dramatic change in loading. These metacarpal features include: metacarpal head morphology and metacarpal diaphyseal curvature.

Previous research suggests that metacarpal morphology, in particular metacarpal head morphology, may experience anatomical alterations with changes in loading (Inouye, 1994a). In a study examining hominoid hand morphology, Susman (1979) found that the distal articular surface of the third metacarpal had a prominent dorsal ridge in adult gorillas and chimpanzees but not in orangutans, gibbons, or humans. This distal metacarpal ridge (DMR) is a raised ridge of bone on the distal end of the metacarpal that stabilizes the metacarpophalangeal joint during hyperextension and is thought to be a morphological feature associated with knuckle-walking (Figure III.1; Tuttle, 1967; Preuschoft, 1973; Susman, 1979; Inouye and Shea, 2004). Inouye (1994a) re-examined the DMR and found that it is present most often (79%) on the third ray in chimpanzees. There is variation in the presence and degree of development of the DMR on other digits (*ibid.*), suggesting that distal ridge formation on the metacarpal might be affected by locomotor variability among individual African apes.

In an ontogenetic study, the distal metacarpal ridge was present more frequently in adult compared to subadult chimpanzee third metacarpals and the height of the ridge scaled with body size (Inouye and Shea, 2004). Since adolescent chimpanzees move in the same manner as adults (Chapter II), it is likely that their anatomy is more similar to adults compared to individuals in other subadult age classes. Because subadults vary in the amount of time they spend knuckle-walking, treating them together as a single group will obscure when any anatomical transitions may occur. In this study, I therefore subdivide subadult chimpanzees into appropriate age categories so that changes in DMR architecture during development can be accurately analyzed and assessed. Based on my observations of locomotor changes during development, I hypothesize that the distal metacarpal ridge will appear in juveniles when individuals begin to knuckle-walk frequently. In addition, I predict that the DMR will continue to develop as chimpanzees age, tracking an increase in knuckle-walking frequency. The DMR is expected to stabilize when knuckle-walking reaches adult proportions.

Metacarpal curvature is a second character of interest. It has been previously hypothesized that when bending is the main loading force on mammalian long bones, diaphyseal curvature acts to increase the predictability of the load environment (Bertram and Biewener, 1988), with numerous studies supporting the idea that diaphyseal curvature of long bone shafts in mammals is responsive to the loading environment (Currey, 1968; Lanyon, 1980; Bertram and Biewener, 1988; Robling et al., 2002; Main and Biewener, 2004). Experiments show that repeated axial loading of the adult rat ulna induces increased mediolateral curvature where a less extreme natural curve was already present (Robling et al., 2002), a response that may make the shaft more efficient in distributing stress (*ibid*.). Another study showed that the tibial curvature greatly decreased in growing rats deprived of normal hindlimb activity, suggesting that long bone curvature depends on functional activity (Lanyon, 1980). During knuckle-walking, the middle phalanges bear most of the weight, with the metacarpals nearly perpendicular to them and serving as load-bearing conduits for the weight of the forelimb (Figure III.1; Richmond and Strait, 2000; Matarazzo, 2008). This angulation and pattern of force transmission is unlike that experienced by any other primate during locomotion. Chimpanzees also exhibit intra-individual variability in the degree of extension/flexion and abduction/adduction at the carpalmetacarpal joint during knuckle-walking (Sarringhaus, preliminary data). This postural variability increases the angle and force variability of the loads experienced by the weight bearing metacarpals. Thus, curvature in the metacarpal shafts may improve load predictability experienced by the bone, thereby increasing the integrity of the load bearing system during knuckle-walking.

Susman (1979) observed that metacarpal curvature varied among hominoids, and suggested that orangutans had the greatest curvature and gibbons the least. Nevertheless, quantitative data that can be used to validate this claim do not exist for adult or subadult hominoids. Like Susman (1979), I hypothesize that metacarpal curvature variation corresponds to bending load differences among species. However, I predict that metacarpal curvature should be greater in species that engage in knuckle-walking behavior (i.e. chimpanzees and gorillas) compared to primarily suspensory (orangutans and gibbons) and digitigrade (baboons) primates.

As previously mentioned, knuckle-walking behavior also varies over the course of development in chimpanzees. With the inception of knuckle-walking, the third metacarpal becomes a load-bearing conduit for the upper arm and I hypothesize that increased longitudinal curvature provides added stability to this bone. Therefore, as chimpanzees age and start to knuckle-walk frequently, I predict that metacarpal curvature will increase to compensate for the high and variable loading experienced by the wrist and hand.

In this study I combine behavioral observations in the field with morphological data from museum specimens to test if increased knuckle-walking frequency over the course of chimpanzee development corresponds to greater load predictability and architectural stability with increased metacarpal longitudinal curvature and distal metacarpal ridge presence.

Methods

Behavioral Methods

Data were collected on the locomotor behavior of chimpanzees at Ngogo, Kibale National Park, Uganda, from February to August 2009. The Ngogo chimpanzee community contains approximately 160 individuals. The unusually large size of the Ngogo community provided a rare opportunity to sample the locomotor behavior of a large number of chimpanzees. Chimpanzees were divided into four age categories: infants (0.1 - 5), juveniles (5.1 - 10), adolescents (10.1 - 14), and adults (20 +). When examining only infants, the largest shift in quadrupedal locomotion occurs when individuals reach three years of age (Chapter II). The infant category therefore was further divided into *young infant* (≤3 years) and *old infant* (>3 years) using this three-year age mark in order to investigate whether knuckle-walking behavior and morphological changes occur before juvenility (Table III.1). These age groupings are based off of known birth dates for individuals. Some adult birth dates are estimated but these individuals are all over 20 years of age. Age groupings are based off of chronological ages and not behavioral markers in order to facilitate morphological comparisons (see Chapter II for age grouping rational).

Focal Observation and Video Data

Rates of arboreal and terrestrial quadrupedal locomotion were calculated using observations of 53 chimpanzees, including 20 infants, 11 juveniles, 11 adolescents, and 11 adults. Each of these chimpanzees was sampled during 5 one-hour-long observation sessions. The positional behavior of focal individuals was recorded every two minutes during instantaneous scan samples. Chimpanzee positional behavior was classified according to body parts that bear the individual's weight, using categories defined in prior studies (Chapter II; Hunt et al., 1996; Thorpe and Crompton, 2006). Quadrupedal locomotion included both quadrupedal walking and quadrupedal running. The percentage of time members of each age class spent in quadrupedal locomotion was calculated for both arboreal and terrestrial substrates.

Hand contact data were recorded during 340 hours of focal observations. The hand placements of chimpanzees were recorded every two minutes during hour-long focal follows. These data included 2069 observations of locomotion including 960 instances of quadrupedal locomotion. Hand contact category was recorded for 799 of the 960 observations of quadrupedal locomotion and included three categories: knuckle, grasp, and palm (Figure III.2). In KNUCKLE the intermediate phalanges on digits II-V contact the substrate. In GRASP the palm and at least two digits are in contact with the substrate and the digits actively grasp the substrate. In PALM the palm contacts the substrate but the fingers do not actively grasp the substrate. Quadrupedal locomotion was also coded as being terrestrial or arboreal.

Since quadrupedal locomotion occurs infrequently in infants, especially young infants, 32 hours of locomotor video footage filmed during February – August 2009 were also analyzed for hand posture usage during quadrupedal locomotion. Video was recorded on two cameras, a

Canon 2GL and a Canon XHAI HDV 3CCD and analyzed frame-by-frame using iMovie. For each locomotor bout, hand posture was recorded from the second visible forearm stride. Data were recorded in the same manner as from the focal observations of wild subjects, resulting in 630 samples of chimpanzees moving quadrupedally. There was no overlap between video recorded bouts and those recorded during focal observation sessions.

Analysis

Hand contact data were derived from 120 individuals, including 21 infants, 17 juveniles, 23 adolescents, and 59 adults. Individuals were coded as using their knuckles during quadrupedal locomotion in one of three ways: not at all (0% of the time), less than 50% of the time, or more than 50 % of the time. Hand contact data were aggregated by individual so that each chimpanzee only contributed a single data point for analysis. Chi-square tests were used to evaluate whether chimpanzees of different ages showed significant heterogeneity in hand usage. Results were considered significant at $p = 0.05$. A 5 x 3 table was employed for the chi-square test with the 5 age categories and 3 categories of knuckle usage. To determine whether hand usage varied with age, I considered observed values with standard residuals greater than two to deviate significantly from expected values at the 95% confidence level (Agresti, 2002).

Skeletal Methods

The metacarpals of 412 individual primates from 6 museums were assessed (see Tables III.3 and III.4). The 206 chimpanzee skeletal specimens were given age estimates using the most likely minimum and maximum ages based on ranges for each tooth eruption (Smith et al., 1994). I also used wear to assess how recently a tooth had emerged. The potential age ranges using eruption and wear of each tooth were averaged and the midpoint taken to represent the most likely age of each specimen. It has recently been shown that wild-caught healthy primates are 0.5 SD behind their captive counterparts in dental eruption ages (Smith and Boesch, 2011). Standard deviations for age of tooth emergence tend to be about 10% of the mean, with 0.5 SD tending to be about 5% of mean age (*ibid.*). Thus, in estimating wild-caught chimpanzee specimen ages, 5% was added to the central tendency mean age for captive chimpanzee tooth eruption data (Smith et al., 1994; Smith and Boesch, 2011, Appendix A). For two individuals, no crania were available, so postcranial material was aged based on epiphyseal fusion using work on both wild and captive chimpanzee postcranial development (Kerley, 1966; Zihlman et al., 2007). After aging chimpanzee skeletal specimens on a numerical scale, I partitioned individuals into one of five age categories that correspond to shifts in locomotor behavior (Table III.1). *Infants* are predominantly upper limb loading in clinging and torso-orthograde suspensory locomotion (Chapter II). *Young infants* are predominantly carried by mothers when traveling any significant distance. *Older infants* move independently from their mothers but still predominantly move in a suspensory fashion that primarily loads the upper limbs. *Juveniles* move entirely independently of their mothers and engage in hindlimb loading quadrupedal walking significantly more than do infants. *Adolescents* and *adults* engage in quadrupedal walking as their primary mode of locomotion and they do this significantly more compared to juveniles (Table III.1).

The metacarpals of gorillas, orangutan, gibbons, and baboons were also analyzed to provide a comparison with primate species of similar and varying locomotor behavior. These species were only divided into subadult and adult specimens since tooth eruption data are not as comprehensive for ape species outside of chimpanzees.

The third metacarpal was chosen for examination because the third ray is consistently used during knuckle-walking by captive African apes while the use of the other digits was more variable (Inouye, 1994b). Even when digits II-V are engaged during knuckle-walking, the third middle phalanx consistently bears the greatest weight (Matarazzo, 2008; Wunderlich and Jungers, 2009) indicating that metacarpal III is the most useful in relaying morphological changes due to the inception of knuckle-walking. Both distal metacarpal ridge and metacarpal curvature were measured from photographs of the bone taken in medial view using ImageJ software (Figure III.3). Measurements were standardized using a 1 cm scale in each image. The presence and degree of the DMR was assessed using Inouye's metacarpal torus measurement method (Inouye 1994a; Inouye and Shea, 2004). The DMR was analyzed using the angle between points A, B, and C (Figure III.4). If the ABC angle is less than 180 degrees, a DMR is considered present; if ABC is approximately 180 degrees (a straight line), the DMR is considered absent; and if ABC is greater than 180 degrees (i.e., it has a rounded edge) then the DMR is also considered absent. The DMR angle was used for comparative analysis since it captures the degree of variation between specimens more aptly than recording the mere presence or absence using the 180 degree threshold. The height was measured as the distance from point C perpendicular to the 180 degree line connecting points A and B (Figure III.4). When present, the DMR height was measured in order to compare the results of this study to those from previous work. While DMR height and angle are part of the same triangle, no correlation is expected between the two variables due to variability in length of the two remaining sides of the triangle.

The degree of metacarpal curvature was analyzed using the included angle method outlined in Susman *et al.* (1984) and Jungers et al. (1997). This method was chosen because metacarpal curvature can be approximated by circularity and because this method is length-independent and measures curvature without a correlation to robusticity (Susman et al., 1984; Stern et al., 1995). Metacarpal total length L, diameter D, and height H, were used to compute the radius of curvature R and the included angle of curvature θ.

$$R = \frac{(H-D/2)^2 + (L/2)^2}{2(H-D/2)}$$

$$\theta = 2 * \arcsin (L/2R)$$

$$\text{Included angle in degrees} = \theta * (180/\pi)$$

In chimpanzees, metacarpals were analyzed with both the distal epiphysis present and not present. Measuring curvature in individuals without the distal epiphyses is less telling of overall curvature but it is representative of shaft curvature, albeit without the influence the epiphysis has on degree of curvature. However, because epiphyses are not yet fully fused and therefore not always present for subadult specimens, curvature assessments without the epiphysis permitted me to increase the sample sizes of the youngest groups.

Distal metacarpal ridge properties and metacarpal curvature measurements for both chimpanzee age classes and other primate species were normally distributed and analyzed using ANOVA (Sokal and Rohlf, 1995). Pairwise post hoc analyses were done using Tamhane T2 procedure due to unequal sample sizes with equal variance not assumed (Sokal and Rohlf, 1995). Sex was also examined for a comparison of individuals in the same age class but potentially different body sizes. The available samples of female and male metacarpals were relatively small and sex differences were thus compared using the nonparametric Mann-Whitney U test.

Results

Chimpanzee Locomotor Development

Knuckle-walking

It has already been established that rates of quadrupedal walking significantly increase as chimpanzees age (Chapter II). In addition, as individuals grow older they spend a larger percentage of that quadrupedal time on the ground (Figure III.5). Young and old infants were predominantly arboreal, only spending 31.7% and 32.4% of quadrupedal time moving terrestrially (Figure III.5). Juveniles spent 63.9% of the time walking on all fours on the ground. Quadrupedal walking, the main locomotor mode for both adolescents and adults, was predominantly a terrestrial activity for both of these age classes (85.4% and 89.4% of quadrupedal locomotion respectively, Figure III.5).

Substrate use was important in determining whether chimpanzees knuckle-walked. To explore this relationship, arboreal and terrestrial quadrupedal locomotion was examined separately. While on the ground, members of the different age groups did not display heterogeneity in hand usage. Terrestrial quadrupedal locomotion took the form of knuckle-walking for individuals in all age classes (Figure III.6). However, variation did exist in the way hands were used during arboreal quadrupedal locomotion.

There were three hand postures displayed during chimpanzee arboreal quadrupedalism: knuckle, grasp, and palm (Figures III.2 and III.6). Young and old infants employed all three of these hand postures but were predominantly graspers (Figure III.6). Analysis of knuckle-walking during arboreal quadrupedal locomotion revealed that members of different age classes differed in the frequency of knuckle-walking (Chi-Square = 49.36, df = 8, $p < 0.001$). More young infants refrained from knuckle-usage than expected (SR for 0% KW = 2.8, Table III.2), while more old infants engaged in knuckle-walking less than 50% of the time (<50% SR = 2.3, Table III.2). Juveniles also used all three hand postures, with over half of their arboreal quadrupedal time consisting of grasping (56.5%). More juveniles than expected engaged in knuckle-walking below 50% of the time (<50% SR = 3, Table III.2). Knuckle was the preferred arboreal hand posture of both adolescents (65.5%) and adults (73.5%) with more adults than expected engaging in knuckle-walking over 50% of the time (>50% SR = 2.3, Table III.2)

While infants knuckle-walk infrequently, they are capable of doing so before one year of age. The youngest chimpanzee videotaped engaging in multiple bouts of terrestrial quadrupedal walking was 10 months old. This individual used knuckle contact for all 6 bouts of terrestrial quadrupedal locomotion videotaped. The next youngest individual in the community was repeatedly observed up until 7 months old and was never seen to engage in any form of quadrupedal locomotion. There were 5 individuals in the Ngogo community during this time that were between 12 and 24 months, and 3 of them were repeatedly followed as focal subjects and video recorded. All three of these individuals consistently used knuckle contact when they engaged in terrestrial quadrupedal locomotion. These findings indicate infants do not move quadrupedally on the ground often, but when they and members of other age classes do so, the default hand posture is knuckle contact.

Overall, quadrupedal locomotion equates to knuckle-walking in adolescents and adults (Figures III.5 and III.6). These individuals use their knuckles while walking quadrupedally whether on the ground or in the trees. Quadrupedal locomotion is predominantly knuckle-walking for juveniles, given the degree of terrestriality during quadrupedal locomotion. However this age class is more variable in hand contact category during arboreal quadrupedalism compared to adolescents and adults (Figure III.6). Given the predominance of using arboreal substrates during quadrupedalism, and the high variability of hand contact usage during this locomotor behavior, quadrupedal locomotion does not often equate to knuckle-walking for individuals in both infant age categories (Figures III.5 and III.6).

Distal Metacarpal Ridge

The distal metacarpal ridge angle differed significantly between individuals in the different age categories of chimpanzees (ANOVA $F = 45.73$, $df = 4$, $p < 0.001$, Table III.3, Figure III.7). The DMR was not present (≤ 180°) until the juvenile category (mean angle = 169.8 degrees, Table III.3, Figure III.7), and then continued to decrease significantly in each subsequent age category until stabilizing between adolescents and adults (Tamhane young infant vs. old infant $p = 0.001$; old infant vs. juvenile $p = 0.001$; juvenile vs. adolescent $p = 0.025$; adolescent vs. adult $p = 1.00$).

The distal metacarpal ridge height also differed significantly between individuals in different age categories of chimpanzees (ANOVA $F = 33.50$, $df = 4$, $p < 0.001$, Table III.3). Post hoc tests revealed that the height of the ridge increased significantly between young and old infants (T's $p = 0.009$) and between old infants and juveniles (Tamhane $p < 0.001$). While the mean height value increased as individuals grew older, no significant difference was found between juveniles and adolescents or between adolescents and adults (Tamhane $p = 0.58$ and $p = 0.57$, respectively) due to the high degree of variation among individuals within the three oldest age categories.

Curvature

The degree of metacarpal curvature, assessed using included angle, increased with age in chimpanzees (ANOVA $F = 74.96$, $df = 4$, $p < 0.001$, Table III.3, Figure III.8). Although post hoc analysis revealed that curvature levels in individuals in the two infant categories were not significantly different from one another (Tamhane $p = 0.726$), they were significantly less compared to the three older age categories (Tamhane all 6 comparisons $p < 0.001$). While juvenile metacarpals were more curved compared to both infant groups, they were less curved compared to both adolescents and adults (Tamhane both comparisons $p < 0.001$). Adolescent and adult metacarpals were not significantly different from one another (T's $p = 0.317$).

The degree of metacarpal curvature in bones without epiphyses was also significantly different between the different age categories (ANOVA $F = 59.86$, $df = 4$, $p < 0.001$, Table III.3). The absolute values of curvature decreased in each age category with no epiphyses present, but the trend between age categories persisted, with an increase in curvature as individuals aged. Post hoc analysis revealed that curvature levels in individuals in the two infant categories were not different from one another (Tamhane young vs. old = 0.107) but were significantly less compared to the three older age groups (Tamhane all 6 comparisons $p < 0.001$). Juvenile metacarpals were not different from adolescents (Tamhane $p = 0.159$) but were less curved compared to adults (Tamhane $p < 0.001$). Adolescents and adults were not different from one another (Tamhane $p = 0.518$). For each age class, the same individual's metacarpal curvature without epiphyses was between 87.11 – 94.7% of the curvature value of the bone measured with epiphysis. To be size independent, the degree of variation (% difference) between curvature measurements with and without the epiphyses for the same individual was compared and found to be significantly different between age classes (ANOVA $F = 8.220$, $df = 4$, $p < 0.001$) with post hoc tests revealing that adult curvature levels decreased more compared to old infant and juvenile individuals (both Tamhane's $p < 0.001$) and that adolescent values decreased more compared to juveniles (Tamhane $p = 0.035$).

Species comparisons

Distal Metacarpal Ridge

The angle for the degree of the distal metacarpal ridge varied between subadult and adult chimpanzees, gorillas, and baboons (ANOVA $F = 25.13$, $df = 4$, $p < 0.001$, Table III.4, Figure III.9). Post hoc analysis revealed differences between both adult chimpanzees and adult gorillas and the three other groups; subadult chimpanzees, subadult gorillas, baboons (Figure III.9, Tamhane all six comparisons $p < 0.001$). No difference was found between the adult chimpanzee and adult gorilla specimens (Tamhane $p = 0.355$) or between the subadult chimpanzees, subadult gorillas, and baboons (Tamhane subadult chimpanzee vs. subadult gorilla $p = 0.990$, subadult chimpanzee vs. baboon $p = 1.000$, subadult gorilla vs. baboon $p = 1.00$). No difference was found between subadult and adult baboons when analyzed separately (Mann-Whitney U $z = 17.50$, $p = 0.19$).

The height of the distal metacarpal ridge also varied between individuals in the different species and age categories (ANOVA F = 41.31, df = 4, $p < 0.001$, Table III.4). Post hoc tests revealed that adult chimpanzee and adult gorillas varied from one another and when compared to the three other groups; subadult chimpanzees, subadult gorillas, baboons (Tamhane all 6 comparisons $p < 0.001$). No difference in height was found between subadult chimpanzees, subadult gorillas, or baboons (Tamhane subadult chimpanzee vs. subadult gorilla p = 0.860; subadult chimpanzee vs. baboon p = 0.230, subadult gorilla vs. baboon p = 0.060).

Curvature

The degree of metacarpal curvature varied greatly between the different species (ANOVA F = 77.26, df = 8, $p < 0.001$, Table III.4, Figure III.10). Subadult and adult specimens of the same species differed in curvature for chimpanzees and gorillas (T's both $p < 0.001$) but not orangutans (Tamhane p = 1.00) and gibbons (Tamhane p = 0.10, Figure III.10). Along with being less curved compared to adult chimpanzees, subadult chimpanzee specimens were significantly less curved compared to those of adult gorillas and significantly more curved compared to metacarpals from both gibbon groups and baboons (Tamhane all 4 comparisons p = 0.00). No difference was found between subadult chimpanzee metacarpal curvature and subadult gorilla, or either orangutan group's curvature (Tamhane SaC vs. SaG p = 0.329, SaC vs. SaO p = 0.797, SaC vs. AO p = 0.625). Similar to subadult chimpanzees, subadult gorilla metacarpals were significantly less curved compared to adult chimpanzees (Tamhane p = 0.00). Unlike subadult chimpanzees, metacarpal curvature of subadult gorillas was significantly different from that found in both subadult and adult orangutans (Tamhane SaG vs. SaO p = 0.020, SaG vs. AO

$p < 0.001$). Subadult gorillas were similar to subadult chimpanzees in that their metacarpals were significantly more curved compared to both gibbon groups and baboons (Tamhane all three comparisons $p < 0.001$). Adult chimpanzee and adult gorillas were significantly different in curvature compared to all other categories, including each other (Tamhane all comparisons $p < 0.001$). Subadult orangutan metacarpals were more curved compared to those of subadult gibbons but not when compared to those of adult gibbons or baboons (Tamhane SaO vs. SaH $p < 0.001$, SaO vs. AH $p = 0.124$, SaO vs. B $p = 0.051$). Adult orangutan metcarpals were significantly more curved compared to those of subadult and adult gibbons as well as baboons (Tamhane all 3 comparisons $p = 0.00$). Both subadult and adult gibbon metacarpals did not differ in curvature from those of baboons (Tamhane SaH vs. B $p = 0.99$, AH vs B $p = 1.00$). No difference was found between subadult and adult baboon specimens (Mann-Whitney U $z = 32.00$, $p = 0.44$).

Adult Sex Differences

There was no sex difference in distal metacarpal ridge angle in either chimpanzees or gorillas (chimpanzees Mann-Whitney U $z = -1.07$, $p = 0.30$; gorilla Mann-Whitney U $z = -1.63$, $p = 0.11$). There was a sex difference in distal metacarpal ridge height between male and female adult gorillas (Mann-Whitney U $z = 41.00$, $p = 0.02$) but not between male and female adult chimpanzees (Mann-Whitney U $z = 67.00$, $p = 0.61$).

There was no difference in degree of metacarpal curvature between male and female adults in any of the ape species (chimpanzees Mann-Whitney U $z = 0.00$, $p = 1.000$; gorillas

Mann-Whitney U z = -1.247, p = 0.225; orangutans Mann-Whitney U z = -0.268, p = 0.815; gibbons Mann-Whitney U z = -0.236, p = 0.864).

Discussion

Knuckle-walking

Overall, increases in chimpanzee knuckle-walking mirror increases in quadrupedal locomotion during different developmental stages. Discovering when transitions in knuckle-walking take place during development required taking 3 variables into consideration: 1) the amount of time individuals engaged in quadrupedal walking, 2) the degree of quadrupedal locomotion that is terrestrial and therefore solely knuckle-walking, and 3) the use of hands during arboreal quadrupedalism. Infants in both categories (young and old) engage in significantly less quadrupedal locomotion compared with members of other age groups. Infants spend a limited amount of time moving quadrupedally, but when they do so, it is done most frequently on arboreal substrates using grasping hand postures. Juveniles are both more quadrupedal and more terrestrial compared to infants. When juveniles engage in arboreal quadrupedalism, they, like infants, utilize all three hand postures of grasp, palm, and knuckle with grasping again being the most prevalent. Adolescents spend more time moving quadrupedally and on the ground than juveniles; unlike members of all younger age classes, adolescents use their knuckles predominantly during quadrupedalism, even on arboreal substrates. There is no shift in habitat use or locomotion between adolescents and adults, as members of these age classes spend a similar amount of time on the ground and moving quadrupedally. Moreover, adults and adolescents do not used their hands differently during arboreal locomotion. These results indicate that a pronounced shift in quadrupedal locomotion takes place at juvenility and again at adolescence when members of the latter begin to knuckle-walk with increasing frequency. As a consequence, morphological features corresponding to knuckle-walking are expected to emerge during these two stages of development.

It had been suggested that infant chimpanzees go through a palmigrade phase of quadrupedal walking before knuckle-walking (Doran, 1992). In contrast, this study found that infants always knuckle-walk during the rare instances when they move quadrupedally on the ground. On arboreal substrates, infants and juveniles primarily used their fingers by grasping when moving quadrupedally with no palmigrade transitional period present for young chimpanzees. Doran's (1992) assessment of locomotor ontogeny suggested that infants 'easily' knuckle-walk on the ground at two years of age, but individuals as young as 10 months old regularly knuckle-walk when on the ground. Thus, the ability to knuckle-walk emerges before one year of age. Moving on arboreal substrates presents a higher risk of falling compared to moving on the ground. This is because arboreal substrates are compliant and may bend and move, especially when large animals walk on them. Reduced substrate stability is especially important for infants compared to older individuals because the former posses lower levels of coordination and therefore risk falling, perhaps fatally (van Lawick-Goodall, 1967; Dunbar and Badam, 1998). Therefore, infants grasp and use their palms to increase stability on arboreal substrates. When there is minimal risk of falling on the ground, infants always use their knuckles. This study highlights that knuckle-walking is possible, but not prevalent, at an early age in chimpanzees. Despite the ability to engage in knuckle-walking, infants rarely do so, and as a consequence, this form of locomotion is not likely to be important in terms of the loading environment. This situation changes dramatically, however, for juveniles, who display a significant increase in quadrupedal walking and knuckle-usage during locomotion.

Distal Metacarpal Ridge

This study explored changes in the DMR through analyzing its height and angle. The DMR is more usefully measured using the angle of the ridge instead of the height of the ridge. The ridge, with an angle less than 180°, emerges during juvenility when individuals begin to knuckle-walk frequently. The DMR again increases in prominence in adolescents at the same time that knuckle-walking continues to increase to become the predominant mode of locomotion.

Prior research on chimpanzees and gorillas suggests that the presence of the DMR varies with age. Measurements of the angle of the ridge and its height revealed that more adults display a DMR on the third metacarpal than do subadults (Inouye and Shea, 2004). My results utilizing ridge height values are consistent with this finding. The problem with using height to define DMR, however, is that there is considerable individual variation with no clear systematic change in the feature during development (Inouye, 1994a). In the present study, individuals were divided into five age categories to examine developmental changes. Mean height increased with each successive age category, with a significant change in angle occurring between the three youngest age classes. The lack of difference between members in older groups, juveniles and adolescents and adolescents and adults, is due to the high degree of variation in height in individuals in these age categories. Inouye, (1994a; Inouye and Shea, 2004) found that DMR height correlated positively with body size in adult chimpanzees and gorillas. In both Inouye's work (1994a) and this study, the mean DMR height for adult gorillas was nearly 60% greater than that of adult chimpanzees. Examining adult sex differences confirmed that body size likely influences the degree of this feature with a sex difference found in the highly sexually dimorphic gorilla. Overall, variation in ridge height indicates that the DMR is a plastic feature. Height, however, does not track knuckle-walking behavior as reliably as does the angle of the DMR.

Because height of the DMR is variable (Inouye and Shea, 2004), I also analyzed the angle of the ridge. Previous research had used the DMR angle only to mark presence (<180 degrees) or absence (>180 degrees) of the trait (Inouye and Shea, 2004). In this study, the DMR angle was ascertained to examine the sharpness of the incline of the ridge instead of its height or mere presence or absence. Sharper angles provide greater resistance against dislocation of the proximal end of the proximal phalange during hyperextension at the metacarpophalangeal joint. Through partitioning the subadult group into four different age categories, this study found that all subadults are not similar. The DMR is present in juveniles and becomes accentuated in adolescents.

In previous work, the presence and absence of the DMR did not correlate with body size (Inouye and Shea, 2004). Unlike DMR height, the DMR angle appears uninfluenced by body size, because it did not differ between sexually dimorphic male and female gorillas. The DMR angle was not different in adult gorillas and chimpanzees although adults in both species displayed much more acute DMR angles than did subadults. This suggests that this stability inducing trait provides more resistance against phalangeal dislocation in adult individuals compared to subadults. Baboons engage in predominantly digitigrade and occasionally palmigrade hand postures during quadrupedal locomotion (Schmitt, 1994; Patel and Wunderlich, 2010), and these types of quadrupedal behaviors do not reliably produce a ridge on the distal metacarpal. Thus, DMR angle reliably tracks knuckle-walking behavior.

Curvature

The degree of metacarpal curvature increased significantly between infancy and juvenility and again between juvenility and adolescence. These increases coincide with times chimpanzees show an increasing dependence on quadrupedal knuckle-walking. By increasing the predictability of force transmission along the shaft, greater curvature likely compensates for the high and variable loading experienced by the hand as individuals start to rely on knuckle-walk (Currey, 1968). Because knuckle-walking primarily loads the third metacarpal in African apes (Matarazzo, 2008), the perfect correlation in timing between increased third metacarpal curvature and the transition to knuckle-walking supports the hypothesis that knuckle walking influences this trait's development. While the assessed degree of curvature is lower when metacarpals are measured without their epiphyses, the same age trends emerge, indicating that the bulk of curvature is due to the bending of the metacarpal shaft. The greater decrease in the percentage of curvature for adults and adolescents when epiphyses are removed indicates that the two oldest age groups have proportionally more curvature in the epiphysis compared to younger individuals. This latter finding is not due to scaling since percentage, and not absolute, difference in curvature with epiphysis present and absent was compared. One important implication of this finding is that knuckle-walking behavior can still be inferred using degree of metacarpal curvature from fossil hominoid third metacarpals without the distal epiphysis present and may also be useful for partial specimens.

The cross species comparisons provide further support for the hypothesis that metacarpal curvature represents a knuckle-walking feature. Adult chimpanzees and gorillas are the only taxa that primarily engage in knuckle-walking, and their metacarpals were significantly more curved than those of non-knuckle-walkers. Subadult chimpanzees moved in a predominantly orthograde suspensory fashion like orangutans and these two groups did not differ in the degree of metacarpal curvature. The baboon group, as previously mentioned, use their digits and palms when walking quadrupedally. Though quadrupedal, baboons displayed curvatures comparable to gibbons supporting the idea that curvature provides stability during a certain type of quadrupedal walking, namely knuckle-walking, when the metacarpals are supporting the weight of the upper limbs and are near perpendicular to the phalanges.

My findings indicate that locomotor behavior and anatomy changes as chimpanzees develop and age. Like chimpanzees, gorillas also experience locomotor transitions. Nonetheless, these are thought to be less drastic compared to chimpanzees because gorillas engage in less suspensory behavior and shift to quadrupedal movement at a relatively younger age (Doran, 1997). It remains to be seen, however, whether more detailed data on developmental changes in gorilla locomotion indicate that morphological and locomotor transitions coincide as they do in chimpanzees.

This study shows that the two predominantly suspensory species, orangutans and gibbons, do not have ontogenetic shifts in metacarpal curvature during development. Of these two species, only orangutan positional behavior has been examined across development. Age class has little influence on locomotor behavior in orangutans, and they do not display distinct locomotor transitions like those documented here in chimpanzees (Chapter II; Thorpe and Crompton, 2006; Manduell et al., 2011). Since subadults practice the same, largely suspensory, behaviors as adults, it is expected that metacarpal curvature should be similar in subadult and adult orangutans, a finding validated in this study.

Curvature does not increase in magnitude with body size. Mean body weight increases two fold between the young and old infant age categories with no accompanying increase in curvature (Gavan, 1971). Mean body weight increases by 150% between old infants and juveniles and again between juveniles and adolescents (Gavan, 1971), with curvature significantly increasing between individuals in both transitions. While there is no way to rule out a threshold effect, with infants too small to induce curvature, the idea that body size is a driving force for curvature is further negated by examining the transition from adolescence to adulthood where individuals vary in body size but not in levels of curvature. That body size does not drive increased curvature is further supported by the lack of sex difference in any of the ape species, including the highly sexually dimorphic gorillas, where males are twice as large as females (Jungers and Susman, 1984). These findings further support the hypothesis that a high degree of metacarpal curvature is *induced* through knuckle-walking behavior.

Lastly, the variation in subadult chimpanzee behavior and morphology caution that "subadult" may not be an appropriate category to describe immature chimpanzees, especially when exploring anatomical correlates of locomotion. For example, a "subadult" skeletal sample composed mainly of adolescents is expected to show little difference in "subadult" and adult morphology whereas a "subadult" sample composed entirely of infants is expected to produce results of greater morphological dissimilarity between the two age categories. Therefore, the composition of a "subadult" skeletal sample could greatly influence how similar or dissimilar "subadults" are to adult morphology.

Conclusion

In summary, changes in both metacarpal ridge angle and metacarpal curvature correspond to developmentally mediated shifts in the frequency of knuckle-walking behavior. High third metacarpal curvature and the distal metacarpal ridge angle are knuckle-walking features present in adult chimpanzees and gorillas but lacking in suspensory orangutans and gibbons. These features are thus indicative of knuckle-walking. Because the timing of the development of the DMR and increased metacarpal curvature are synchronous with the transition to knuckle-walking, the loads produced by knuckle-walking likely influence the development of these traits. To date, only a handful of epigenetic features have been identified and used to reconstruct the locomotor behavior of fossil hominoids. These include the femoral bicondylar angle (e.g. Tardieu and Trinkaus, 1994; Tardieu, 1999) and lumbar lordosis (e.g. Nakatsukasa and Hayama, 1996; Nakatsukasa, 2004). These characteristics provide a means to infer the locomotor behavior of early hominins (e.g. Lovejoy et al., 1973, Susman et al., 1984; Sanders, 1998; Latimer and Ward, 1993; Ward, 2002; see also Lovejoy et al., 1999). Results from this study furnish provisional support for two additional plastic features that are diagnostic of a particular locomotor mode, knuckle-walking. The presence or absence of the distal metacarpal ridge angle and metacarpal curvature can be assessed in fossil hominoids that may have included knuckle-walking in their behavioral repertoire, including *Kenyapithecus* (Benefit and McCrossin, 1995) and *Ardipithecus* (Lovejoy et al., 2009a). Results of such analyses could then help resolve whether a knuckle-walking phase characterized human evolution.

CHAPTER III TABLES

Table III.1 Morphological and behavioral markers of chimpanzee age categories.

Category	Age	Dental eruption markers*	Locomotor Behavior**
Young Infant	0 - 3	Deciduous dentition erupts during this time, M1 not erupted	Predominantly suspensory with the highest levels of suspensory behavior for any age group.
Old Infant	3 - 5	M1 erupted or near eruption, I1 not erupted	Still predominantly suspensory but higher levels of independence from mother and higher levels of quadrupedal locomotion compared to young infants.
Juvenile	5-10	I1 erupted or near eruption, I2, M2, P3, P4 erupts during this time, C not erupted or just erupting, M3 not erupted	Completely independent from mother, a drastic decrease in suspensory locomotion and a drastic increase in quadrupedal walking and running compared to older infants.
Adolescent	10-~15	C fully erupted M3 erupts at this time postcrania not all fused	A drastic decrease in suspensory locomotion and vertical climb and a drastic increase in quadrupedal walking compared to juveniles.
Adult	~15+	Some wear on teeth, postcrania all fused***	No significant change in locomotion compared to adolescents.

*from Smith *et al.* 1994; Smith and Boesch, 2011 ** from Chapter II ***from Zihlman et al. 2007

Table III.2. Percentage of individuals in each age category that fall within a given knuckle usage category during arboreal quadrupedalism.

Age Class	Never	<50%	>50%
Young Infant			
%	71	29	0
SR	2.8*	0.2	-1.9
Old Infant			
%	25	58	17
SR	0.3	2.3*	-1.8
Juvenile			
%	19	62	19
SR	-0.2	3.0*	-1.9
Adolescent			
%	24	5	71
SR	0.2	-1.8	1.1
Adult			
%	11	8	81
SR	-1.4	-2.0*	2.3*

*SR standard residual, considered significant if over 2. Negative values have observed values less than expected and positive values have observed values greater than expected.

Sample size for each groups young infant = 7, old infant =12, juvenile = 16 adolescent = 21,adult = 37 This is smaller than the overall sample because some individuals only engaged in quadrupedal walking on terrestrial substrates.

Table III.3 Curvature, DMR angle, and DMR height for each age class of chimpanzee.

Category	Curvature			No Epiphysis Curvature			DMR Angle			DMR height in mm		
	N	Mean θ	SD	N	Mean θ	SD	N	Mean ∠	SD	N	Mean H	SD
Young infant	20	28.7°	3.8	31	24.9°	4.7	18	191.8°	6.1	15	0.00	0.00
Old infant	42	30.5°	4.9	48	28.0°	5.8	40	180.9°	12.9	33	0.10	0.18
Juvenile	55	36.7°	5.6	61	34.3°	4.9	51	169.8°	11.4	51	0.77	0.69
Adolescent	20	43.0°	5.7	20	37.6°	5.2	20	160.3°	11.1	19	1.11	0.71
Adult	46	46.1°	4.6	46	40.1°	4.5	46	158.8°	8.6	46	1.48	0.86
ANOVA		F = 74.96			F = 59.86			F = 45.73			F = 33.50	
		df = 4			df = 4			df = 4			df = 4	
		$p < 0.001$			$p < 0.001$			$p < 0.001$			$p < 0.001$	

Chimpanzee specimens were from the American Museum of Natural History, Cleveland Museum of Natural History, Harvard Museum of Comparative Zoology, the University of Zurich, and the Quex Museum (Kent, U.K.).

Table III.4 Curvature and distal metacarpal ridge angle for different age classes and species of primates.

Category	Curvature			DMR <			DMR height in mm		
	N	Mean θ	SD	N	Mean ∠	SD	N	Mean H	SD
Chimpanzee subadult	137	34.5°	6.9	129	174.6°	14.8	118	0.54	0.67
Chimpanzee adult	46	46.1°	4.4	46	158.8°	8.6	46	1.48	0.86
Gorilla subadult	44	37.5°	6.3	44	176.4°	16.2	43	0.73	0.81
Gorilla adult	30	52.0°	6.7	29	152.6°	14.0	29	2.62	1.45
Orangutan subadult	26	31.7°	6.1						
Orangutan adult	30	32.4°	4.1						
Gibbon subadult	30	24.2°	4.4						
Gibbon adult	30	27.5°	3.8						
Baboon subadult and adult	20	26.1°	5.1	17	176.4°	13.9	10	0.33	0.22
ANOVA		F = 77.26			F = 25.13			F = 41.31	
		df = 8			df = 4			df = 4	
		$p < 0.001$			$p < 0.001$			$p < 0.001$	

Primate specimens were from the American Museum of Natural History, Cleveland Museum of Natural History, Harvard Museum of Comparative Zoology, London Natural History Museum, the University of Zurich, and the Quex Museum (Kent, U.K.).

CHAPTER III FIGURES

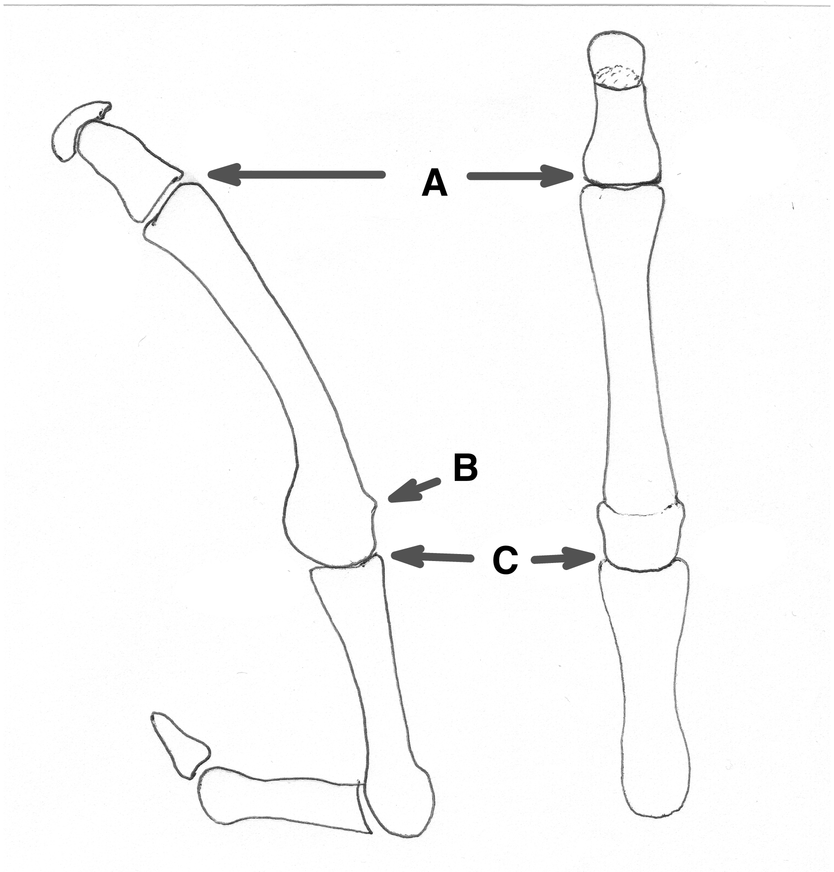

Figure III.1 Third digit of chimpanzee in knuckle-walking posture.
Left figure side view and right figure anterior view. A) carpalmetacarpal joint B) distal metacarpal ridge C) metacarpalphalangeal joint. Left figure loosely based on Richmond and Straight, 2000.

Figure III.2 Three hand contact categories for chimpanzees.
From left to right, knuckle, grasp, and palm. In KNUCKLE the intermediate phalanges on digits II-V contact the substrate. In GRASP the palm is in contact with the substrate and the fingers actively grasp the substrate. In PALM the palm contacts the substrate but the fingers do not actively grasp the substrate.

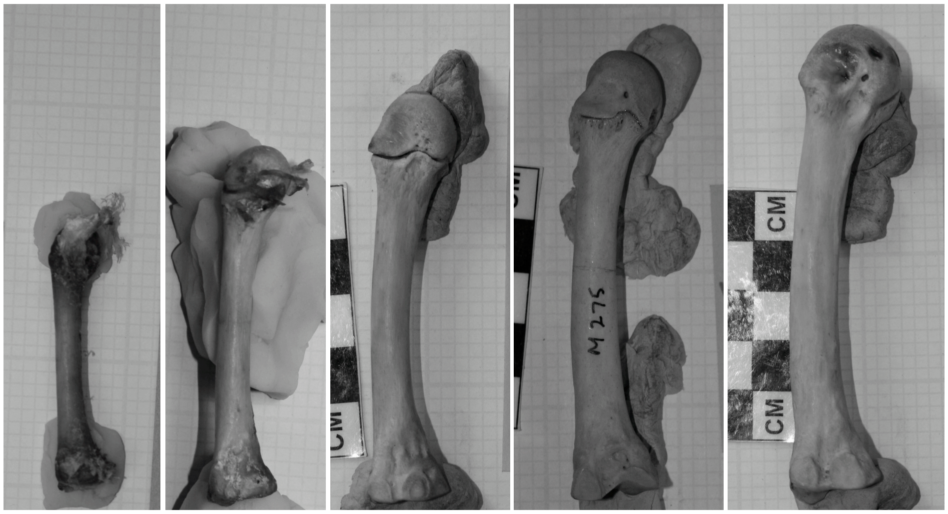

Figure III.3 Third metacarpals of chimpanzees.
From left to right, young infant, old infant, juvenile, adolescent, and adult.

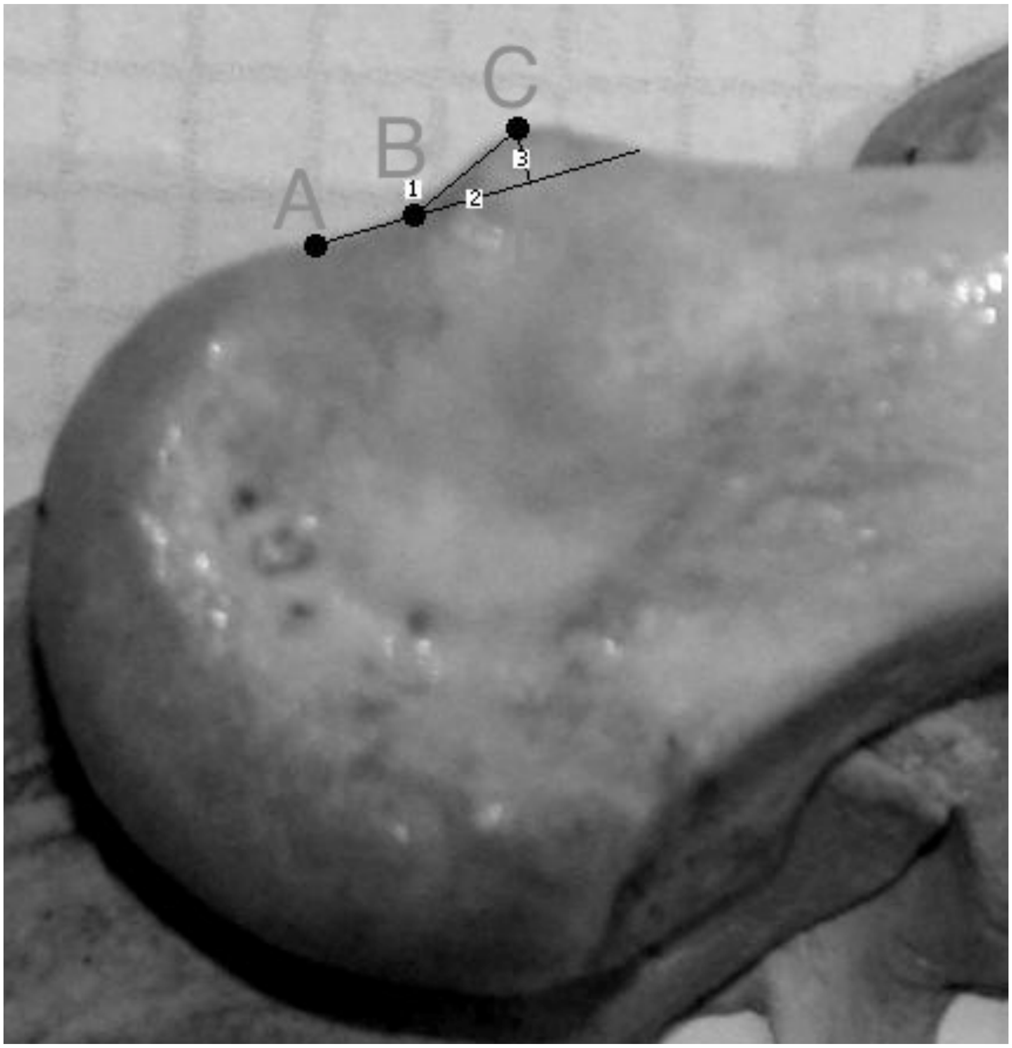

Figure III.4 Measurement of the distal metacarpal ridge.

Angle <ABC is used to quantify the presence of the DMR. The height is measured as the distance from point C perpendicular to the 180 degree line connecting points A and B.

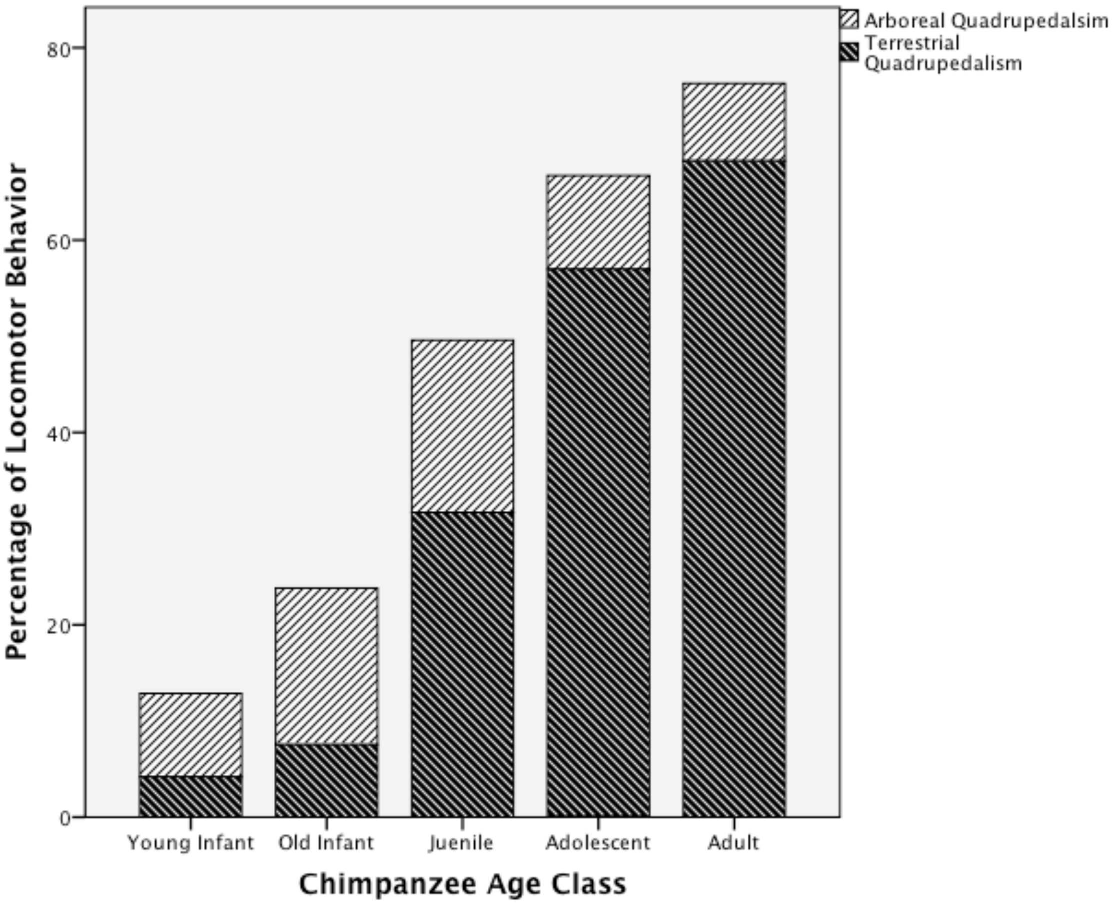

Figure III.5 Rates of arboreal and terrestrial quadrupedal locomotion for different age classes of chimpanzee.

There is a significant difference in the rates of quadrupedal locomotion between infants and juveniles and between juveniles and adolescents (Chapter III). When infants and juveniles were further subdivided into 6 different age groups, the only difference in quadrupedal locomotion occurred between the infant groups and the juvenile groups and not within either of these two groups (*ibid.*).

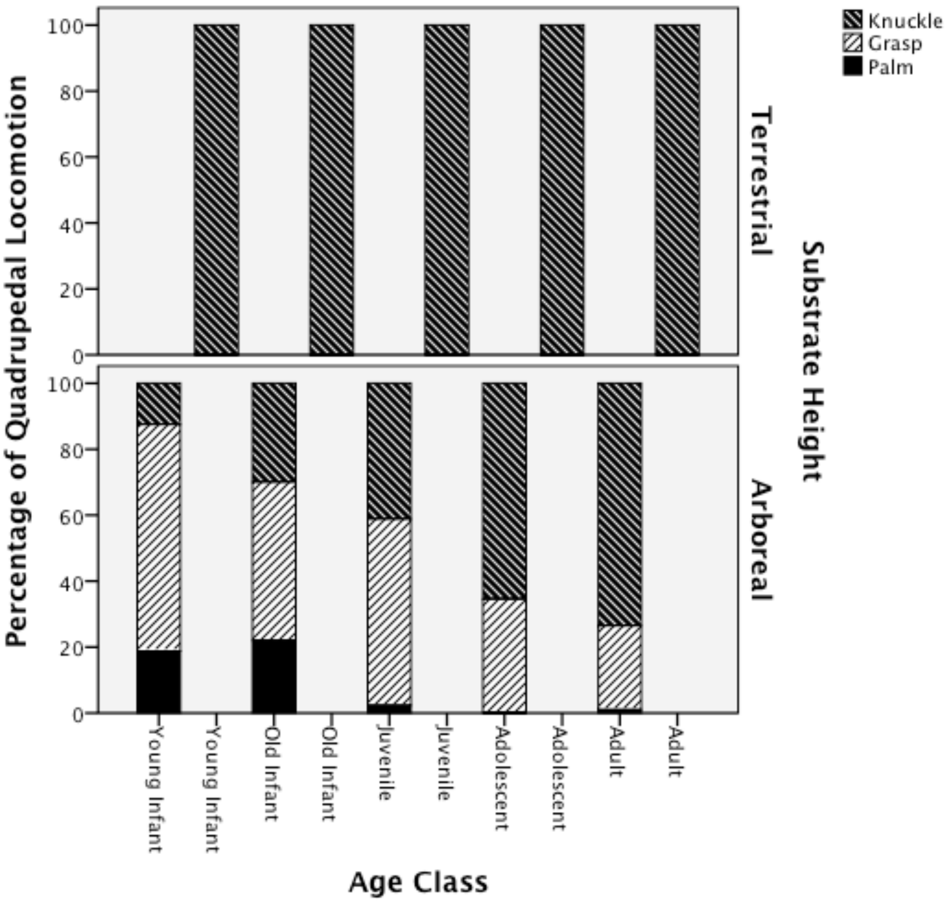

Figure III.6 Percentage of time spent in each of the hand contact categories during arboreal and terrestrial quadrupedal locomotion for each age class of chimpanzee.

Video and frequency data combined for percentage results. Arboreal and terrestrial percentages given separately.

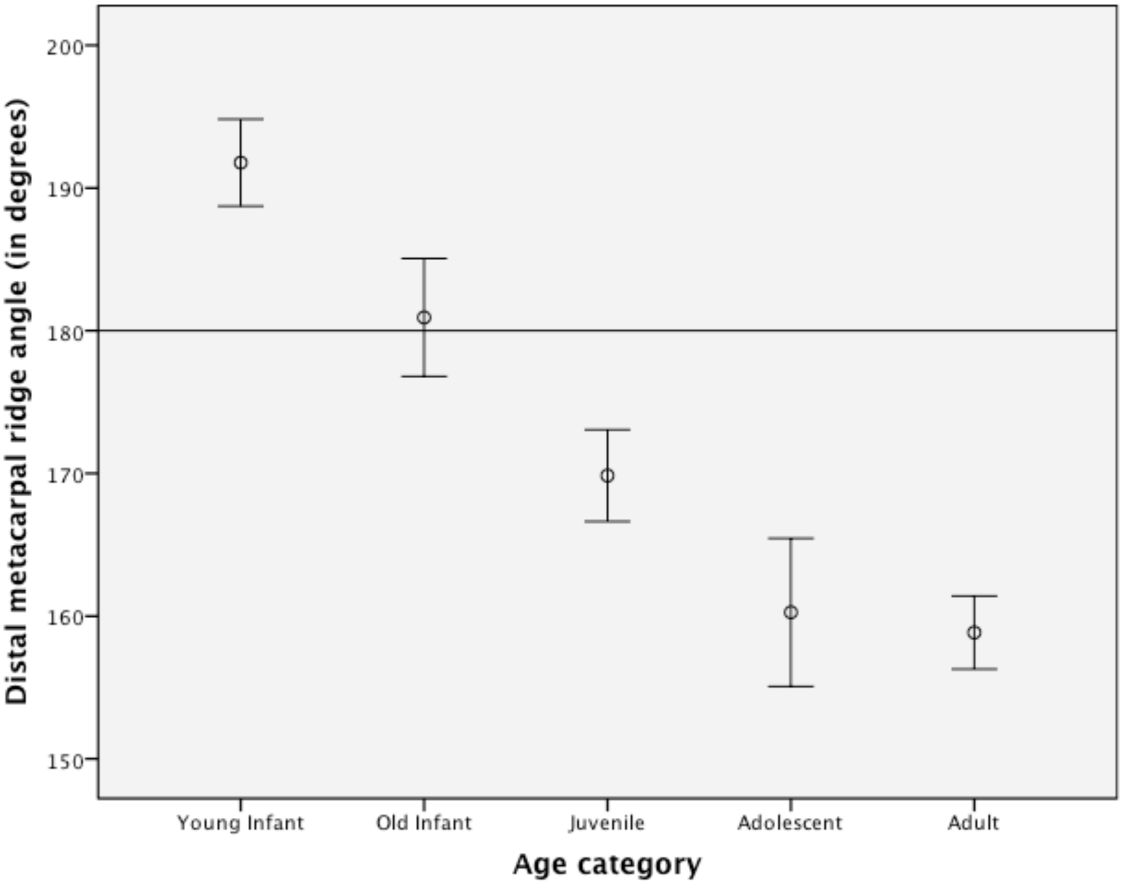

Figure III.7 Distal metacarpal ridge angle of differently aged chimpanzees.

CI at 95%. The DMR angle was significantly different between groups. The 180 degree line indicates that the epiphyseal area is straight. Above 180 degrees the epiphysis is rounded, below 180 degrees there is a distal metacarpal ridge present. Post hoc analysis revealed that DMR angle significantly decreases with each subsequent age category except between adolescents and adults.

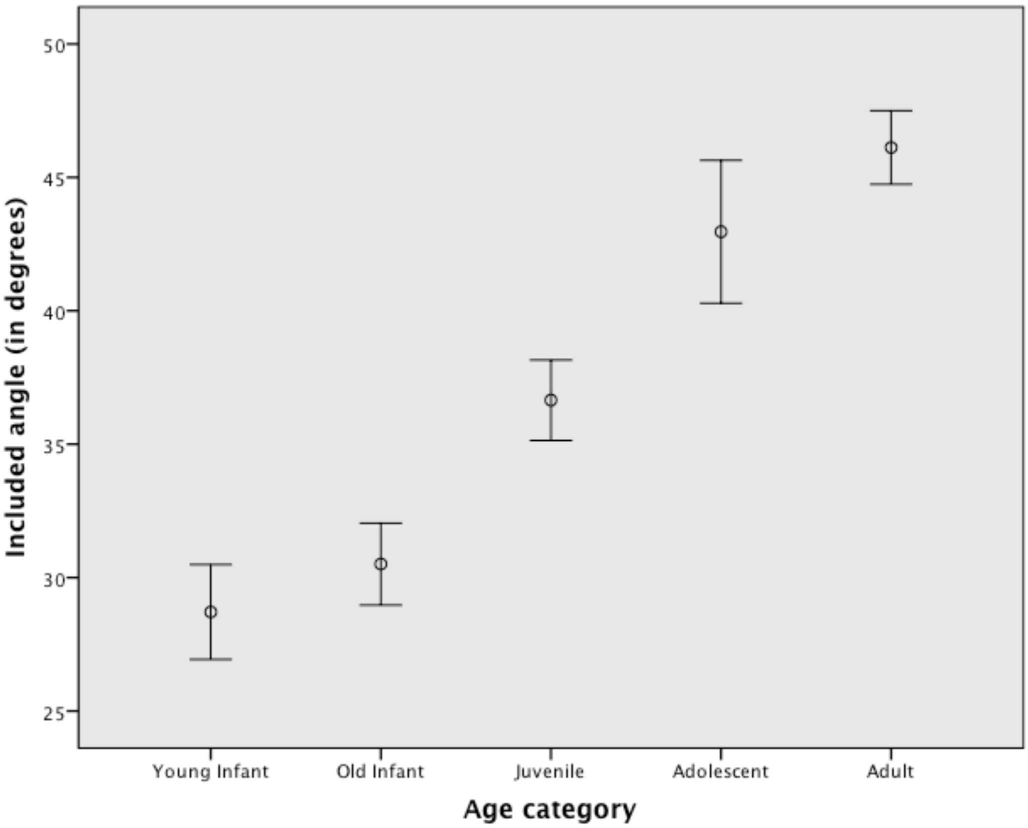

Figure III.8 Degree of metacarpal curvature of differently aged chimpanzees.

CI at 95%. The included angle was significantly different between groups. Post hoc analysis revealed all age groups different from one another except between the two infant groups and between adolescents and adults.

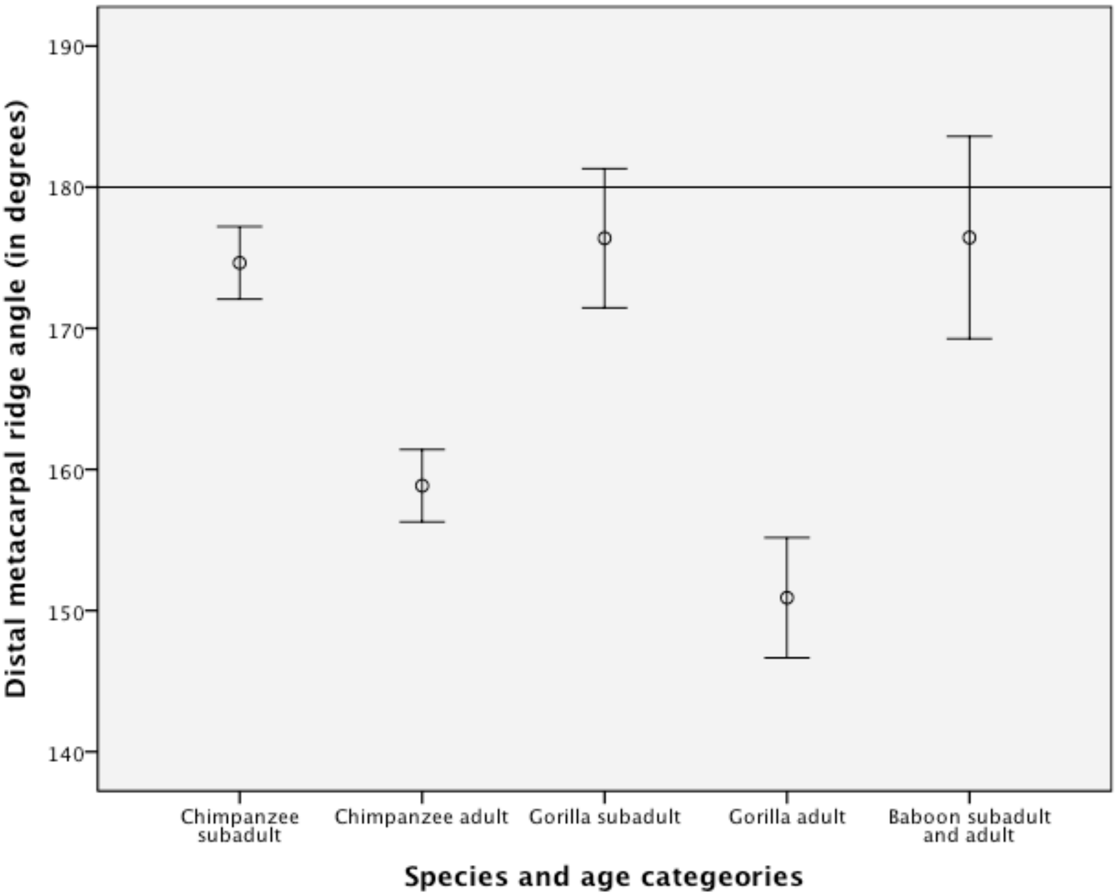

Figure III.9 Distal metacarpal ridge angle of differently aged chimpanzees, gorillas, and baboons. CI at 95%. The DMR angle is significantly different between groups. The 180 degree line indicates that the epiphyseal area is straight. Above 180 degrees the epiphysis is rounded, below 180 degrees there is a distal metacarpal ridge present. Post hoc analysis revealed that adult chimpanzees and adult gorillas had significantly less angled DMR compared to the three other categories. No difference was found between subadult and adult baboons when analyzed separately (Mann-Whitney U = 17.50, p = 0.19).

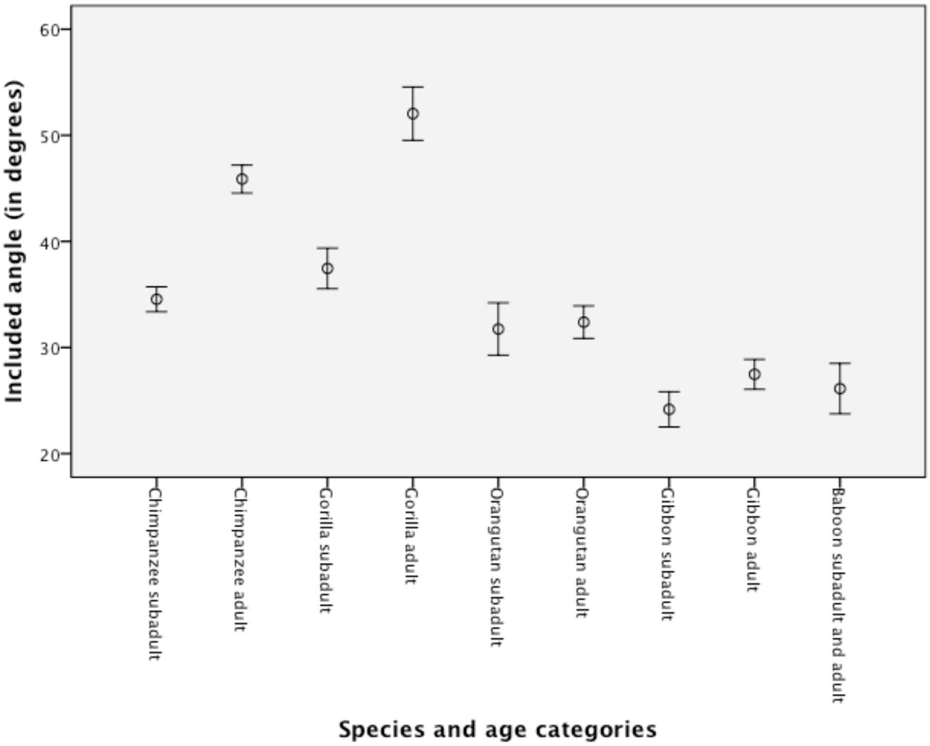

Figure III.10 Degree of metacarpal curvature of differently aged primate species.

CI at 95%. Included angle is significant different between groups.

Post- hoc comparisons T's subadult chimpanzee vs. adult chimpanzee $p < 0.001$, subadult chimpanzee vs. subadult gorilla $p = 0.329$, subadult chimpanzee vs. adult gorilla $p < 0.001$, subadult chimpanzee vs. subadult orangutan $p = 0.797$, subadult chimpanzee vs. adult orangutan $p = 0.625$, subadult chimpanzee vs. subadult gibbon $p < 0.001$, subadult chimpanzee vs. adult gibbon $p < 0.001$, subadult chimpanzee vs. baboon $p < 0.001$, adult chimpanzee vs. subadult gorilla $p < 0.001$, adult chimpanzee vs. adult gorilla, $p < 0.001$, adult chimpanzee vs. subadult orangutan $p < 0.001$, adult chimpanzee vs. adult orangutan $p < 0.001$, adult chimpanzee vs. subadult gibbon $p < 0.001$, adult chimpanzee vs. adult gibbon $p < 0.001$, adult chimpanzee vs. baboon = 0.00, subadult gorilla vs. adult gorilla $p < 0.001$, subadult gorilla vs. subadult orantutan $p = 0.02$, subadult gorilla vs. adult orangutan $p < 0.001$, subadult gorilla vs. subadult gibbon $p < 0.001$, subadult gorilla vs. adult gibbon $p < 0.001$, subadult gorilla vs. baboon $p < 0.001$, adult gorilla vs. subadult orangutan $p < 0.001$, adult gorilla vs. adult orangutan $p < 0.001$, adult gorilla vs. subadult gibbon $p < 0.001$, adult gorilla vs. adult gibbon $p < 0.001$, adult gorilla vs. baboon $p < 0.001$, subadult orangutan vs. adult orangutan $p = 1.00$, subadult orangutan vs. subadult gibbon $p < 0.001$, subadult orangutan vs. adult gibbon $p = 0.124$, subadult orangutan vs. baboon $p = 0.051$, adult orangutan vs. subadult gibbon $p < 0.001$, adult orangutan vs. adult gibbon $p < 0.001$, adult orangutan vs. baboon $p < 0.001$, subadult gibbon vs. adult gibbon $p = 0.10$, subadult gibbon vs. baboon $p = 0.99$, adult gibbon vs. baboon $p = 1.00$. No difference was found between subadult and adult baboon specimens (Mann-Whitney $U = 32.00$, $p = 0.44$).

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CHAPTER IV

Long bone cross-sectional properties reflect changes in locomotor behavior in developing chimpanzees.

Introduction

Prior research reveals that loading behavior correlates with cortical bone cross-sectional geometry in human and nonhuman primates (Schaffler et al., 1985; Demes et al., 1991; Ruff and Runestad, 1992; Ruff, 2002; Carlson, 2005; Shaw and Stock, 2009, Cowgill et al., 2010). Using this relationship, the locomotor behavior of primates has been inferred from the strength and shape of midshaft long bones (Ruff et al., 1994; MacLatchy et al., 2000; Stock and Pfeifer, 2001; 2004; Ruff, 2008; 2009). Bone is most responsive to loading during development (Lieberman et al., 2003; Pontzer et al., 2006; Gosman and Ketcham, 2009), so examining changes in behavior and morphology during growth is especially important in interpreting adult form. Relatively few studies have focused on the development of midshaft cortical bone geometry, with humans being well characterized, and baboons (*Papio*) only preliminarily so (Ruff et al., 1994; Sumner and Andriacchi, 1996; Ruff, 2003a; Cowgill et al., 2010). This study introduces a third taxon to this new field, as the first to track femoral and humeral strength and shape change during development in chimpanzees. I analyze these femora and humeri in relation to observations of the development of locomotor behavior in the wild.

Strength

Ruff (2003a; 2003b; 2005) showed that cross-sectional properties of long bones in developing humans are responsive to changes in mechanical loading during growth. Human children undergo a major change in mechanical loading of the limbs when they transition to unsupported walking around the age of 1 (Variot and Gotcu, 1927; Cheron et al., 2001). Ruff (2003a) demonstrated that strength increases with age for both the femur and humerus but the proportional strength, and therefore rate of growth, of each bone varies. The femur is initially stronger than the humerus but the humerus increases in relative strength at a faster rate (the proportion of femoral/humeral (F/H) strength decreases) in the first year of life when humans are crawling (*ibid.*). Proportional strength of the femora and humeri again change drastically from about 1 to 3 years of age with the femur surging in relative strength with the onset of bipedal walking (*ibid.*). This increase in femoral relative to humeral shaft strength continues, albeit less dramatically, into the teenage years when adult strength levels are reached (Sumner and Andriacchi, 1996; Ruff, 2003a).

Similar to humans, the *Papio cynocephalus* femur is relatively stronger than the humerus in young infants. In the baboon, the femoral/humeral strength ratio increases until about 2.5 years at which time adult-level strength proportions are reached (Ruff, 2003a). Adult baboon femoral to humeral strength ratios are below those found in adult humans (Ruff, 2003a; Shaw and Ryan, 2012). This is expected since, unlike in humans, both forelimb and hindlimb are habitually used in this primarily quadrupedal species. Quantitative locomotor data on wild baboons during ontogeny is lacking so morphological transitions in this species cannot be assessed with regard to locomotor change. However, a qualitative study has reported that yellow baboon infants begin riding dorsally on their mothers as early as two months of age and are independent quadrupedal locomotors (only carried in times of suspected danger) by around 8 months of age (Altman et al., 1981). These findings indicate that baboon F/H strength ratios may be reached after adult locomotor behavior is established, but prior to skeletal maturation (dental maturation >8 yrs, Kahumbu and Eley, 1991).

Diaphyseal cross-sectional proportions of the humerus and femur correlate with differences in locomotion in adult primates. Indriids who engage in hindlimb dominated saltatory locomotion, have significantly stronger femora compared to humeri (five different species examined in the family Indriidae, Demes et al., 1991). Slow climbing *Loris* and *Nycticebus* engage in locomotion that is not dominated by one set of limbs and have forelimbs and hindlimbs equally able to resist mechanical loading (Demes and Jungers, 1989). Schaffler et al. (1985) found the forelimb dominated suspensory species *Hylobates lar* had stronger femora compared to humeri but that their femoral/humeral (F/H) ratios are much lower compared to Old World monkey species that are more quadrupedal (Schaffler et al., 1985). Cross-species comparisons among hominoids have also shown that different locomotor repertoires are correlated with differences in F/H bending and torsional strength ratios (e.g. Ruff, 2002; Shaw and Ryan, 2012). For example, adult *Pongo*, who predominantly use forelimb dominated locomotion, have greater humeral than femoral midshaft bending strengths, with F/H strength proportions significantly lower than those of more quadrupedal chimpanzees and *Gorilla* (Ruff, 2002; Shaw and Ryan, 2012). Gorillas engage in the least amount of upper limb suspensory behavior among great apes. Correspondingly, this species is the great ape with the highest F/H ratios, with the mountain gorilla subspecies even higher than their more arboreal lowland counterparts (Ruff, 2002).

Overall, greater F/H strength ratios are correlated with higher levels of hindlimb locomotion. Thus, the relationship between strength ratios and locomotion are likely to emerge in developing chimpanzees as they become more quadrupedal. Chimpanzees go through several locomotor transitions during development. As individuals grow older, they display a decrease in upper limb loading suspensory behavior and an increasing reliance on quadrupedal knuckle-walking (Chapter II; Doran and Hunt, 1994). Infants primarily engage in upper limb loading suspensory behavior, while juveniles are both suspensory and quadrupedal (Table IV.1; Chapter II; Doran, 1992; Doran and Hunt, 1994). Alternatively, adolescents and adults are primarily quadrupedal knuckle-walkers (*ibid.*). During knuckle-walking, chimpanzees experience higher peak vertical forces on the hindlimbs than forelimbs, in contrast with nonprimate mammals for whom the reverse is typical (Demes et al., 1994). Adult chimpanzees have stronger femoral than humeral midshafts but the difference between the two bones is not as great as in humans (Ruff 2002; 2003b; Shaw and Ryan, 2012). This is because chimpanzees still load their arms during knuckle-walking and arboreal travel even in adulthood (Chapter II; Doran and Hunt, 1994), unlike humans, who are freed from the constraints of mandatory arm support during positional behavior after infancy. Chimpanzee locomotor transitions are more gradual than the abrupt discontinuity that occurs between crawling and walking in humans. Therefore, the F/H strength changes are also likely to be more gradual. Despite more subtle locomotor changes, I predict a positive correlation between age and F/H strength over the course of development in chimpanzees with initial forelimb usage making humeral strength greater or equal to that of the femur in infants. In older individuals, I predict that hindlimb loading during frequent quadrupedalism will lead to significantly greater femoral compared to humeral strength. Locomotor transitions are greatest when individuals reach juvenility and adolescence (Ch II). If shifts in strength closely map changes in locomotion then F/H strength ratios are expected to significantly increase at these times during development.

Shape

The midshaft shape of primate long bones is also influenced by loading patterns. In general, loading the limb in multiple directions is thought to lead to greater circularity of long bone cross-sectional shape while repeated directional loading on the limb (especially anteroposterior bending) is thought to produce more elliptical cross-sections. For example, young humans (4 - 5.9) go through a waddling phase of high mediolateral loading during bipedal locomotion which corresponds to increased femoral circularity during this time (Cowgill et al., 2010). In nonhuman primates, slow climbers load their limbs in multiple directions and have more circular shaped cross-sections equally able to resist bending from multiple directions compared to higher unidirectional loading leapers who have more elliptical femora (Demes and Jungers, 1989; Ruff 1989; Ruff and Runestad, 1992).

Relating specific locomotor behaviors with shape has been difficult in adult great apes and other primates who have diverse locomotor repertoires (Ruff and Runestad, 1992; Carlson, 2005; Carlson et al., 2006; 2011). No difference in humeral or femoral midshaft shape (I_{max}/I_{min}) was found among chimpanzee subspecies in an analysis of adult specimens (Carlson, 2005). This is likely due to generally similar locomotor patterns among subspecies (Doran and Hunt, 1994; Chapter II). Differences in shape have been found at the community level in chimpanzees but with no definitive correlation with locomotor mode differences (Carlson et al., 2006; 2011). At the species level, there is a significant difference in midshaft shape between gorillas and chimpanzees in the femur and humerus, with a trend of increased circularity with increased levels of arboreal locomotion in these African apes (Carlson, 2005).

Demes and Carlson (2009) found that even linear (quadrupedal) arboreal locomotion loaded the forearm in more directions compared to terrestrial locomotion in capuchins. The difference between overall arboreal and terrestrial loading environments should be even more pronounced in chimpanzees. This is because chimpanzee arboreal locomotion is comprised of multiple locomotor modes and submodes compared to the handful of locomotor modes they engage in while moving terrestrially (Chapter II). Increased time spent in arboreal locomotion is therefore expected to correlate with increased circularity in femoral and humeral midshaft shape in chimpanzees.

During development chimpanzees go through a shift from primarily engaging in arboreal locomotion as infants to predominantly terrestrial locomotion as adults (Chapter II, Chapter III, unpublished data). As individuals age, they also engage in fewer locomotor modes and submodes, again making the loading environment more predictable (Chapter II). I therefore predict that the midshaft of the humeri and the femora will become more elliptical as individuals age, coinciding with the developmental transition of decreased locomotor variability.

Methods

The predictions outlined above regarding changes in midshaft strength and shape were tested using 74 skeletons of wild-caught individuals from the American Museum of Natural History, the Cleveland Museum of Natural History, and the Harvard Museum of Natural History (Table IV.2). Only seemingly healthy individuals with no apparent atrophy of the upper or lower limbs were used, as this could reflect atypical patterns of locomotion. Individuals were aged using dental eruption patterns (Smith et al., 1994; Smith and Boesch, 2011; Table IV.3). In some cases where individuals were not association with teeth, individuals were aged using epiphyseal fusion of postcrania (N = 4; Kerley, 1966; Zihlman et al., 2007). Ages were assigned on an integer scale and in categorical form (Table IV.3; see Chapter III for a detailed description of aging techniques). Specimens were classified into five age categories that corresponded to changes in locomotion that occurred during development: young infant 0.1 - 3.0 years; old infant 3.1 - 5 years; juvenile 5.1 - 10 years; adolescent 10.1 - 15 years; adult 15+ years (Table IV.1)

Long bone geometric properties were derived from micro computed tomographic (micro CT) scans of the humerus and femur. Scans were performed on one bone at a time in the center of the scan field. Scans were conducted at the Orthopaedic Research Laboratory at the University of Michigan (45 µm, 80 kVp, 400ms exposure time), and the Cleveland Clinic (93 µm, 80 kVp, 100ms exposure time) with both facilities using General Electric Explore Locus microCT system. The scale of analysis was adjusted for each image to account for the difference in resolution between the two machines. This was accomplished by setting the distance in pixels to a known distance in each image. Bones were leveled using foam and scanned with the posterior surface of the bone facing the scan bed. Bone alignment for the anterior-posterior, medial-lateral, and longitudinal planes was based off of reference points outlined in Ruff (2002).[1] Bones were scanned in 3D with a 4cm field of view (FOV) so that bone alignment could be rechecked in MicroView 3D volume viewer and altered after scanning if required to ensure that the

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[1] The femur is positioned so that the AP midpoints of the shaft just distal to the lesser trochanter and just proximal to the condyles are equidistance from the support surface. “The coronal plane is then defined as parallel to the supporting surface through the most distally projecting points on the two condyles. The sagittal plane is perpendicular to the coronal plane and contains the M-L midpoint of the shaft just distal to the lesser trochanter and the deepest point in the intercondyle notch. The intersection of the coronal and sagittal planes defines the longitudinal axis of the femur…The humerus the AP midpoints of the shaft just distal to the head and lesser tubercle and at the proximal edge of the olecranon fossa. Coronal planes are then parallel to the supporting surface and run through the midpoint of the….long axis of the trochlea/capitulum. The sagittal plane(s)… in the humerus the M-L midpoint of the shaft at the surgical neck and the lateral lip of the trochlea.” Ruff, 2002 pg 337-339.

longitudinal axis of the shaft was parallel to the underlying surface (i.e. leveled) at the point of interest. This was more of a concern in the femur due to AP curvature in older individuals.

Humeral length was measured as the maximal length from proximal to distal end of the long bone. Femur length was measured from the average distal projection of the condyle to the most distal point on the femoral neck with the long axis of the diaphysis perpendicular to the vertical osteometric board. Bone lengths, including those for subadult individuals, were measured with epiphyses. Unfused epiphyses were re-approximated and held in place with clay to accurately measure total length. Cross-sections were obtained at 50% from the distal end on the femoral and humeral shafts and again at 40% from the distal end on the humeral shaft to avoid the influence of the deltoid tuberosity (Ruff, 2002). Areas of interest were marked with adhesive tape, thick enough to be visible in the scans. On the humerus, the tape was placed just proximal to the 50% region of interest (ROI) and just distal to the 40% ROI. On the femur, the tape was placed just distal to the 50% ROI. A 2D image at the exact point of interest on the Z axis was exported as a DICOM file into ImageJ (version 1.45s) and BoneJ (version 1.3.2, Doube et al., 2010). The 2D scan images were thresholded and checked for any distortion in BoneJ (Figure IV.1).

These 2D cross-sectional images of bone slices were then cleaned and analyzed using Slice Geometry in BoneJ (Figure IV.1, Figure IV.2). Bone continues to change in both composition and density as individual's age. This is especially apparent in developing individuals where bone is still being laid down (Currey, 2002; Scheuer and Black, 2000). It can be difficult to distinguish the difference between cancellous and cortical bone when there is a high degree of porosity in bone closest to the medullary cavity. Any obvious trabecular bone was "cleaned" from the scans to the level of the neighboring endosteal envelope using the erasure tool in ImageJ (Figure IV.2, a - d; Carlson, 2005). In scans with porosity in the endosteal area, when a foramen was less than

50% enclosed by cortical bone, tissue towards the medullary cavity was erased until the bone in question increased in thickness and was structurally congruent with the cortical bone (Figure IV.2, e - f). This conservative approach was taken because leaving possible trabecular bone was preferred over omitting cortical or "nearly" compact bone. This is because cancellous bone of the diaphysial midshaft region has negligible impact on bone strength and rigidity and can therefore essentially be ignored since including or excluding the bone has little impact on results when cancellous bone comprises less than 40% of the total cross-sectional area (Ruff, 1983).

Bones are subject to stress from bending and twisting and the strength of resisting these forces is best measured by second moments of area (Ruff, 1995). Second Moments of Area (I_{max}, I_{min}) and Polar Moments of Area (J, Z) were calculated from the images to assess bending and torsional rigidity (see Table IV.3). The polar second moment of area, J, has been found to be the best single indicator of second moments of area in cross-section geometry in the absence of experimental data on loading (Lieberman et al., 2004). Z_p was also calculated to compare results of this study to work published by Ruff (2003a, 2003b). I_{max} and I_{min} ratios were used to examine shape. I_{max} and I_{min} were used over I_x and I_y because principle axes have been found to be more indicative of shape compared to anatomical axes in African apes given individual variation in principle angles (Figure IV.3; Carlson, 2005; Carlson et al., 2011, Morimoto et al., 2011). Principle axis values were also used because they are less influenced by observer error in bone orientation.

Body mass influences long bone loading and therefore cross sectional properties of bones. Unlike body mass estimates for adult chimpanzees, methods for accurately estimating body mass from skeletal remains of subadult specimens are lacking. Therefore, examining changes in femur and humeral strength were conducted comparing one bone to another bone in the same individual. Using femur to humerus ratios of strength in the same individual negates the problem of accurate body mass estimates and allows comparison between individuals of differing body masses. Values for the humerus and femur are also plotted against one another to illustrate change in each bone that might be influencing the ratio.

Prior research has compared strength and shape variables in relation to locomotor behavior of individuals without taking into consideration body size (Ruff, 2002; Carlson, 2005; Cowgill et al., 2010). This method offers a comparable dataset for immature nonhuman primate or fossil specimens when scaling measures (i.e. to body mass or limb length) are not available (Ruff, 2009).

All variables were normally distributed based on Kolmogorov-Smirnov tests (all $p > 0.05$). Femoral/humeral strength ratios (J, Z_{pol}) and shape ratios (I_{max}/I_{min}) were transformed using natural logarithms. Strength ratios showed homogeneity of variance based on Levene's tests (all $p > 0.05$). The humeri but not the femora showed homogenence of variance in shape (Levene's test: humerus $p > 0.05$; femur < 0.05). One-way ANOVAs were used to asses strength and shape differences between age groups with Bonferroni *post hoc* comparisons conducted on variables with equal variance and Tamhane's on variables with unequal variance. Paired t-tests of humerus and femur J values were conducted on individuals within each age category. Z_{pol} mean values and graphical depictions were also given so comparisons could be made with Ruff (2003a). Patterns of shape change in the humerus and femur over the course of development were evaluated through bivariate correlations and linear regressions of second polar moment area ratios (I_{max}/I_{min}) on age (Cowgill et al., 2010).

Results

Strength

There was a positive relationship between F/H strength (J) and age in developing chimpanzees with the youngest individuals having the lowest mean ratios (on either side of the femur J = humerus J reference line) and adults having the highest mean values (Table IV.4; Figure IV.4). The bivariate plots for lnF and lnH illustrate that an increase in strength in one bone corresponded to an increase in strength in the other bone in the same individual. In addition, the F/H proportion increase with age was due to a larger increase in femoral strength and not a decrease in humeral strength (Figure IV.5).

When data were partitioned into age categories, the mean F/H J ratio increased in each subadult age group with significant variation in strength between groups for both the F/H50 (ANOA F = 7.78, df = 4, $p < 0.01$; Figure IV.4; Tables IV.4 and IV.5) and F/H40 ratios (ANOVA F = 15.67, df = 4, $p < 0.01$; Figure IV.4; Tables IV.4 and IV.5). *Post hoc* comparisons revealed that the variation between age categories was mainly due to the young infant group (Table IV.5). Young infants had significantly lower F/H50 and F/H40 ratios compared to juveniles, adolescents, and adults (Table IV.5). The F/H40 ratio showed additional differences between groups with the older infant group having a significantly higher F/H40 ratio compared to young infants but lower F/H40 ratio compared to adolescents and adults (Table IV.5; Figure IV.4).

Paired t-tests (lnJ) revealed no difference between femoral and humeral limb strength at either humerus location in young infants (Table IV.4). Older infants had significantly stronger femora compared to H40 but not compared to H50 (Table IV.4). Individuals in the three oldest age classes possessed femora that were significantly stronger than their humeri (Table IV.4,

Figure IV.4). The same general relationship of increased F/H ratios with increased age existed for Z_{pol} as in J (Figure IV.6, Table IV.4).

Shape

Femur shape and age were linearly correlated (Pearsons Correlation r (73) = 0.50, $p < 0.001$; linear regression line $R^2 = 0.252$; Figure IV.7). Neither humerus region of interest showed a linear correlation with age (H50 Pearson's correlation = -0.05, p = 0.67; H40 Pearson's Correlation = -0.21 p = 0.07; Figure IV.8). Figure IV.8 illustrates that humerus shape (I_{max}/I_{min}) is variable at all ages. A few young infants have the most elliptical (highest ratios) humeral shafts at H40 but the majority of young infants display values indistinguishable from individuals in other age categories.

Femoral shape differed between individuals of different age classes (ANOVA F = 6.54, df = 4, $p < 0.01$, Table IV.5). *Post hoc* tests revealed that the femur was more elliptical in adults compared to both groups of infants (Tamhane A vs. YI $p < 0.001$; Y vs. OI p = 0.027; Table IV.5; Figure IV.7). Femoral shape values of juveniles and adolescents did not differ (Tamhane $p > 0.05$; Table IV.4). Nevertheless, only juvenile femora were more elliptical than the femora of young infants (Tamhane J vs. YI p = 0.002; Table IV.5). Humeral shape at H40 but not at H50 displayed heterogeneity among members of different age classes (H40 F = 2.57, df = 4, p = 0.046; H50 F = 1.71, df = 4, p = 0.16). However, *post hoc* comparisons of H40 revealed no differences between individuals in different age classes (Bonferoni all $p > 0.05$). The bivariate plots for femoral and humeral shape indicate that no clear relationship between the two bones exist for either H50 or H40 location (Figure IV.9).

Discussion

Strength

Both femoral and humeral strength increased with age in chimpanzees. The relationship between the bones differed as predicted with femoral strength increasing more than humeral strength as individuals aged. Young infant chimpanzee mean ratios for H40 and H50 are just under 1 and an analysis revealed no difference between femoral and humeral strength in these individuals (Table IV.4). The pattern in older infants was less clear with the femur being significantly stronger compared to H40 but not H50. The bias towards stronger femora started definitively at the juvenile period. The strength of juvenile chimpanzee femora was significantly greater compared to that of their humeri measured at both H50 and H40.

Despite a general trend of increased F/H ratios with age, the distinctive shifts in locomotion that occur during juvenility and adolescence did not manifest in drastic changes in strength ratios between members of different age classes (Table IV.5; Figure IV.4). Mean values for strength ratios increase in each subsequent age category until adolescence but the differences are not significant due to considerable variability within each group (Table IV.4, Table IV.5). It is possible that longitudinal data, like that used by Ruff (2003a,b) for the human sample, would minimize individual variation and show a clearer relationship to locomotion. While juveniles engage in intermediate rates of suspensory and quadrupedal behavior, they engage in significantly higher rates of quadrupedal running compared to any other age group. This form of locomotion, which loads heavily on hindlimbs, may contribute to a surge in relative femoral strength and may help to explain why no difference was found between juveniles and older individuals.

While methodological differences[2] make it unwise to directly compare absolute Z_{pol} values from this study with Ruff's data (2003a), general comparisons of trends show some differences between humans, baboons, and chimpanzees (Figure IV.10). Chimpanzee infant F/H ratios in Z_{pol} appear to be unique realtive to human and baboon infants. Ruff (2003a) found the femur to be relatively stronger in both human and baboon infants which was not the case for chimpanzees who have humeri and femora with relatively equal strength (Figure IV.10; Table IV.4; youngest baboon specimen 7 months, chimpanzee 5 months, and human 6 months). Adult ratios of strength are reached at 2.5 years in baboons and at about 15 years for humans (Ruff, 2003a). This is before long bone growth has ceased in both taxa. Adult F/H ratios are reached by 6-8 years in chimpanzees. In accordance with overall patterns of development, this is later than in baboons but earlier than in humans (Figure IV.5; Figure IV.10).

Shape

The femoral midshaft of developing chimpanzees becomes increasingly elliptical with age, as knuckle-walking becomes the dominant form of locomotion. Contrary to expectation, however, the humerus does not undergo this change in shape with a high degree of variability in I_{max}/I_{min} ratios in all age categories. Adult mean values for both humeral and femoral principle moment of area ratios fall within the range of mean values previously reported for adult chimpanzees (I_{max}/I_{min}, Carlson, 2005).

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[2] Ruff (2003a, b) used both anatomical axis and 2x AP in calculating Z_p in the femur but used AP + ML in calculating the humerus midshaft in his study on baboon and human ontogeny, therefore caution was used in comparing exact values.

The highest mean value for femoral shape (I_{max}/I_{min}) for any chimpanzee age class was lower than the reported mean values for any human age class over the course of development (Cowgill et al., 2010). However there was considerable overlap in absolute values between the two species (*ibid.*). The spread of mean values was also similar between the two species (0.20 for chimpanzees and 0.17 for humans), but the overall trends were divergent with human femoral shape showing a quadratic relationship with age and chimpanzees femoral shape demonstrating a linear relationship (*ibid.*).

Morimoto et al. (2011) found no difference in ontogenetic trajectories between captive and wild individuals in terms of femoral midshaft shape using femoral length as an age proxy. Since body mass was not controlled for in either Morimoto et al. (2011) or this study, the increase in elliptical shape with age could be due to an increase in mass. With increasing body size there is a trend of increasing femoral ML/AP bending rigidity in most primate species (Ruff and Runestad, 1992). However, if body mass was a predominant determining factor in shape, one would expect to see some relationship between humeral shape and age. Likewise, if the femoral trend was predominantly genetically determined as Morimoto et al. (2011) suggest, the humerus would also be expected to show a pattern with age. In a study on a small sample of wild living chimpanzees, where skeletal samples and individual locomotor behavior were known, Carlson et al. (2006) found that shape was more highly correlated with the proportion of arboreal locomotion than it was with body mass.

It is noteworthy that, even if the femoral trend is in part influenced by body mass, a different pattern is found in the humerus. In a study of forelimb and hindlimb morphometrics across a range of catarrhines (including apes), forearm measures (including midshaft diameters) were found to be significantly more variable than were hindlimb measures (Buck et al., 2010).

The authors proposed that variable loading patterns in suspensory behavior was a possible explanation (*ibid.).* While forelimb loading is not stereotypical throughout development in chimpanzees, infants are even more variable in their loading behavior compared to adults, leading to the hypothesis that circularity (I_{max}/I_{min}) would decrease with age. Since this hypothesis was not supported, an alternate model of how the forelimb is loaded during development must be sought. The lack of any significant change in shape over time may be indicative of one or more of the following: variation in the frequency of locomotor modes engaged in, the performance of these modes, and/or variation in muscle attachment sites.

The first potential factor influencing humeral shape is individual variation in locomotor frequency. I have previously shown that developing chimpanzees undergo considerable changes in their locomotor behavior, especially with regard to knuckle-walking and suspensory movement (CH II). Variation between members of different age classes was greater than individual variation within an age class. Because of this, a trend would have occurred between age classes if locomotor mode frequency primarily influences humeral shape. However, there may be high individual variation in submode frequencies, preventing a transparent relationship between function and shape. For example, infant and adult chimpanzees vertically descend substrates a similar proportion of their locomotor time, however, they do differ in the way in which they descend. Infants frequently utilize forelimb dominated descent submodes, such as *head-first descent*. Adolescents and adults, in contrast, tended to use more hindlimb dominated vertical descent submodes such as *rump first symmetrical descent* (CH II). Degree of individual variation with regards to submode frequencies was not analyzed due to small sample size and warrants further investigation.

Secondly, there is likely a high degree of variation in how individual chimpanzees perform the same behavior, as has been shown in humans with regard to bipedality. Cowgill et al. (2010) found that bipedal performance style varies in humans over the course of development, and that femoral cortical bone shape changes correspondingly. In addition, there was a high degree of individual variability in performance with regard to ground reaction forces, especially in individuals under 4 years of age (*ibid.*). This study shows that performance variation influences shape in a species that engages in only one primary type of locomotion. Chimpanzees engage in a greater array of types of locomotion and any individual variation in performance of those behaviors is likely to produce differences in the shape of bones. The lower variability in shape of the femur compared to the humerus may be due to the lower variability in performance for hindlimb loading behaviors like quadrupedalism compared to forelimb loading behaviors like torso-orthograde forelimb suspension.

Lastly, the higher variation in humeral shape compared to that of the femur may be due to muscle attachment site variability being higher in the former. Several femoral muscles attach posteriorly at one location, the linea aspera. The humeral shaft has a greater number of bony muscle attachment sites such as the deltoid plane and tuberosity proximally, and the supinator crest distally. Variation in the size and location of these humeral muscle attachment sites may influence the shape of the humeral cross-section and warrants further investigation.

Further research is required to determine if variation in frequency, variation in performance, or variation in muscle attachment sites contribute most substantially to the high variation seen in humeral shape. Regardless of the cause, this high forelimb variability coupled with the distinctive hindlimb pattern of increased elliptical shape with age, implies that the loading environment is a contributing factor in determining midshaft shape in the chimpanzee humerus and femur.

Conclusion

Overall there is a positive relationship between F/H strength ratios and age in chimpanzees. Forelimbs and hindlimbs have equal strength in early infancy, but the femur becomes significantly stronger than the humerus in individuals by juvenility. The distinctive shifts in locomotion that occur at the juvenile and adolescent periods did not manifest in drastic changes in strength ratios between individuals in different age classes. However, the general trend of increased femur to humerus strength ratios with age makes this a usable feature in determining degree of suspensory behavior in fossil specimens. For example, there is a longstanding debate over the locomotor repertoire of Australopithecines (e.g. Lovejoy et al., 1973; Susman et al., 1984; Latimer and Lovejoy, 1990; Ward, 2002). A recent study examining an *Australopithecus afarensis* subadult specimen from Dikika argues that this species engaged in suspensory behavior over the course of development (Green and Alemseged, 2012). The present study provides data to test this claim of suspensory behavior in the Dikika specimen as well as any other subadult specimen where the humerus and femur are present.

Shape, in addition to strength, changes over the course of development in the femur. The femur becomes more elliptical with age in chimpanzees likely reflecting the increase in quadrupedal walking. However, there is no clear relationship between shape and age in the humerus. This latter result may reflect individual variation in humeral loading from arboreal locomotion throughout an individual’s lifetime in chimpanzees. The difference in humeral and femoral shape trends indicate that function is likely influencing form. However, further study is required to investigate this possibility and to better understand what variables are most influential in determining bone shape in developing chimpanzees.

CHAPTER IV TABLES

Table IV.1 Markers of chimpanzee age categories.

Category	Age	Dental eruption markers*	Locomotor Behavior**	N
Young Infant	0 - 3	Deciduous dentition erupts during this time, M1 not erupted	Predominantly suspensory with the highest levels of suspensory behavior for any age group.	11
Old Infant	3 - 5	M1 erupted or near eruption, I1 not erupted	Still predominantly suspensory but higher levels of independence from mother and higher levels of quadrupedal locomotion compared to young infants.	9
Juvenile	5-10	I1 erupted or near eruption, I2, M2, P3, P4 erupts during this time, C not erupted or just erupting, M3 not erupted	Completely independent from mother, a drastic decrease in suspensory locomotion, and a drastic increase in quadrupedal walking and running compared to older infants.	26
Adolescent	10-~15	C fully erupted M3 erupts at this time postcrania not all fused	A drastic decrease in suspensory locomotion and vertical climb and a drastic increase in quadrupedal walking compared to juveniles.	8
Adult	~15+	Some wear on teeth, postcrania all fused***	No significant change in locomotion compared to adolescents.	20

*from Smith *et al.,* 1994; Smith and Boesch, 2011, ** from Chapter 1 ***from Zihlman et al., 2007

Table IV.2 Age and museum distribution of skeletal sample.

	Subadult	Adult	Total
American Museum of Natural History	19	12	31
Cleveland Museum of Natural History	27	8	35
Harvard Museum of Natural History	8	0	8

Table IV.3 Cross-sectional geometric properties of interest.

Symbol	Definition	Mechanical significance
I_{max}	Second moment of area around major axis	Maximum bending strength
I_{min}	Second moment of area around minor axis	Minimum bending strength
I_{max}/I_{min}	Principle moment of area ratio	Indication of shape, higher values indicate greater deviation from circularity
J	Polar second moment of area	The sum of any perpendicular second moments of area. Indicator of torsional strength and twice the average bending strength.
Z_{pol}	Polar section modulus	J divided by half the total superiosteal breadth Indicator of torsional strength

Table IV.4 Age category means and paired t-test results of cross-sectional properties.

		Femur	Humerus 50	Humerus 40
0.1 – 3.0	N	11	11	11
	I_{max}/I_{min}	1.09(0.04)	1.23(0.15)	1.27(0.13)
	F/H J		0.99(0.14)	0.96(0.15)
	Paired t-test J lnF/lnH		-0.53(0.15)	-1.06(0.16)
	F/H Z_{pol}		1.05(0.10)	1.04(0.10)
3.1 – 5.0	N	9	9	9
	I_{max}/I_{min}	1.15(0.08)	1.24(0.08)	1.15(0.05)
	F/H J		1.13(0.20)	1.20(0.19)
	Paired t-test J lnF/lnH		1.69(0.19)	3.15(0.16)*
	F/H Z_{pol}		1.15(0.13)	1.18(0.13)
5.1 – 10.0	N	26	26	25
	I_{max}/I_{min}	1.20(0.13)	1.30(0.13)	1.18(0.10)
	F/H J		1.28(0.25)	1.35(0.26)
	Paired t-test J lnF/lnH		5.34(0.22)**	6.69(0.21)**
	F/H Z_{pol}		1.26(0.17)	1.28(0.17)
10.1 – 15.0	N	8	8	8
	I_{max}/I_{min}	1.20(0.11)	1.27(0.16)	1.14(0.07)
	F/H J		1.36(0.13)	1.50(0.09)
	Paired t-test J lnF/lnH		8.32(0.10)**	19.37(0.06)**
	F/H Z_{pol}		1.30(0.08)	1.37(0.52)
15. 1 + adult	N	20	20	20
	I_{max}/I_{min}	1.29(0.14)	1.22(0.13)	1.18(0.10)
	F/H J		1.37 (0.20)	1.50(0.21)
	Paired t-test J lnF/lnH		10.13(0.13)**	13.48(0.13)**
	F/H Z_{pol}		1.32(0.17)	1.27(0.19)

t values given for paired t-tests (2-tailed) . Standard deviation in parentheses. *$p < 0.05$;** $p < 0.01$

Table IV.5 ANOVA comparisons of cross-sectional properties.

	F	df	*p*	*post hoc* analysis*
J				
LN F/H50	7.78	4	<0.01	A, Adol, J >> YI
LN F/H40	15.67	4	<0.01	A, Adol, J, >> YI; OI > YI A >> OI; Adol > OI
I_{max}/I_{min}				
LN F	6.54	4	< 0.01	A, J >> YI; A > OI
LN H50	1.71	4	0.16	
LN H40	2.57	4	0.05(0.046)	NS

post hoc $p < 0.05$; $p << 0.01$

A = adult, Adol = adolescent, J = juvenile, OI = old infant; YI = young infant

*Bonferonni tests used in all cases but LNF $I_{max}/I_{min}$where Tamhane test was used due to unequal variance between age classes.

CHAPTER IV FIGURES

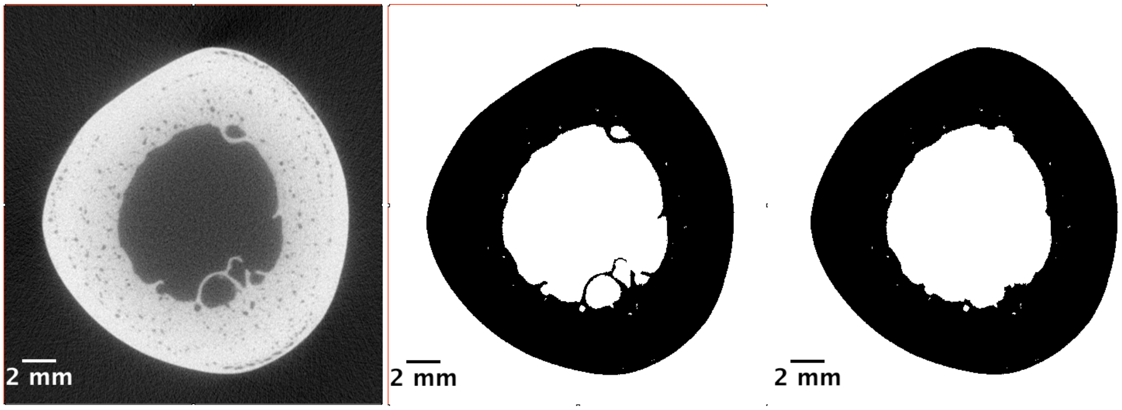


Figure IV.1 CT image of transverse cross-section of a subadult humerus at 50%.
From left to right 2D DICOM image of CT scan, thresholded, and cleaned.

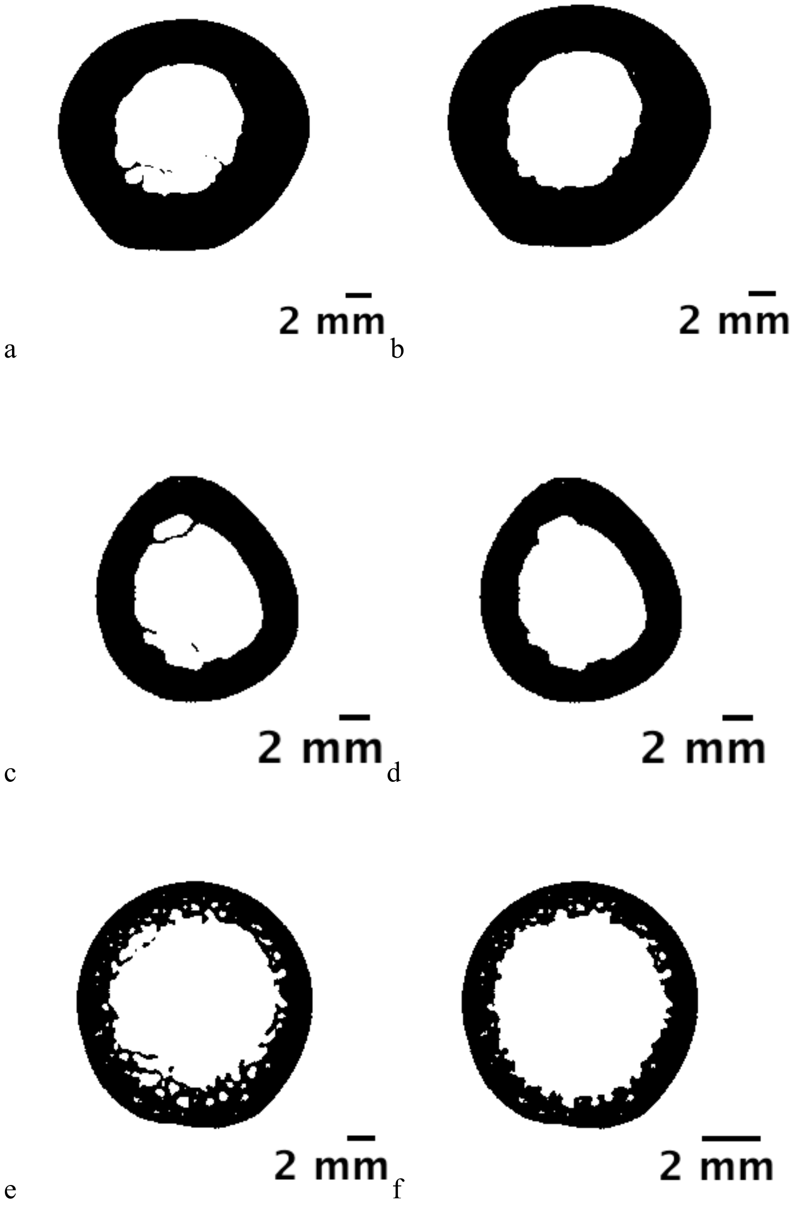


Figure IV.2 Binary images of transverse cross-sections of long bones at the midshaft pre (left) and post (right) cleaning of trabecular bone. a.b. Femur at 50% of an estimated 10.4 year old individuals. c.d. Humerus at 50% of an estimated 4.6 year old individual. e.f. Femur 50% of an estimated 0.6 year old individual (Images not scaled to one another).

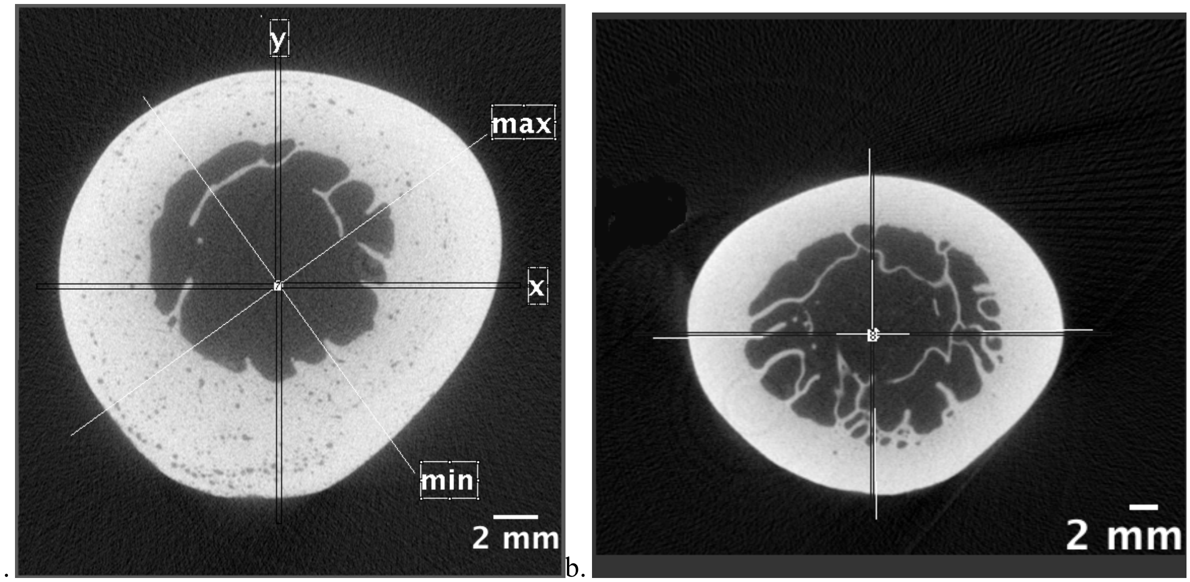


Figure IV.3 Anatomical and principle axis of CT transverse cross-section at the femur midshaft in two individuals. Anatomical axes x and y drawn in black while principle axes I_{max} and I_{min} drawn in white. In image a. the two axes vary considerably while in image b. they are nearly identical. (Images not scaled to one another).

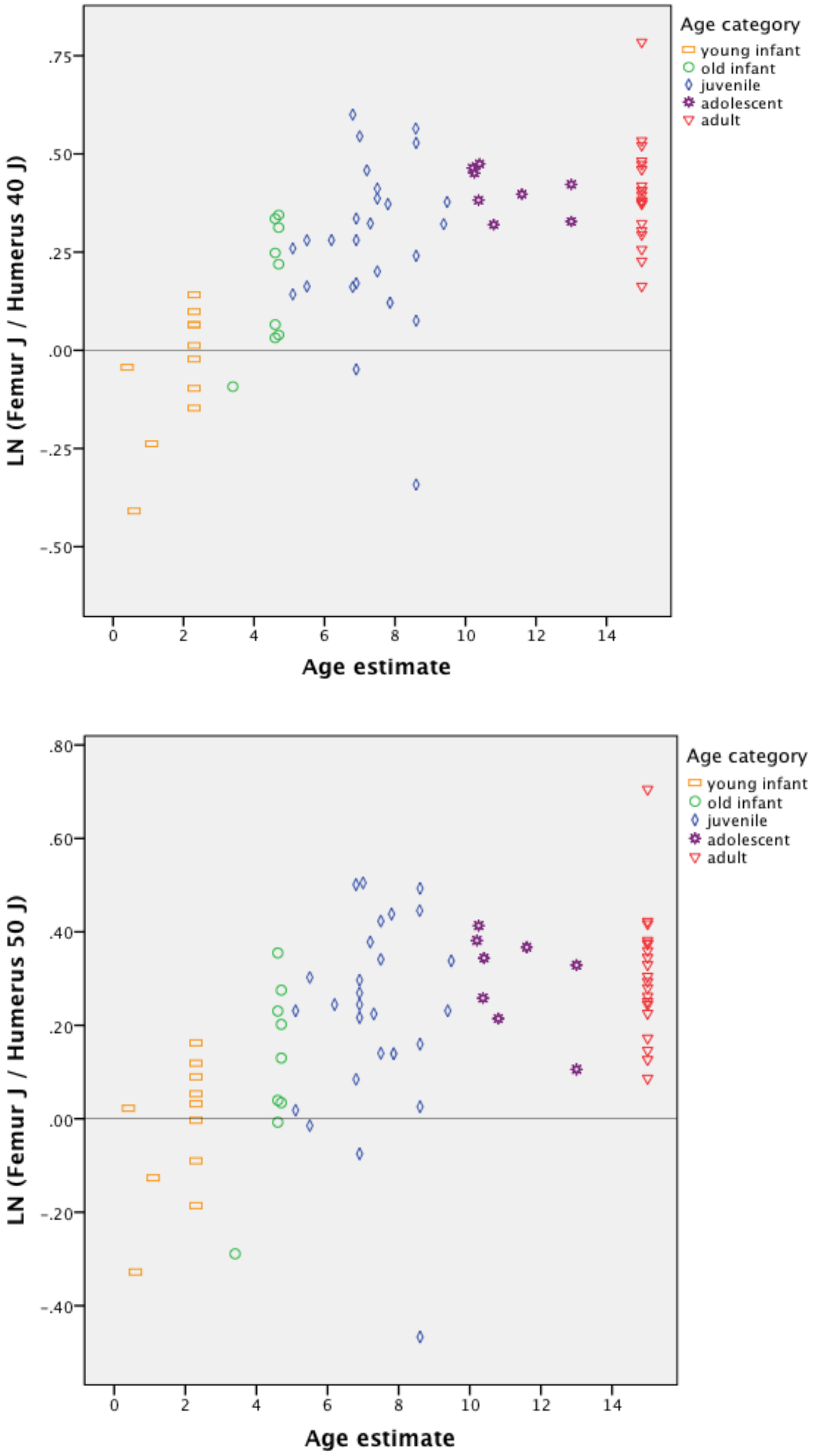
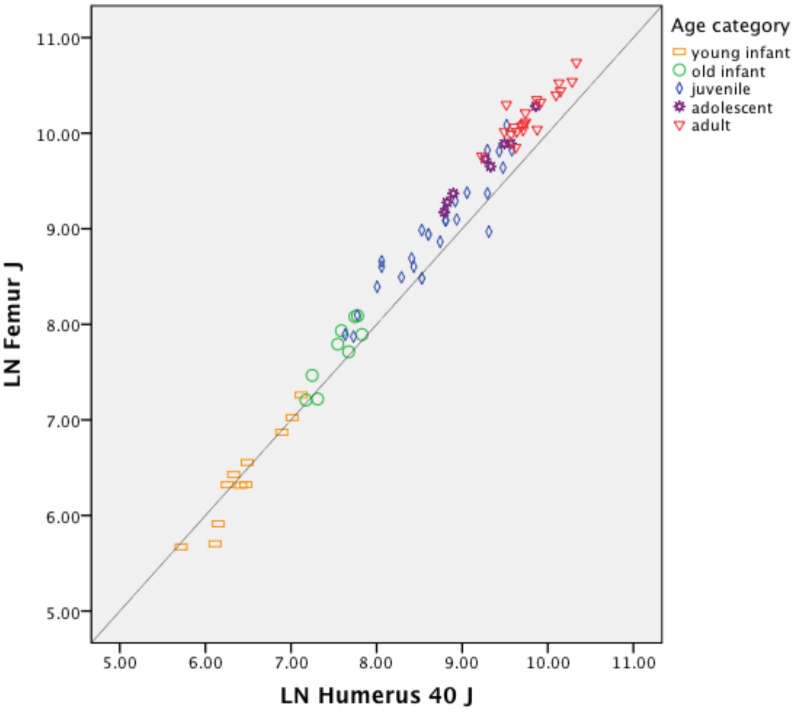


Figure IV.4 Femoral to humeral polar second moment of area ratio changes with age.

Ratio is of the natural log transformed. Colors depict different age classes. Top figure is with humerus at 40% and bottom figure is with humerus at 50%. Reference line for femur = humerus.



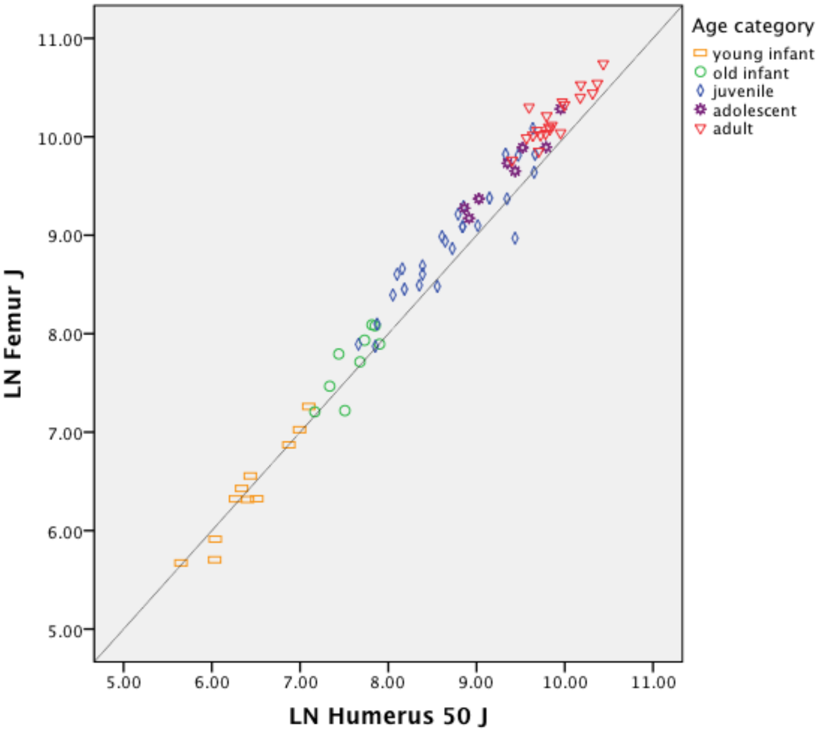


Figure IV.5 Femoral to humeral polar second moment of area for differently aged chimpanzees. Data are natural log transformed. Colors depict different age classes. Top figure is with humerus at 40% and bottom figure is with humerus at 50%. Isometric reference line for femur = humerus.

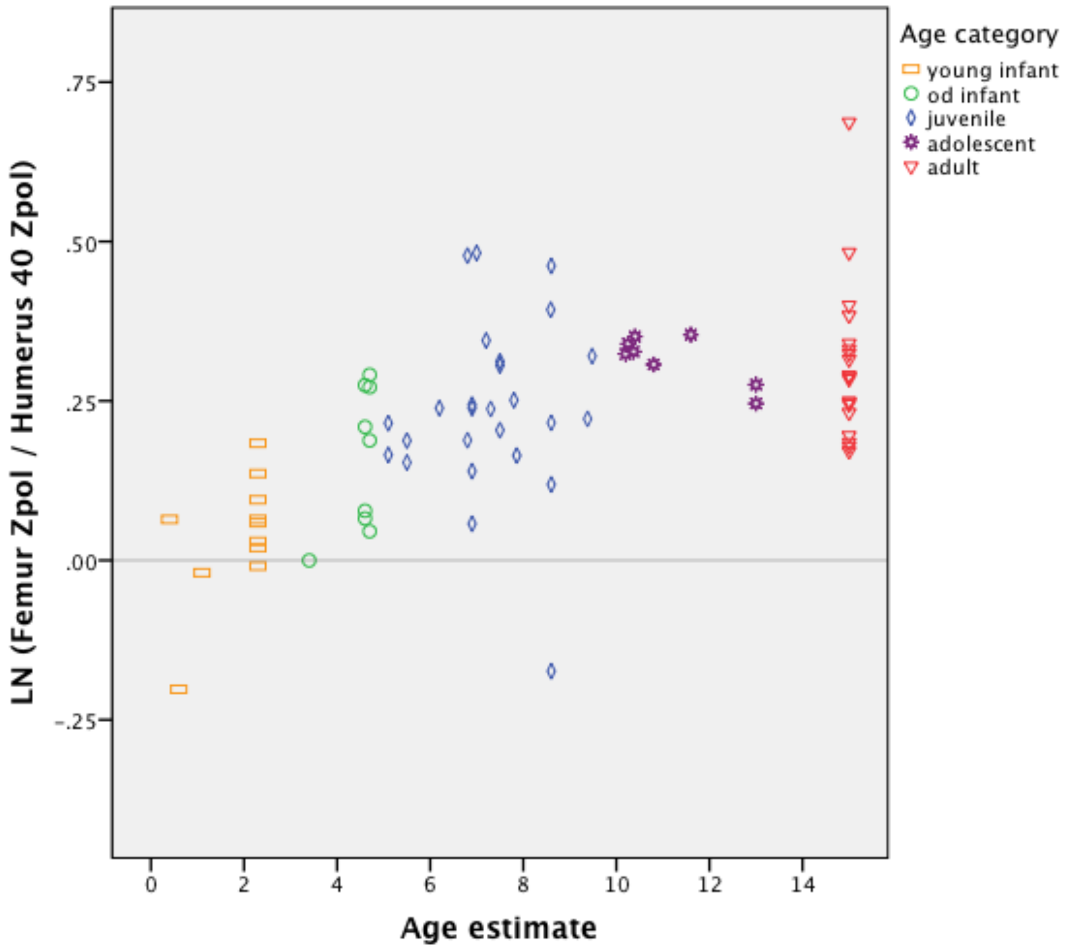


Figure IV.6 Femoral and humeral section modulus changes with age.

Data are natural log transformed. Colors depict different age classes. Reference line for femur = humerus.

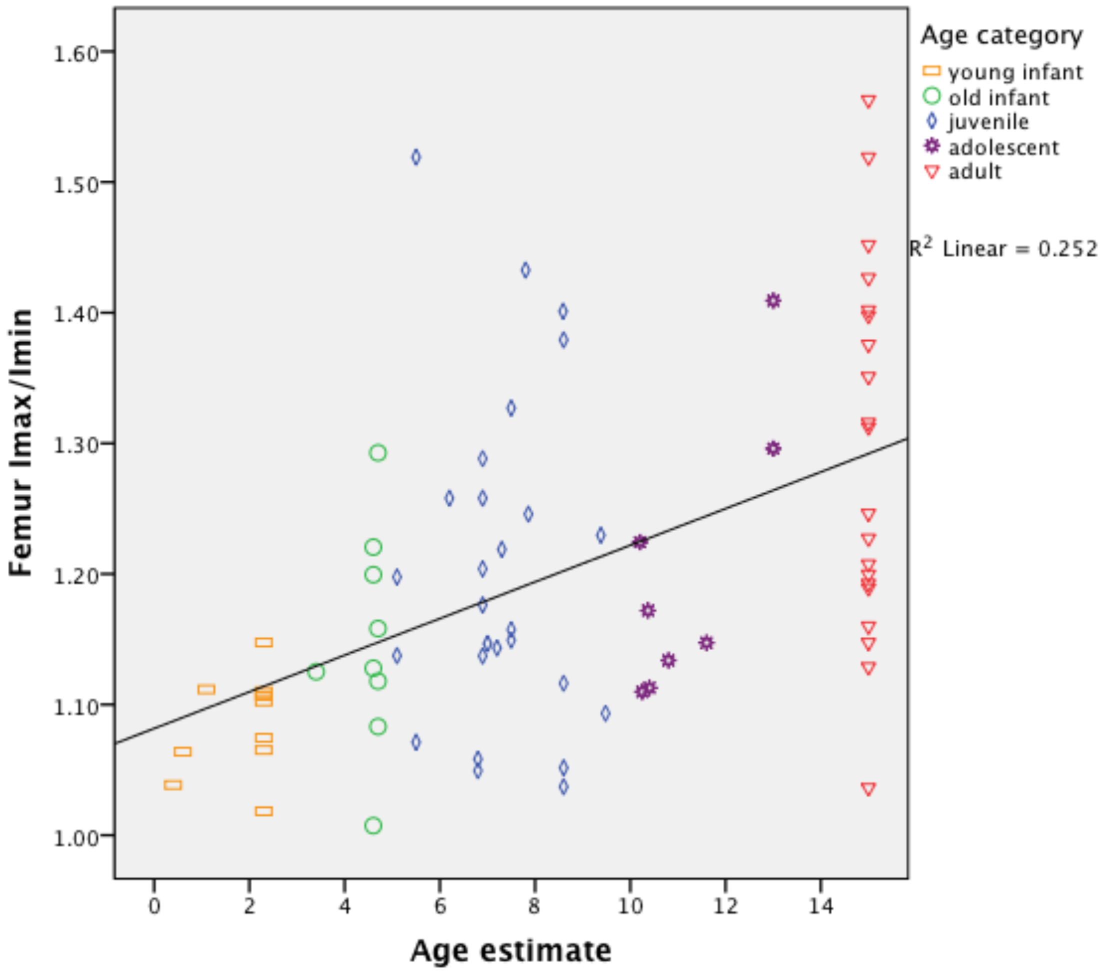
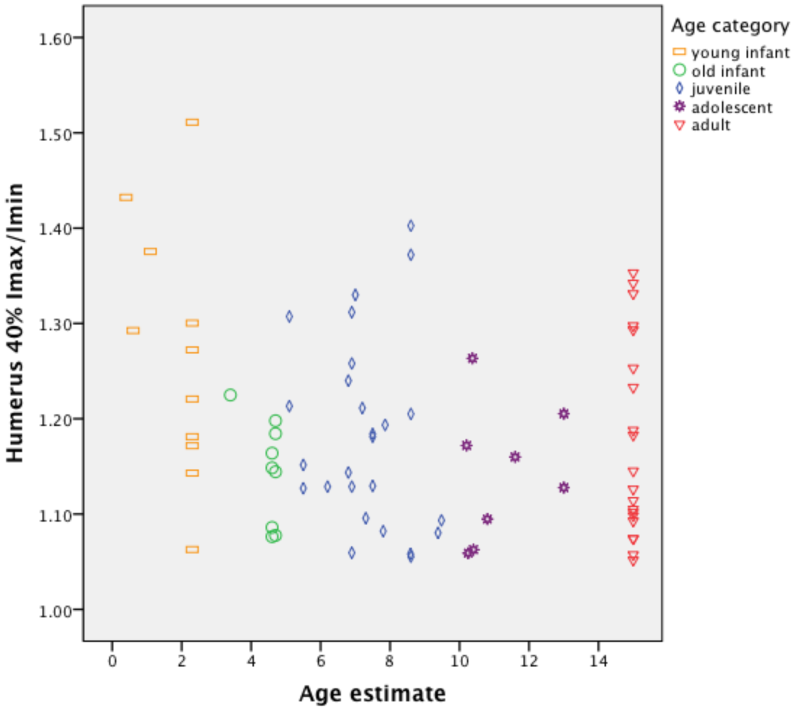


Figure IV.7 Femoral shape changes with age.
Colors depict different age classes. Linear regression line.



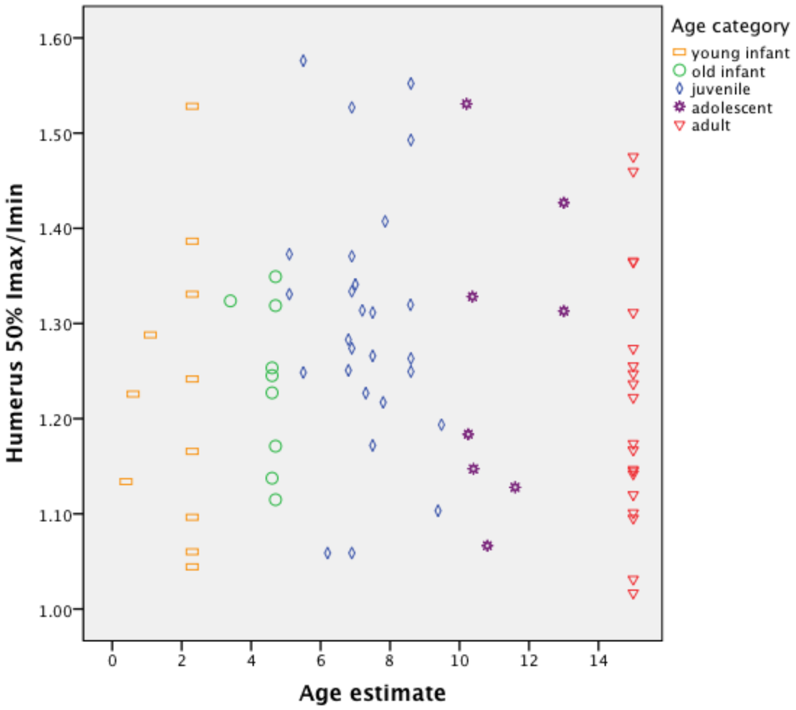


Figure IV.8 Humeral shape changes with age.

Colors depict different age classes. Top figure is with humerus at 40% and bottom figure is with humerus at 50%.

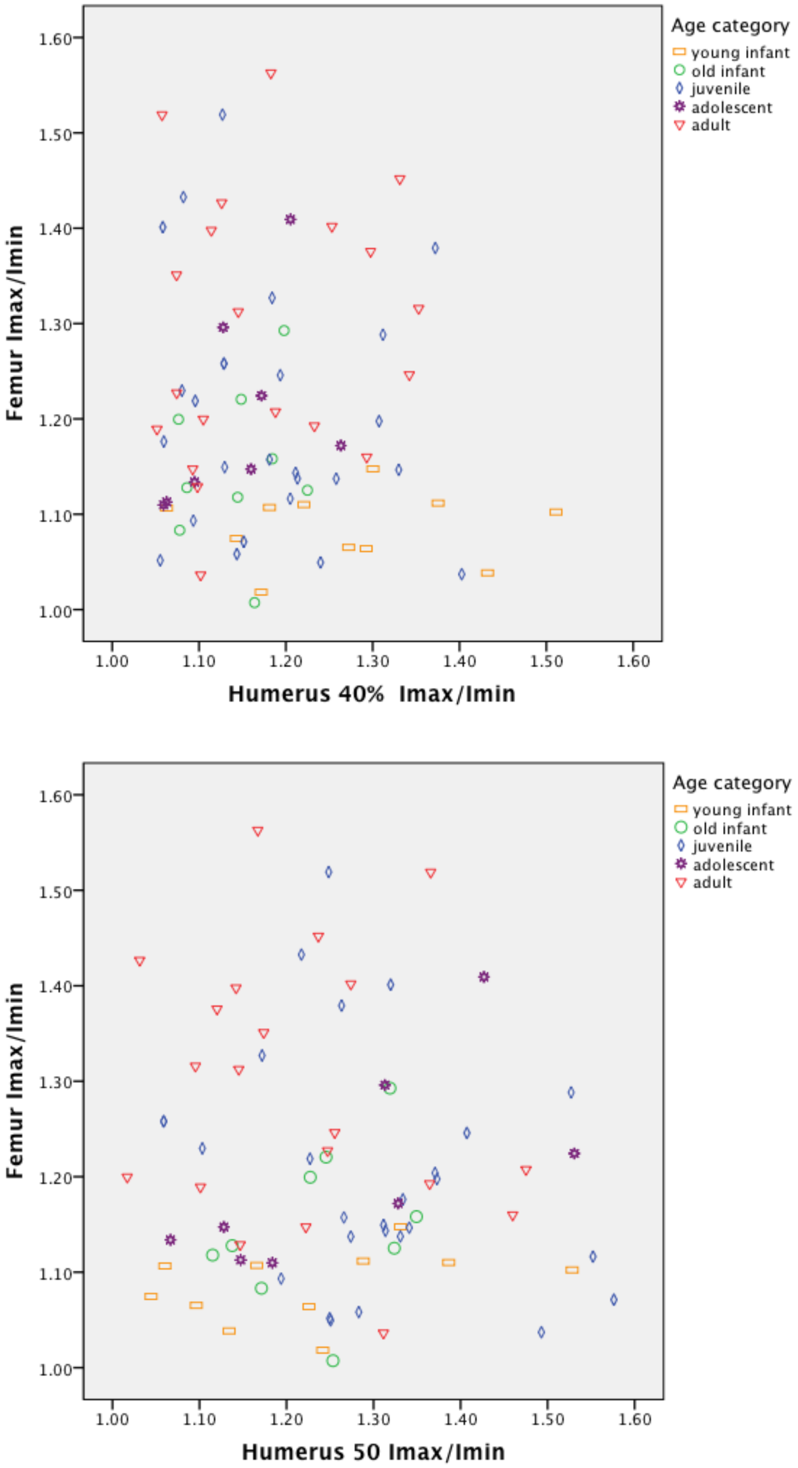


Figure IV.9 Femoral to humeral shape for differently aged chimpanzees.

Colors depict different age classes. Top figure is with humerus at 40% and bottom figure is with humerus at 50%.

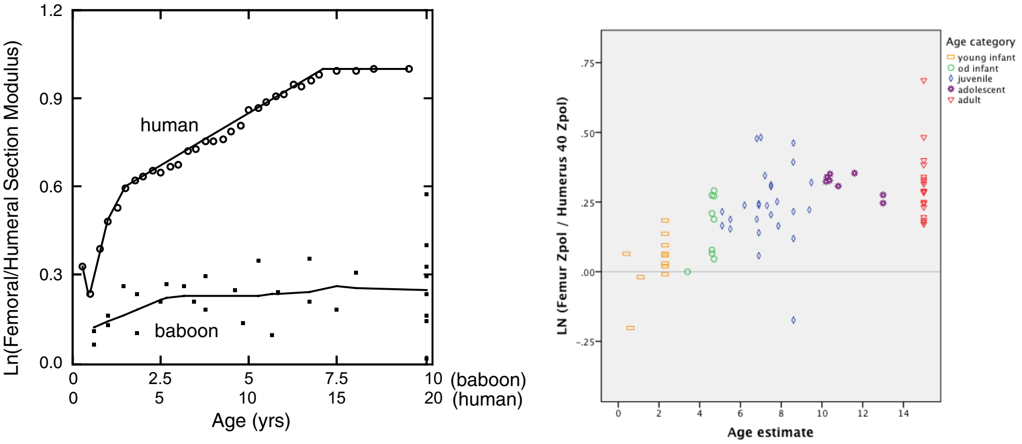


Figure IV.10 Comparison of results for Z_{pol} ratios and age.

Left graph from Ruff 2003a his Figure 11 on page 332. Used with author's permission. Showing femorur/humerus Zpol changes with age in humans and baboons. Points are age averages for humans and individuals for baboon sample. Right graph Figure IV.6 from this study.

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CHAPTER V

Conclusion

In order to better understand how function influences form, the behavior and morphology of developing chimpanzees were examined. This project sought to find morphological traits indicative of suspensory or knuckle-walking behavior that could then be used to infer the presence or absence of these behaviors in skeletal specimens. This was accomplished through analyzing observational and video data of the postural and locomotor behavior of wild chimpanzees and then analyzing morpholometric and CT data of wild-caught museum specimens. Morphometric analysis was conducted on the degree of third metacarpal curvature and distal metarpal ridge and CT analysis done on humerus and femur cross-sectional properties to compare how changes in morphology over the course of development corresponded to changes in behavior. Overall, a significant relationship was found between shifts in positional behavior and morphological changes over the course of development.

In Chapter II I showed that chimpanzee infants principally load their upper limbs in locomotion and that the loading environment changed to more hindlimb dominated locomotion as individuals aged. Infants displayed more diversity in their forms of positional behavior than did members of any other age-sex class, engaging in behaviors not habitually exhibited by adults at all. The most dramatic transitions in positional behavior occurred during juvenility and adolescence. In the juvenile period (at ~5 years), with the advent of complete independent locomotion, there was a drastic decrease in the amount of clinging and an increase in the time spent sitting; compared with subjuveniles. There was also a decrease in the amount of torso-orthograde suspensory locomotion and an increase in both quadrupedal walking and running. Relative to all younger individuals, adolescent chimpanzees (10-13 years) experienced a further decrease in the amount of time in torso-orthograde suspensory locomotion, but also vertical climbing, and orthograde forelimb suspension, and continued to increase the amount of time they walked quadrupedally.

I used the previous results from Chapter II to examine whether changes in morphology track changes in behavior. In Chapter III I found that the degree of metacarpal curvature in subadult chimpanzees, who knuckle-walk rarely and are often suspensory, is similar to that of subadult and adult orangutans who are predominantly suspensory. During this period of development, the distal metacarpal is also rounded with no raised ridge. The degree of metacarpal curvature and the distal metacarpal ridge angle increase as chimpanzees age and begin to knuckle-walk frequently. The metacarpals of knuckle-walking adult chimpanzees and gorillas are more curved than those possessed by primates that do not knuckle-walk, presumably in order to increase the predictability of stress transmission in the shaft. In addition, adult chimpanzees and gorillas possess ridges on their metacarpals that are not present in non-knuckle-walking species. Results of these analyses indicate that metacarpal curvature and distal metacarpal ridge angle are diagnostic features that can be used to determine whether fossil hominoid taxa were knuckle-walkers.

In Chapter IV I found that cross-sectional properties of the humerus and femur also changed during development with femur:humerus (F/H) strength ratios as well as femoral principal moment of area ratios increasing with age in chimpanzees. Young infants were found to have similar strength in the humerus and femur with a shift to significantly stronger femora occurring at the juvenile period. The infant femur was also more circular and able to resist loads from multiple directions (i.e. as consistent with more diverse loading from arboreal behaviors) compared to the more elliptical midshaft of adults. However, the general relationship between anatomical and behavioral changes is more subtle in long bone cross-sectional properties than that observed with the metacarpal in Chapter III, reflecting overall locomotor trends in the species but not fine grain shifts between age classes with regard to specific locomotor mode shifts. Furthermore, ontogenetic trends in shape were also quite disparate between the femoral and humeral midshaft leading to further questions on the nature of the determinants of midshaft shape.

The findings presented here show that chimpanzee positional behavior proceeds developmentally through a number of distinct stages, each characterized by its own loading regime. Overall, the growing bones of chimpanzees track locomotor transitions. Specifically, the more arboreal, suspensory infants have straight metacarpals with no distal ridge, rounded femoral midshafts, and humeri and femora equally able to bear loads. The more terrestrial and quadrupedal adults have curved metacarpals, prominent DMR angles, elliptical femora, and proportionally stronger hindlimbs than forelimbs. Metacarpal morphology was found to be a more sensitive gauge of locomotor transition timing compared to cross-sectional properties. This is likely because metacarpal morphology is primarily influenced by one behavior, knuckle-walking, while strength and shape changes in response to several, sometimes opposing, forces created by a suite of different positional modes.

APPENDIX

Appendix A. Average dental eruption age for wild chimpanzees (5% added to Smith numbers)

Chimpanzee tooth	i1	i2	p3	p4	dc	M1	I1	I2	M2	P3	P4	C	M3
Female Upper						3.43	5.92	7.13	7.09	7.31	7.84	9.48	11.90
Female Lower						3.35	6.13	6.35	6.77	7.69	7.96	9.06	11.25
Male Upper						3.55	5.90	7.01	7.16	7.28	7.59	9.42	11.93
Male Lower					1.00	3.50	5.93	6.53	6.79	7.75	7.76	9.70	10.78
All Upper	0.26	0.35	0.40	0.84	1.07	3.49	5.91	7.07	7.12	7.29	7.72	9.45	11.91
All Lower	0.27	0.38	0.41	0.79	1.18	3.43	6.03	6.44	6.78	7.72	7.86	9.38	11.01