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Metacarpal Ratio and Its Relation to Sexual Dimorphism in Primates with Different Mating Strategies

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METACARPAL RATIO AND ITS RELATION TO SEXUAL DIMORPHISM IN PRIMATES WITH DIFFERENT MATING STRATEGIES

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ABSTRACT

The digit ratio (2D:4D) is a sexually dimorphic trait in mammalian hands that is a result of levels of prenatal androgen exposure (PNAE) during limb development. Previous studies have shown that females have a higher ratio than males and that sexual dimorphism in the ratio is greater in species with polygynous mating strategies and high levels of intermale aggression compared to monogamous species with low intermale aggression. This study used metacarpals instead of phalanges to test the hypotheses that the metacarpal ratio (2Mc:4Mc) will be higher in females than males within a species and that the ratio would be more sexually dimorphic in species with high intermale competition compared to species with low intermale competition. Intermale competition is defined as the frequency and intensity of aggression found in adult males within a species. Second and fourth metacarpals were measured on skeletonized animals for six species with different mating strategies (M=monogamy; P=polygyny) and levels of intermale aggression (H=high; I=intermediate; L=low; F=female; M=male). All animals used in the study were designated by the museum as wild-caught. Sample sizes for each species including mating strategy and level of intermale aggression were as follows: *Aotus azarae* (M,L; 9F, 11M), *Hylobates lar* (M,L; 49F, 51M), *Presbytis rubicunda* (P,I; 18F, 19M), *Trachypithecus cristatus* (P,I; 31F, 18M), *Alouatta seniculus* (P,H; 17F, 19M), and *Macaca fascicularis* (P,H; 19F, 18M). Results comparing medians fail to reject the null hypotheses that the metacarpal ratio is the same between sex within the species and the ratios will be the same regardless of competition level. The sexes are non-significantly different in metacarpal ratio in *A. seniculus*, *A. azarae*, *H. lar*, and *M. fascicularis*; males have a significantly higher ratio than females in *P. rubicunda*, but females have a significantly higher ratio than males in *T. cristatus*. Results are not

consistent with previous research on digit ratios indicating that metacarpals and phalanges may

respond differently in their growth and PNAE.

CHAPTER 1. INTRODUCTION

Sexual dimorphism is a characteristic found in different organisms that can be associated with different social behaviors such as aggression and mating strategy. These characteristics can be seen in canines, body size, and dichromatism. One characteristic that has been the recent subject of much research is the ratio of the 2nd to the 4th digit (2D:4D) of the hand which is used to interpret the extent of prenatal androgen exposure (PNAE) during limb development. This ratio is computed by dividing the length of the second digit by the length of the fourth digit. Ratios that are closer to 1.0 are found in females while ratios less than 1.0 are found in males (Manning et al., 1998). These sexually dimorphic ratios can also be found in the digits in the feet, although most studies focus on the ratios in the hand.

Manning et al. (1998) were among the first to determine that there was a relationship between prenatal hormonal influences and the 2D:4D ratio and that this relationship is instrumental in the understanding of testosterone levels within individuals. The low 2D:4D ratio characteristic of males indicates higher levels of PNAE in osteogenesis (Nelson and Shultz, 2010). This low 2D:4D ratio has since been linked to increased intrasexual competition and high levels of aggression among males within a species (Bailey and Hurd, 2004; Benderlioglu and Nelson, 2004; Hönekopp et al., 2005). This thesis examines these relationships using metacarpals to determine the metacarpal ratio (2Mc:4Mc ratio) instead of the phalangeal ratio with the assumption that the metacarpal and the phalangeal development occurs during the same period of exposure to androgens.

This study is a comparative analysis of metacarpal ratios in six species of primates. Since sexual dimorphism is increased in canine and body size in species with high intermale competition and decreased in low intermale competition (Nelson et al., 2011), this dimorphism

can be tested in the hand bones. The questions that this study addresses are: 1) is there a sexual difference in the 2Mc:4Mc ratio as in the 2D:4D ratio, and 2) is the intraspecific level of intermale competition (or alternatively, mating strategy) associated with this ratio? In accord with results for the 2D:4D ratio, the hypothesis in this study is that females will have a higher 2Mc:4Mc ratio than males of species with high intermale competition (i.e., polygynous species), whereas the sexes will not differ in 2Mc:4Mc ratio in species with low intermale competition (i.e., monogamous species). The difference between the sexes is also expected to be greater in species with higher intermale competition than species with low intermale competition. The species used in this study are: *Alouatta seniculus* (Venezuelan red howler), *Aotus azarae* (Azara's night monkey), *Hylobates lar* (lar gibbon), *Macaca fascicularis* (crab-eating macaque), *Presbytis rubicunda* (maroon leaf-monkey), and *Trachypithecus cristatus* (silvery lutung). These specific species were chosen for their representation of the Competition Levels used for this research and their availability within museum collections.

Metacarpals are used instead of phalanges to determine whether they too show sexual dimorphism in relative lengths. McFadden and Bracht (2005) measured gorilla and chimpanzee metacarpals and found that the sex differences in the digit ratios are larger than the differences in the metacarpals but that the difference is still measurable justifying this research. McFadden and Bracht (2005) hypothesized that the variation in the differences was attributed to the digit and metacarpal growth being influenced by different mechanisms at different times during fetal development. In addition to the use of metacarpals, metatarsals will also be used because research measuring metacarpals and metatarsals found differences in both metapodials (McFadden and Bracht, 2003; 2005). This research analyzes the effect of intermale competition

and sex on the 2Mc:4Mc and 2Mt:4Mt ratios and does not include or control for potential factors such as interfemale competition, geographic region, locomotion, and body size.

1.1 Focus of this research

This research will evaluate whether there is a relationship between social behavior and 2Mc:4Mc ratios within six primate species. In species with high intermale competition such as *A. seniculus* and *M. fascicularis*, the female 2Mc:4Mc ratio is expected to be greater than that of the male 2Mc:4Mc ratio. This study will test whether the same sexual dimorphism based on mating strategies in the phalanges is seen using metacarpals and metatarsals. Since this study compares the extent of the sexually dimorphic ratio in the metapodials between different intermale competition levels, the species with the same competition levels as predetermined by Plavcan and van Schaik (1992) are expected to have similar ratio differences between sexes in their metapodials. If results are consistent with research on 2D:4D, then use of metacarpals or metatarsals will facilitate future research into the relationship among prenatal exposure to androgens, skeletal development, and social behavior because the number of specimens in museum collections with usable and identifiable metapodials is far greater than specimens with usable and identifiable phalanges. However, if results are not consistent with those based on the digit ratio, the important issue is to explain why metapodial development differs from that of phalanges.

Other researchers have found significant sexually dimorphic patterns in different metacarpal ratios. For gorillas, McFadden and Bracht (2003) found that the largest sex difference was in the 4Mc:5Mc ratio for both hands. For chimpanzees, the largest sex difference was in the 2Mc:3Mc ratio only in the left hand, and for baboons the largest differences were in the 3Mc:5Mc and the 4Mc:5Mc ratios in the right hand (McFadden and Bracht, 2003). While the

2D:4D ratio is known to show a significant difference in humans, another metacarpal ratio that has a difference is the 2Mc:5Mc in the left hand (McFadden and Bracht, 2002). Tague (2002) also found sex differences in the 3Mc:4Mc ratios although he did not specifically look for sex differences in ratios with his research on metacarpal lengths. Because the difference between the sexes in these ratios was considered meaningful in other research, this study will test all ratios in the metacarpals to determine whether another metacarpal ratio was sexually dimorphic relative to level of intermale competition.

Using the identification of levels of intermale competition outlined by Plavcan and van Schaik (1992), the species were grouped into three categories: Competition Level 1, Competition Level 3, and Competition Level 4. Plavcan and van Schaik's (1992) system put the species in their study on a spectrum based on the frequency and intensity of intermale aggression and found a positive correlation between this behavior and canine dimorphism. Type 2 will not be used for this research because of small available sample sizes.

The first competition level (Type 1) can be identified as monogamous with little to no intermale aggression within the species. The second competition level (Type 2) is a multiple male and multiple female society but with low intermale aggression. Competition Level 3 (Type 3) consists of species with multiple males and multiple females with seasonal intermale competition. Competition Level 4 (Type 4) consists of polygynous species with heightened intermale competition throughout the entire year. There is expected to be a gradient in the 2Mc:4Mc (and 2D:4D) ratio difference between females and males, with no significant difference in Type 1 species, a slight difference in Type 3 species, and the largest difference in Type 4 species. Based on Plavcan and van Schaik (1992), the species in this study classified by

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competition level are as follows: Type 1: *A. azarae* and *H. lar,* Type 3: *P. rubicunda* and *T. cristatus*, and Type 4: *A. seniculus* and *M. fascicularis*.

CHAPTER 2. THEORETICAL BACKGROUND

The foundational research that led to the examination of the relationship between digit length and exposure to prenatal androgens was conducted more than 50 years ago. In this research, Phoenix et al. (1959) exposed female guinea pigs to androgens which in turn "masculinized" the guinea pigs' behavior. Phoenix et al. (1959) concluded that PNAE alters the normal expected behavior in adult guinea pigs. In another research project, Goy and Phoenix (1972) removed the testes of a male rhesus monkey after the second trimester of prenatal development, which is the time of heightened androgen exposure, and found that despite the absence of the male testes, the postnatal rhesus monkeys continued normal levels of male play behavior but less mounting behavior. The results from this early research and other research mentioned later in this literature review emphasize the importance in learning more about sex hormones and behavior which has the potential to increase our understanding of the proximate causes behind social bonding, aggression, and other behaviors (Nelson and Shultz, 2010).

Robertson et al. (2008) conducted a study on the 2D:4D ratio and 2Mc:4Mc ratio in humans. Their results showed an average 2D:4D ratio of 0.908 for males and 0.922 for females with a standard deviation of 0.02 for both sexes with a statistical significance of $p<0.01$ and an average 2Mc:4Mc of 1.152 for males and 1.157 for females with a standard deviation of 0.03 for both sexes and a p-value of 0.01 (Robertson et al., 2008). Robertson et al. (2008) stated that metacarpals were advantageous over phalanges because of "finger problems" such as interphalangeal joint osteoarthritis and other trauma. They were able to use a larger sample size of metacarpals than phalanges of the same population, with 99% of usable metacarpals compared to 84% of usable phalanges in a sample size of 3172 participants (Robertson et al., 2008). One

difference between the current study and Robertson et al.'s is that this study will include the categorical variable of intermale competition in the analysis.

2.1 Prenatal fetal development and testosterone

The sexually dimorphic characteristics in the 2D:4D ratio are established during prenatal development based on exposure to androgens. This difference in the ratio is first evident in humans as early as the ninth week of fetal development, is established by week 14, and is sustained throughout puberty (Malas et al., 2006; Manning, 2002; Nelson and Shultz, 2010; Shaw et al., 2012). The production of testosterone in fetal development is at maximum capacity in week 13, which is before the establishment of the sexual difference in the ratio (Malas et al., 2006; Manning, 2002; Nelson and Shultz, 2010; Shaw et al., 2012). The temporal association between the establishment of sexual dimorphism in the 2D:4D ratio and heightened testosterone secretion suggests a causal relationship.

Some structures of the body develop as a suite, independently of other structures. This is a concept known as modularity (Callebaut and Rasskin-Gutman, 2005). The presence of testosterone during a critical period of fetal development can change reproductive structures to male-like structures and sensitize the brain to male hormones, while the absence of testosterone can change the structures to female-like structures and sensitize the brain to female hormones (Mitchell, 1979). While this period can vary in different mammalian species, in monkeys it occurs during the 19th day for reproductive tissues and 46th day for the brain of fetal development (Mitchell, 1979; Neuman et al., 1970).

The whole limb bud is a module, developing at the same time independently from the rest of the body (Raff, 1996). Therefore, the metacarpals may be influenced by the same hormonal stimuli as the digits, but the second and fourth digits seem to differ in their interaction with

androgen and estrogen exposure. In the fourth digit, the androgen receptors increase the length while estrogen receptors decrease the length (Howlett et al., 2015). Therefore, the length of the fourth digit is dependent on the balance of androgen and estrogen exposure beginning at the ninth week of development for humans. Generally, males are exposed to more testosterone and less estrogen (i.e., resulting in a longer fourth digit) while females are exposed to more estrogen and less testosterone (resulting in a shorter fourth digit), which creates the sexually dimorphic 2D:4D ratio. The fourth digit can then be identified as the defining factor of the sexually dimorphic 2D:4D ratio.

Berenbaum and Beltz (2011) made an interesting connection between hormones and development. They argued that social experience can cause hormone deficiencies in individuals (Berenbaum and Beltz, 2011). They identified this effect from social experience as something that occurs at puberty; however, there could be lasting epigenetic effects on the individual because of this hormone deficiency. Primate adults have behavioral patterns that are strongly correlated with their reproductive system creating sexually differentiated behavior. According to Neuman et al. (1970), these behaviors are affected by estrogens and androgens which are sex-specific hormones. This relationship with androgens and behavior could be indicative of social experiences being an influence on the growth and development of an individual.

More specifically, Berenbaum and Beltz (2011) were able to ascertain the relationship between testosterone and growth during fetal development. They found that the difference between the sexes begins in early development and finishes at puberty; however, social and biological experiences could influence this development as they could cause hormone deficiencies at puberty (Berenbaum and Beltz, 2011). Berenbaum and Beltz's research shows that sexual differentiation is existent before puberty, the time when there is the highest lifetime

amount of secretion of estrogen or testosterone excluding pregnancy. Thus, studying characteristics that are evident in prenatal development should be further researched to better understand the prenatal androgen levels in different species prior to the influences of social experiences.

The masculinized digit ratio (low 2D:4D ratio) has been found in human fetuses that have high levels of amniotic testosterone (Lutchmaya et al., 2004; Nelson and Shultz, 2010). Interestingly, van Anders et al. (2006) stated that in a study on dizygotic twins, females with a male twin have a lower 2D:4D ratio (masculine ratio) than females with a female twin, which was attributed to hormone-transfer during development and not postnatal behavior associated with females growing up with male co-twins. The amniotic testosterone levels have also been found to affect postnatal growth and metabolism (Manikkam et al., 2004; Smith et al., 2010; Wolf et al., 2002). In other research on amniotic levels of testosterone, Resko (1974) found higher levels of testosterone in the umbilical artery in normal male rhesus monkey fetuses than normal female fetuses. This was to be expected; however, he also performed an experiment in which he castrated male rhesus monkey fetuses on day 100 of gestation (during week 14, which is when digit ratio is fixed) and found that this did not affect the testosterone level of these male fetuses compared to normal male fetuses (Resko, 1974). This is significant because it shows that prenatal testosterone levels are secreted prior to the fixation of the digit lengths.

2.1.1 Uterine environment and its effect on the fetus

As previously stated, the uterine environment influences many aspects of the embryo during integral periods of development. The method of examining hormones in the amniotic fluid and relating them to postnatal behavior was first conducted by Finnegan et al. (1989). Finnegan et al. (1989) used amniocentesis during the second trimester and concluded that

hormone levels of the fetus were not determined by the fetal sex. In a study conducted on

Callithrix geoffroyi (white-headed marmoset) to determine the relationship between a mother's

level of testosterone and the level in her offspring during prenatal and postnatal development,

Smith et al. (2010) found that changes in maternal androgen levels can affect prenatal and

postnatal growth rates. The maternal androgens that are exposed to the fetus are not influenced

by the fetal sex both in marmosets and in humans (Glass and Klein, 1981; Meulenberg and

Hofman, 1991). Smith et al. (2010) found that this influence depended on the life stage the infant

was in when exposed to the androgens. For example, marmoset mothers with high levels of

androgens during their first trimester gave birth to smaller infants with slower growth rates than

mothers with low levels of androgens (Smith et al., 2010), showing the significance of maternal

androgens during the first trimester. The marmosets made up for this decreased growth during

late infancy and with an increased growth rate as juveniles (Smith et al., 2010). The evidence in

this research shows that growth rates of individuals at different life stages, whether prenatally or

postnatally, depend on the androgen levels of the mother during the first trimester of their

pregnancy, which is the same trimester in which the limbs develop. The relationship between

maternal androgens and fetal development shown in Smith et al. (2010) indicates that the first

trimester is an integral time in development relating to hormones that have organizational effects

on the individual.

2.1.2 Masculinization and feminization as a result of hormones

Digit growth in mammals is determined by the levels of androgens and estrogens secreted

during fetal development along with activational effects during postnatal development. During

normal fetal development for males, testosterone is synthesized from the Leydig cells of the

interstitial testicular tissue which leads to male secondary sex characteristics, masculinized

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behavior, and spermatogenesis (Manning, 2002; Smith et al., 2010). Exposure to high prenatal testosterone stimulates the growth of the fourth digit creating a more masculine ratio, whereas exposure to prenatal estrogen reduces the growth of the fourth digit resulting in a more feminine ratio (Howlett et al., 2015; Manning, 2002). The relationship between the two receptors for testosterone and estrogen determines the sexual dimorphism in this ratio, with a positive relationship between testosterone receptors and the length of the fourth digit and a negative relationship between estrogen receptors and the fourth digit. Therefore, the extent of the sexual difference in the ratios in different species should indicate the interspecific differences in number of androgen and estrogen receptors which can then be used for further analyses on the behavior of these animals.

Hormones can have masculinizing effects on individuals that could permanently influence their growth and development. One example is through Congenital Adrenal Hyperplasia (CAH). CAH is an autosomal recessive disorder that is caused by an enzyme defect that affects cortisol production, thus resulting in high levels of prenatal androgen exposure (Berenbaum and Beltz, 2011). The common case of a person with CAH has a deficiency of the 21-hydroxylase enzyme which negatively affects cortisol synthesis (Mathews et al., 2009; New, 1998). The enzyme deficiency increases androgens by inhibiting cortisol synthesis through the adrenal cortex, thus preventing androgens from converting into cortisol (New, 1998). This causes an overall increase in androgen production, creating a more masculinized effect because of this decrease in cortisol secretion (Mathews et al., 2009). Mathews et al. (2009) found that CAH in both male and female individuals alters sex-specific behaviors. Also, women with CAH have a masculinized 2D:4D ratio caused by them being exposed to an increased amount of prenatal androgen hormones (Shaw et al., 2012). There is also evidence that the ratio of testosterone to

progesterone to which a fetus is exposed can affect their sexual differentiation (Mitchell, 1979; Resko, 1974). In addition to CAH, another indicator of imbalanced hormones is polycystic ovarian syndrome (PCOS), whose symptoms include hyperandrogenism which causes women to give birth to smaller offspring at gestational age (Smith et al., 2010). As previously discussed, this could influence the growth rate of the individual and shows the effect of maternal androgens on the fetal growth. Also, men born with androgen insensitivity have a feminized 2D:4D ratio indicating the relationship between hormonal imbalance and digit length is evident in men (Shaw et al., 2012).

Sex-specific hormones play a part in organizing the brain and the body (Nelson and Shultz, 2010). Therefore, feminine hormones can also influence certain aspects of the brain and the body. One such influential hormone is progesterone. According to Resko (1974), there are higher levels of progesterone in the umbilical vein and artery of female fetuses than found in male fetuses which act as an antagonist to androgens. Thus, more progesterone means less androgen (Mitchell, 1979). Because of this negative correlation, progesterone could have an indirect effect on the influences that different androgens have on the growth and development of the fetus.

Growth and development of an individual are affected by testosterone sensitivity and insensitivity. This sensitivity peaks at perinatal development, declines throughout puberty and ends in late adolescence/early adulthood (Berenbaum and Beltz, 2011). The time between birth and puberty is also influential on the later development of the individual. The previous research on marmoset growth conducted by Smith et al. (2010) emphasizes that maternal androgens affect prenatal and postnatal growth rates and shows that this sensitive period can influence the growth and physiology of the individual.

2.2 Genetic effects

The codon, CAG, repeats on exon 1 of the androgen receptor gene, and more CAG repeats on the exon causes an increased insensitivity to androgens during development (Shaw et al., 2012). Manning et al. (2003) tested the correlation between CAG repeats and 2D:4D ratio and concluded that the sensitivity resulting from the number of CAG repeats can partially explain the 2D:4D ratio. The repeats of CAG and 2D:4D ratio have a positive allometric relationship, meaning that the more CAG repeats there are on the androgen receptor, the higher the 2D:4D ratio because the cells are less responsive and, therefore, more insensitive to androgens keeping the fourth digit shorter (Manning et al., 2003).

2.2.1 Homeobox genes

Modules are evident in the osteological structures and respond the same way to the same stimulus in development. One of these modules is the distal zeugopod/posterior digit module, as suggested by Reno et al. (2008), which is regulated by *Hoxd11* of the group of homeobox genes (Reno et al., 2008). The modules are regulated through different *Hox* genes. *Hox* genes affect the overall pattern of development by regulating the digits and testes based on different extents of androgen sensitivity in the *Hox* gene clusters (Manning et al., 1998; Manning, 2002; Reno et al., 2008). However, knowledge is limited regarding the exact targets of *Hox* gene expression (Reno et al., 2008).

This research will focus on the *Hoxa* and *Hoxd* genes, as they are associated with the organization of the distal zeugopod and regulate parts of the reproductive system including the gonads and the penis which are all associated with testosterone levels within an individual (Nelson and Shultz, 2010). Additionally, these *Hox* genes regulate the mesenchyme allocated to the growth of digits which could induce a reduction or an increase in the length of the digits

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(Tague, 2002). *Hox* gene expression in the distal limbs is divided into separate phases. In the first phase, as outlined by Reno et al. (2008), the zeugopod is organized (Tarchini and Duboule, 2006) and then, in the second phase, the *Hoxd* genes pattern the digits (Reno et al., 2008; Spitz et al., 2003). Reno et al. (2008) believe that since there is a strong correlation between *Hox* gene expression and limb development, then any research into the evolution of mammalian limbs should consider the influence of these genes and their "downstream targets."

In the zeugopod, *Hoxd11*, *Hoxd12*, and *Hoxd13* are the only *Hox* genes known to influence the posterior digit morphology (Reno et al., 2008). For example, a posterior extension of *Hoxd13* expression has shown to expand the wing of a bat (Chen et al., 2005). Also, deletion of *Hox* genes negatively affects the development of the distal zeugopod. If *Hoxd12* and *Hoxd13* are deleted, then *Hoxd11* action is unmodified and causes deformations in the wrist and hand such as partially fused metacarpals and shortened phalangeal lengths (Kmita et al., 2002; Reno et al., 2008). Another example of how *Hox* genes can affect development is through complete ablation of *Hoxa11* and *Hoxd11*, which Davis et al. (1995) have shown to result in the appearance of shorter radii and ulnae.

While complete ablation of these *Hox* genes shortens bones, an increase in *Hox* gene dosage can also influence bone lengths, as seen with *Hoxd11* and *Hoxd13* (Boulet and Capecchi, 2002; Reno et al., 2008). Altered expression of *Hoxd11* in mutated mice caused reductions in metacarpals and phalanges (Davis and Capecchi, 1996). The *Hox* dosage influences the length of metacarpals and phalanges as shown in experiments with mice (Boulet and Capecchi, 2002). This experiment showed that there is a relationship with *Hox* genes and metacarpal/digit growth in mice. This difference in the amount of *Hox* gene dosage among different species could explain the specialization of different digits in the hands of some primates (Reno et al., 2008). *Hoxa* and

Hoxd expressions are significant because they control different anatomical features that essentially include the positional identity of the feature's function and, most importantly, they control cell adhesion and proliferation that specify the anatomy of the limbs (Reno et al., 2008). In research altering *Hoxd11* and *Hoxd13* on mice, when mutated to be homozygous, the *Hoxd13* mice had shorter metacarpal lengths, missing phalanges, and deformed carpals (Davis and Capecchi, 1996) while *Hoxd11* mice had reduced lengths in the metacarpals and phalanges carpals (Davis and Capecchi, 1996; Reno et al., 2008). Reno et al. (2008) conclude that *Hoxd11* is one of the primary regulator genes for the distal zeugopod and posterior digits.

There is an evidentiary relationship between *Hox* gene regulation and the developing forelimb. Fluctuations in *Hox* gene expression have been shown to affect the length of the forelimb module. Results found in the previously mentioned research could also explain the derived traits in the digit lengths in certain primates that result in a change in one or more digits with little to no effect on the rest. For example, the digit elongation in different ateline and colobine monkeys could be attributed to an increase in *Hoxd11*/*Hoxd12* expression, a decrease in *Hoxa13*/*Hoxd13* expression, or some sort of modification of their *Hox* response systems (Goff and Tabin, 1997; Reno et al., 2008).

2.3 Hormonally influenced behavior

Males and females are observed to have different roles in many primate groups. Often, their social roles differ regarding dominance and status rankings (Mazur, 1976). Dominance and social ranking depend on the effect that testosterone has on different behaviors (Mazur, 1976). Therefore, the feedback loop relationship between prenatal and postnatal testosterone levels, behavior, and social ranking should be examined in research involving a combination of the three. While there is weak evidence for PNAE effects on sex-typed behavior, characteristics such

as aggression, autistic-like features, and cognition have been found to be influenced by prenatal androgens to a moderate degree (Berenbaum and Beltz, 2011).

Other examples of hormonally influenced characteristics are "maternal investment; growth and developmental patterns; body and canine size; scent glands and scent-marking behavior; vocalisations and various visual ornaments such as manes, flanges, coloured skin and fur; as well as interspecific variation in traits such as relative testes size and penile morphology, and the presence of sexual swellings" (Kappeler and van Schaik, 2004:3-4). In a society that depends on a hierarchical structure of dominance to maintain social stability, a change in an individual's social status could affect an individual's fitness and, by inference, could also be affected by an individual's PNAE (Howlett et al., 2015). Males and females have competitive regimes that can be associated with one another; however, the intermediate Competition Level (Type 3) used in this study had no discrepancy between the extent of male and female competition (Nelson and Shultz, 2010). If the 2D:4D ratio and 2Mc:4Mc ratio can be informative of PNAE levels, then these ratios can be used as additional variables in studies involving androgen exposure and other behaviors associated with these hormones such as intrasexual competition.

2.4 Sexual dimorphism and intermale competition

There are two different types of hormonal effects on the structure of the brain. The first is organizational effects which "produce permanent changes to brain structures and the behaviors they subserve" (Berenbaum and Beltz, 2011:183). The second is activational effects which are "hormones acting later in life to produce temporary alterations to the brain and behavior (through ongoing changes to neural circuitry) as the hormones circulate in the body throughout adolescence and adulthood" (Berenbaum and Beltz, 2011:183). The importance of the

relationship between organizational and activational hormonal effects is that PNAE presents variability during fetal development which, in turn, causes variability in these networks during adulthood (Shaw et al., 2012). These prenatal sex hormones have been found to influence masculine behaviors such as foot-clasp mounting and rough-and-tumble play in different anthropoids (Nelson and Shultz, 2010) and feminine behaviors such as sociality and affiliative behavior (Howlett et al., 2015). The prenatal hormones that determine the 2D:4D ratio are considered to have organizational effects because they occur early in development and are more permanent. This indicates that any variation in sex hormone exposure with pubertal timing could influence aspects of brain organization and associated behavior (Berenbaum and Beltz, 2011).

The organizational and activational hypothesis is examined in a longitudinal study on PNAE and the growth rates over time in marmoset monkeys, *C. geoffroyi*. In this study, Smith et al. (2010) measured the growth rate of marmosets born with "normal" PNAE from birth to 300 days old. In addition to the growth, Smith et al. (2010) documented intra- and interindividual variation in the marmosets' urinary androgen levels. The growth rates in these marmosets were found to be contingent upon the level of androgen exposure during the first trimester (Smith et al., 2010). The relationship between growth rate and androgen exposure was negatively correlated because, as the androgen exposure during the first trimester increased, the weight and postnatal growth rate decreased (Smith et al., 2010). The conclusions in this study suggest that PNAE during the early stages of development can have lasting effects on the postnatal development of the individual, such that a heightened exposure to androgens could inhibit the morphological size of certain characteristics (Smith et al., 2010). This study supports the organizational and activational hypothesis because the PNAE produces permanent changes to the structure that become more prominent later in life.

2.4.1 Notable research on sexual dimorphism

Previous research on the 2D:4D ratio across primates shows consistency with sexually dimorphic 2D:4D ratios. Nelson and Shultz (2010) conducted the first study of 2D:4D ratio variation among primates comparing the ratios of species with different mating strategies. They found that 2D:4D ratio among males is lower (higher PNAE, masculinized) in polygynous species with high intrasexual competition and that 2D:4D ratio among males is higher (lower PNAE, feminized) in pair-bonded species with low levels of intrasexual competition (Nelson and Shultz, 2010). Within pair-bonded and nonpair-bonded species, all species examined had a significant sexual difference in the ratio (Nelson and Shultz, 2010). In addition to high intermale competition being associated with low 2D:4D ratio, interfemale competition and 2D:4D ratio was also strongly associated (Nelson and Shultz, 2010). Nelson and Shultz (2010) controlled for phylogeny and locomotion, which removed different influences on hand morphology, and found the 2D:4D ratios and social behaviors to be maintained with consistent results in Anthropoidea.

Nelson and Shultz (2010:401) believe that their results are "consistent with prenatal androgens in non-human primates potentially promoting the development of competitive and aggressive behaviors, which can ultimately be manifested in increased intrasexual competition, polygynous social systems and dominance hierarchies." This consistent relationship in this study and others mentioned in this chapter shows that PNAE could be considered a mechanistic explanation for the evolutionary development of sex-specific behavior, predominantly behavior associated with aggression (Nelson and Shultz, 2010). Nelson and Shultz (2010) believe that one evolutionary mechanism that is a result of PNAE is female philopatry in nonhuman primates, which is now believed to be a derived response to competition versus an ancestral trait response. The hormones that influence the 2D:4D ratio and the associated behaviors originate from the

fetal gonads or the maternal adrenal glands and can therefore be either fetally or maternally derived (Mesanio and Jaffe, 1997; Rabinovici and Jaffe, 1990), meaning that mothers and their uterine environment could be considered an influence for the evolution associated with these sex hormones in addition to the male fetal secretion of testosterone. This is significant especially in species with female dominance hierarchies that could have an epigenetic effect on offspring (Nelson and Shultz, 2010). Nelson and Shultz (2010) continued to speculate whether the shifts in PNAE with associated genetic changes may have contributed to flexibility and dexterity in the hands of apes and, consequentially, modern humans. They found that there was a dimorphic ratio in relation to interfemale competition (Nelson and Shultz, 2010). Their results show that lower 2D:4D ratios in females were associated with high interfemale competition and female philopatry, while high 2D:4D ratios in females were associated with low interfemale competition and heterosexual or female dispersal (Nelson and Shultz, 2010). Overall, they found a more extreme difference in the ratios of nonpair-bonded species than in pair-bonded species (Nelson and Shultz, 2010).

 2.5 Evidence in other species

Testosterone levels have been proven to be varied among different mating strategies in nonprimate animals. A study on the polygynous pectoral sandpiper (*Calidris melanotos*) and the monogamous semipalmated sandpiper (*Calidris pusilla*) has found that the polygynous males had higher levels of testosterone than the monogamous males and sustained the testosterone levels for a longer period during their breeding season (Steiger et al., 2006). This study supports the organizational and activational hypothesis and suggests that certain behavior is sensitive to levels of testosterone (Steiger et al., 2006).

Further information that the 2D:4D ratio and 2Mc:4Mc ratio can provide is an understanding of the social relations in extinct species. Nelson et al. (2011) examined proximal phalanges and their ratios in early hominoids to predict the social systems of these species. The early hominins (Middle to Late Miocene) were estimated to have generally polygamous, high intermale competition social systems using the proximal phalangeal ratio (2PP:4PP) (Nelson et al., 2011). In contrast, *Australopithecus africanus* had the proximal phalangeal ratio of a monogamous species. Nelson et al. (2011) found Neandertals and other early anatomically modern humans to have a 2PP:4PP ratio suggesting higher intermale competition compared to modern human populations. With further research into the accuracy of the association between ratios in the hand and mating strategies, the findings in this study suggest that the social systems of extinct primates can be inferred through the utilization of 2D:4D ratios in postcranial analysis of fossils and can assist with the understanding of the evolution of human social behavior (Nelson et al., 2011).

CHAPTER 3. MATERIALS AND METHODS

3.1 Materials

Table 3.1 presents sample sizes for each species and their level of intermale competition. Two species were used to represent each competition level and its corresponding ordinal variable. For the research, 100 *H. lar* specimens (Type 1; 51 male; 49 female) and 20 *A. azarae* specimens (Type 1; 11 male; 9 female) were measured. There were 37 *P. rubicunda* specimens (Type 3; 19 male; 18 female) and 49 *T. cristata* specimens (Type 3; 18 male; 31 female). For this sample, 36 *A. seniculus* specimens (Type 4; 19 male; 17 female) and 37 *M. fascicularis* specimens (Type 4; 18 male; 19 female) were measured. Adults were used in this research and were defined as specimens with their metacarpal epiphyses fused. Metacarpals that were articulated or damaged were disregarded. Sex, species, and locality were determined using museum records. The specimens measured at the museums were all indicated as wild-caught.

Table 3.1 Sample sizes and competition level of species

Species	Competition Level	Males	Females	Total
Alouatta seniculus	4	19	17	36
Aotus azarae	1	11	9	20
Hylobates lar	1	51	49	100
Macaca fascicularis	4	18	19	37
Presbytis rubicunda	3	19	18	37
Trachypithecus cristatus	3	18	31	49

3.2 Methods

Digital calipers were used to measure the maximum length of each metapodial to the nearest 0.01 mm. I measured all available metapodials 1-5 of the specimens but am only reporting metapodials 2-5 because they are the metapodials in ratios mentioned in previous

literature. The average 2Mc:4Mc and 2Mt:4Mt is defined as the average of the left and right side combined or the single left or right side if either was unavailable. To determine intra-observer error and precision, *A. seniculus* was measured twice and using the first 100 double measurements of the metapodials, the intra-observer error was estimated using the equation: (|original value-repeated value|/original value). This mean value was 0.0623. The precision was then calculated as 1- intra-observer error. The precision value was 0.9377.

 3.3 Statistical analysis

SPSS was used for all statistical analyses. Statistical tests included Mann-Whitney U tests and two-way factorial ANOVA (Analysis of Variance) using the independent variables Competition Level and Sex for each ratio used as the dependent variables. The Wilcoxon signed-rank test was used to determine asymmetry in the metapodial ratios. The null hypotheses and the corresponding alternative hypotheses were as follows. Null Hypothesis 1: Female ratio values will be the same as male ratio values averaged across species; Alternative Hypothesis 1: Female ratios will not equal male ratios. Null Hypothesis 2: The average 2Mc:4Mc ratios of the species are the same averaged over sex among the competition levels; Alternative Hypothesis 2: The average 2Mc:4Mc ratios of the species are different averaged over sex among the competition levels. Level of statistical significance was set at $p \leq 0.05$ for analyses.

CHAPTER 4. RESULTS

4.1 Descriptive statistics for metapodials

Tables 4.1 and 4.2 show the descriptive statistics found for each variable in the

metapodials. Among 88 comparisons for each metapodial between the sexes, the male average

was greater than female average seven times out of eleven for metacarpal 2 on either side, nine

times for metacarpals 3 and 5 out of eleven, ten times out of eleven for metacarpal 4 and

metatarsals 3 and 5, and all eleven times for metatarsals 2 and 4. The female average was larger

than the male average four times for metacarpal 2 out of eleven, twice for metacarpals 3 and 5

out of eleven, and once for metacarpal 4 and metatarsals 3 and 5 out of eleven comparisons.

These results show that in general males have longer metapodials than females, but that the

prevalence of this dimorphism is the least frequent for metacarpal 2. Left metapodial values for

male *P. rubicunda* were unavailable and therefore left out of the comparison of the descriptive

statistics.

Table 4.3 presents the results of the Wilcoxon signed-rank test for asymmetry between

the left and right metapodial ratios: 2Mc:4Mc and 2Mt:4Mt. The only species with a significant

difference in the ratios was *T. cristatus* in the metacarpals. There were no significant differences

for the left and right side of the other species in the 2Mc:4Mc and 2Mt:4Mt ratios.

Table 4.1 Descriptive statistics for individual metacarpals in mm

		Female			Male		
Species	**Metacarpal**	**N**	**Mean**	**Std. Dev.**	**N**	**Mean**	**Std. Dev.**
Alouatta seniculus	Left Second	10	29.92	2.29	13	30.31	2.94
(Type 4)	Left Third	9	33.04	2.40	14	34.04	3.17
	Left Fourth	12	30.48	4.19	13	32.87	3.22
	Left Fifth	11	27.24	4.28	15	28.86	3.17
	Right Second	14	30.78	4.94	16	30.03	3.18
	Right Third	14	33.23	4.45	14	33.64	3.60
	Right Fourth	15	31.55	4.39	15	31.92	3.49
	Right Fifth	15	28.04	4.56	15	28.43	3.18

(table cont'd)

Species	Metacarpal	Female			Male		
		N	Mean	Std. Dev.	N	Mean	Std. Dev.
Aotus azarae (Type 1)	Left Second	3	17.94	0.33	6	18.10	0.55
	Left Third	5	19.36	0.41	6	19.66	0.68
	Left Fourth	5	17.86	0.50	5	18.46	0.67
	Left Fifth	7	13.98	0.93	5	14.12	0.42
	Right Second	3	18.09	0.52	7	18.29	0.39
	Right Third	3	19.19	0.39	7	19.88	0.49
	Right Fourth	4	17.73	0.47	7	18.66	0.50
	Right Fifth	5	13.66	0.77	7	13.95	0.31
Hylobates lar (Type 1)	Left Second	39	64.27	4.61	39	65.14	3.50
	Left Third	40	60.50	4.56	39	61.39	3.87
	Left Fourth	39	55.38	3.96	41	56.80	2.91
	Left Fifth	38	49.18	3.52	39	50.13	2.99
	Right Second	40	64.55	3.43	38	64.54	3.38
	Right Third	42	60.61	4.07	39	60.93	3.47
	Right Fourth	42	55.56	3.04	40	55.97	2.92
	Right Fifth	41	49.33	2.93	46	50.40	2.94
Macaca fascicularis (Type 4)	Left Second	4	28.56	1.01	2	27.94	0.36
	Left Third	4	27.78	1.54	2	27.50	0.60
	Left Fourth	4	26.53	1.50	3	27.26	3.72
	Left Fifth	6	23.84	1.28	1	23.42	
	Right Second	17	27.72	1.13	15	31.14	2.00
	Right Third	18	26.76	1.21	14	30.19	1.91
	Right Fourth	17	25.65	1.20	15	28.66	1.97
	Right Fifth	14	23.55	1.03	15	26.38	2.01
Presbytis rubicunda (Type 3)	Left Second	2	41.59	1.07	0		
	Left Third	2	42.96	1.33	0		
	Left Fourth	2	41.40	1.61	0		
	Left Fifth	2	40.08	2.36	0		
	Right Second	17	40.83	1.03	18	41.85	1.09
	Right Third	16	42.18	1.08	17	42.74	1.23
	Right Fourth	17	39.87	1.15	18	40.58	1.10
	Right Fifth	18	38.44	1.11	17	38.98	1.28
Trachypithecus cristatus (Type 3)	Left Second	10	37.13	3.24	3	35.71	2.29
	Left Third	10	36.60	1.79	4	36.34	2.02
	Left Fourth	9	35.53	1.61	4	34.70	1.48
	Left Fifth	10	33.79	1.57	4	33.59	1.48
	Right Second	28	36.04	1.57	16	36.43	1.92
	Right Third	31	36.38	1.44	16	37.20	2.15
	Right Fourth	29	35.33	1.31	15	36.43	2.13
	Right Fifth	29	33.72	1.50	16	34.82	1.98

Table 4.2 Descriptive statistics for individual metatarsals in mm

Species	Metatarsal	Female N	Mean	Std. Dev.	Male N	Mean	Std. Dev.
Alouatta seniculus (Type 4)	Left Second	14	37.58	5.60	12	40.49	4.42
	Left Third	13	38.91	4.72	13	40.89	3.66
	Left Fourth	15	37.51	4.58	12	40.29	3.37
	Left Fifth	15	34.41	6.19	11	38.64	3.45
	Right Second	14	39.84	3.16	9	41.36	4.89
	Right Third	13	39.54	2.99	13	41.16	3.85
	Right Fourth	15	37.80	4.93	11	40.07	3.48
	Right Fifth	15	35.24	4.93	11	37.38	4.37
Aotus azarae (Type 1)	Left Second	4	30.75	0.57	7	31.72	1.01
	Left Third	4	31.77	0.28	4	32.62	0.93
	Left Fourth	5	32.81	0.68	8	34.06	0.90
	Left Fifth	4	32.51	1.24	9	33.87	0.59
	Right Second	5	31.52	1.08	7	32.20	0.74
	Right Third	5	32.48	0.88	7	33.48	1.20
	Right Fourth	5	33.35	1.10	7	34.65	1.08
	Right Fifth	4	32.50	1.27	8	34.23	0.94
Hylobates lar (Type 1)	Left Second	36	46.18	2.34	43	47.44	3.49
	Left Third	39	43.68	2.81	45	44.81	3.21
	Left Fourth	33	41.87	2.56	43	42.82	2.89
	Left Fifth	33	38.18	3.58	43	38.51	2.90
	Right Second	37	46.10	2.67	31	46.72	2.63
	Right Third	37	43.69	2.69	30	44.36	2.77
	Right Fourth	38	41.69	2.42	35	42.44	2.74
	Right Fifth	38	37.89	2.21	35	38.59	2.71
Macaca fascicularis (Type 4)	Left Second	4	35.40	1.54	2	38.67	4.67
	Left Third	4	37.66	2.03	3	40.63	3.91
	Left Fourth	4	37.37	2.06	1	37.40	
	Left Fifth	5	34.79	1.80	3	38.06	2.30
	Right Second	18	34.55	1.49	13	38.26	3.26
	Right Third	18	36.80	1.40	14	40.29	4.64
	Right Fourth	19	36.32	1.36	14	39.90	4.78
	Right Fifth	19	34.54	1.36	11	38.43	4.89
Presbytis rubicunda (Type 3)	Left Second	2	52.52	0.99	0		
	Left Third	2	57.13	0.79	0		
	Left Fourth	2	58.68	0.33	0		
	Left Fifth	2	59.19	0.28	0		
	Right Second	17	52.07	1.35	18	53.73	1.46
	Right Third	16	57.09	1.11	19	58.91	2.19
	Right Fourth	17	58.24	1.20	17	60.23	1.79

(table cont'd)

	Metatarsal	Female			Male		
		N	Mean	Std. Dev.	N	Mean	Std. Dev.
Trachypithecus cristatus (Type 3)	Right Fifth	17	58.13	2.39	18	60.72	2.14
	Left Second	9	45.57	4.01	3	45.66	2.89
	Left Third	6	50.21	1.63	3	48.93	2.88
	Left Fourth	9	49.41	5.39	3	50.26	3.50
	Left Fifth	7	50.94	1.93	3	50.45	3.88
	Right Second	27	45.81	1.80	17	46.53	2.44
	Right Third	29	48.98	1.95	17	49.72	2.53
	Right Fourth	26	50.48	1.80	17	51.24	2.80
	Right Fifth	28	49.91	1.95	16	51.19	2.55

Table 4.3 Test for asymmetry in the metacarpals and the metatarsals of each species (* indicates significance)

Test for Asymmetry		
Species	Metapodial Ratio	*p*- value
Alouatta seniculus	2Mc:4Mc	0.117
	2Mt:4Mt	0.520
Aotus azarae	2Mc:4Mc	0.686
	2Mt:4Mt	0.917
Hylobates lar	2Mc:4Mc	0.656
	2Mt:4Mt	0.162
Macaca fascicularis	2Mc:4Mc	1.000
	2Mt:4Mt	0.273
Presbytis rubicunda	2Mc:4Mc	0.317
	2Mt:4Mt	0.678
Trachypithecus cristatus	2Mc:4Mc	0.036*
	2Mt:4Mt	0.655

4.2 Mann-Whitney U test results

The Mann-Whitney U test was used to compare the male 2Mc:4Mc ratio to the female 2Mc:4Mc ratio to determine whether this difference was significant (Table 4.4). The left 2Mc:4Mc ratios for *M. fascicularis* and *P. rubicunda* were excluded from this analysis because their sample sizes were too small. For the Mann-Whitney U tests, the only ratios that were significantly different were the right 2Mc:4Mc ratios of *A. azarae* (p=0.048), the average and

right 2Mc:4Mc ratio of *P. rubicunda* (p=0.017; p=0.025), and the average and right 2Mc:4Mc

ratio of *T. cristatus* (p=0.01; p=0.001). For these ratios, the results would reject the Null

Hypothesis 1 that the male and female 2Mc:4Mc ratios are equal. The Null Hypothesis 2 states

that the average 2Mc:4Mc ratios of the species are the same averaged over sex among the

competition levels; however, since all of the results from Competition Level Type 4 and Type 1

species fail to reject the hypothesis of a sexual difference in the 2Mc:4Mc ratio, neither

difference is significant, and therefore, the Null Hypothesis 2 cannot be rejected.

Table 4.4 Comparisons of 2Mc:4Mc ratio between sex within the species (* indicates significance)

Species	Competition Level	Mann-Whitney U Test Results		
		Variable	*p*- value	Decision on Null Hypothesis 2
Alouatta seniculus	4	Average 2Mc:4Mc	0.217	Fail to reject
		Left 2Mc:4Mc	0.722	Fail to reject
		Right 2Mc:4Mc	0.134	Fail to reject
Aotus azarae	1	Average 2Mc:4Mc	0.052	Fail to reject
		Left 2Mc:4Mc	0.250	Fail to reject
		Right 2Mc:4Mc	0.048*	Reject
Hylobates lar	1	Average 2Mc:4Mc	0.064	Fail to reject
		Left 2Mc:4Mc	0.375	Fail to reject
		Right 2Mc:4Mc	0.107	Fail to reject
Macaca fascicularis	4	Average 2Mc:4Mc	0.299	Fail to reject
		Right 2Mc:4Mc	0.401	Fail to reject
Presbytis rubicunda	3	Average 2Mc:4Mc	0.017*	Reject
		Right 2Mc:4Mc	0.025*	Reject
Trachypithecus cristatus	3	Average 2Mc:4Mc	0.010*	Reject
		Left 2Mc:4Mc	0.497	Fail to reject
		Right 2Mc:4Mc	0.001*	Reject

4.3 Interaction of competition levels and sex on the metacarpal ratios

Table 4.5 presents the results for the interaction between sex and competition level on the

2Mc:4Mc ratio and 2Mt:4Mt ratio for the left, right, and average of the two ratios testing Null

Hypothesis 2 that the average 2Mc:4Mc ratios and 2Mt:4Mt ratios of the species are the same among the competition levels. The ratios 2Mc:4Mc and 2Mt:4Mt are significant for the competition level for the left, right, and average ratios. For sex, average, and right side 2Mc:4Mc ratios are significant. For the interaction, average and left side 2Mt:4Mt ratios are significant.

For left 2Mc:4Mc, the relationship with level of competition is significant but the relationship with sex is not significant. The interaction of competition level and sex with left 2Mc:4Mc ratio is not significant. Therefore, we cannot conclude that the effect of sex on the 2Mc:4Mc ratio for each competition level is different.

For the average and the right 2Mc:4Mc ratio values, the effect of the level of competition is significant. The relationship with sex is also significant. From the interaction of sex and competition level for the average and the right 2Mc:4Mc ratios, the results are not significant and we cannot conclude that the effect of sex on the average and right 2Mc:4Mc ratios for each competition level is different.

Table 4.5 Interaction between the variables competition level and sex on the ratios using ANOVA (* indicates significance)

	p-values		
Variable	Competition Level	Sex	Competition Level and Sex
Average 2Mc:4Mc	<0.001*	<0.001*	0.372
Left 2Mc:4Mc	<0.001*	0.062	0.105
Right 2Mc:4Mc	<0.001*	0.004*	0.696
Average 2Mt:4Mt	<0.001*	0.163	0.001*
Left 2Mt:4Mt	<0.001*	0.139	0.019*
Right 2Mt:4Mt	<0.001*	0.343	0.216

4.4 Results for the interaction of competition levels and sex on the metatarsal ratios

The average 2Mt:4Mt ratio is significantly affected by the level of competition ($p<0.001$) and the interaction of competition level and sex ($p<0.001$) but the effect of sex on the ratio is not

significant. For the left 2Mt:4Mt, the main effect of the level of competition is significant

($p<0.001$). For the effect of sex on the left 2Mt:4Mt, the main effect of sex on the left metatarsal

ratio is not significant ($p=0.139$). The p-value of the interaction of competition level and sex on

the left 2Mt:4Mt ($p=0.019$) means that there is a significant relationship between competition

level and sex on the ratio. In the right 2Mt:4Mt, the p-value for the main effect of competition

level on the ratio is significant ($p<0.001$). The other effects, sex and the interaction variable, are

not significant on the right 2Mt:4Mt ($p=0.343$ and $p=0.216$).

 4.5 Other results in other ratios

All ratios for the remaining combinations of metacarpals 2-5 are presented in Table 4.6

for each species. These additional ratios were used because of other research that found a sexual

difference in ratios besides 2Mc:4Mc (see Chapter 5; Tague, 2002; McFadden and Bracht, 2003).

Comparing these Mann-Whitney U tests between sexes within species, results show that only the

right 3Mc:4Mc for *H. lar* ($p<0.001$), right 2Mc:3Mc and 2Mc:5Mc for *P. rubicunda* ($p=0.040$;

$p=0.031$), and right 2Mc:3Mc, 2Mc:5Mc, and 3Mc:4Mc for *T. cristatus* ($p=0.006$; $p<0.001$;

$p=0.011$) are significant.

Table 4.6 Comparisons of other ratios for metacarpals 2-5 between sex within the species (*
indicates significance)

		Mann-Whitney U Test Results		
Species	**Competition Level**	**Variable**	**p-value**	**Decision on Null Hypothesis 1**
Alouatta seniculus	4	Left 2Mc:3Mc	0.917	Fail to reject
		Right 2Mc:3Mc	0.265	Fail to reject
		Left 2Mc:5Mc	0.571	Fail to reject
		Right 2Mc:5Mc	0.102	Fail to reject
		Left 3Mc:4Mc	0.554	Fail to reject
		Right 3Mc:4Mc	0.667	Fail to reject
		Left 3Mc:5Mc	0.473	Fail to reject

(table cont'd)

		Mann-Whitney U Test Results		
		Variable	***p*-value**	**Decision on Null Hypothesis 1**
		Left 4Mc:5Mc	0.738	Fail to reject
		Right 4Mc:5Mc	0.486	Fail to reject
Aotus azarae	1	Left 2Mc:3Mc	0.571	Fail to reject
		Right 2Mc:3Mc	0.262	Fail to reject
		Left 2Mc:5Mc	0.571	Fail to reject
		Right 2Mc:5Mc	0.262	Fail to reject
		Left 3Mc:4Mc	0.222	Fail to reject
		Right 3Mc:4Mc	0.117	Fail to reject
		Left 3Mc:5Mc	0.548	Fail to reject
		Right 3Mc:5Mc	0.667	Fail to reject
		Left 4Mc:5Mc	0.690	Fail to reject
		Right 4Mc:5Mc	0.788	Fail to reject
Hylobates lar	1	Left 2Mc:3Mc	0.959	Fail to reject
		Right 2Mc:3Mc	0.554	Fail to reject
		Left 2Mc:5Mc	0.490	Fail to reject
		Right 2Mc:5Mc	0.328	Fail to reject
		Left 3Mc:4Mc	0.070	Fail to reject
		Right 3Mc:4Mc	0.001*	Reject
		Left 3Mc:5Mc	0.258	Fail to reject
		Right 3Mc:5Mc	0.081	Fail to reject
		Left 4Mc:5Mc	0.656	Fail to reject
		Right 4Mc:5Mc	0.335	Fail to reject
Macaca fascicularis	4	Right 2Mc:3Mc	0.710	Fail to reject
		Right 2Mc:5Mc	0.905	Fail to reject
		Left 3Mc:4Mc	0.400	Fail to reject
		Right 3Mc:4Mc	0.830	Fail to reject
		Right 3Mc:5Mc	0.667	Fail to reject
		Right 4Mc:5Mc	0.458	Fail to reject
Presbytis rubicunda	3	Right 2Mc:3Mc	0.040*	Reject
		Right 2Mc:5Mc	0.031*	Reject
		Right 3Mc:4Mc	0.217	Fail to reject
		Right 3Mc:5Mc	0.780	Fail to reject
		Right 4Mc:5Mc	0.322	Fail to reject
Trachypithecus cristatus	3	Left 2Mc:3Mc	0.600	Fail to reject
		Right 2Mc:3Mc	0.006*	Reject
		Left 2Mc:5Mc	0.376	Fail to reject
		Right 2Mc:5Mc	0.001*	Reject

(table cont'd)

	Mann-Whitney U Test Results		
	Variable	**p-value**	**Decision on Null Hypothesis 1**
	Right 3Mc:4Mc	0.011*	Reject
	Left 3Mc:5Mc	0.503	Fail to reject
	Right 3Mc:5Mc	0.088	Fail to reject
	Left 4Mc:5Mc	0.503	Fail to reject
	Right 4Mc:5Mc	0.899	Fail to reject

Table 4.7 lists the descriptive statistics for all the ratios used in this analysis. While the Null Hypothesis 1 was not rejected for the majority of the metapodial ratios, the average values of the ratios can still be compared to determine the difference between sexes. For the 2Mc:4Mc ratio regardless of side, the female ratio is larger eleven times out of the seventeen comparisons. For the 2Mt:4Mt ratio regardless of side, the female ratio is larger ten times out of the seventeen comparisons. The ratios are the same across the sexes for 2Mc:4Mc zero times and 2Mt:4Mt five times. Out of 53 comparisons, females in the other ratios compared were larger thirty-three times. In the other ratios, females and males were equal fifteen times. Males were larger in these ratios five times.

Table 4.7 Descriptive statistics for ratios used in this study in mm

		Descriptive Statistics of Ratios						
		Female			**Male**			
Species	**Ratio**	**N**	**Mean**	**Std. Dev.**	**N**	**Mean**	**Std. Dev.**	**Female-Male**
Alouatta seniculus (Type 4)	Left 2Mc:4Mc	10	0.95	0.02	12	0.94	0.04	0.01
	Right 2Mc:4Mc	14	0.96	0.04	15	0.94	0.03	0.02
	Average 2Mc:4Mc	15	0.96	0.02	15	0.94	0.03	0.02
	Left 2Mt:4Mt	13	1.00	0.05	11	1.02	0.02	-0.02
	Right 2Mt:4Mt	14	1.03	0.02	9	1.03	0.04	0.00
	Average 2Mt:4Mt	13	1.03	0.03	15	1.02	0.02	0.01
	Left 2Mc:3Mc	9	0.91	0.02	12	0.90	0.02	0.01

(table cont'd)

	Descriptive Statistics of Ratios							
		Female		Male				
							Std.	Female-
	Ratio	N	Mean	Std. Dev.	N	Mean	Std. Dev.	Male
	Right 2Mc:3Mc	14	0.92	0.04	14	0.91	0.03	0.01
	Left 2Mc:5Mc	8	1.07	0.03	12	1.05	0.06	0.02
	Right 2Mc:5Mc	14	1.08	0.03	15	1.06	0.04	0.02
	Left 3Mc:4Mc	9	1.05	0.01	12	1.04	0.02	0.01
	Right 3Mc:4Mc	14	1.04	0.02	14	1.04	0.02	0.00
	Left 3Mc:5Mc	8	1.18	0.04	12	1.17	0.05	0.01
	Right 3Mc:5Mc	14	1.18	0.05	14	1.17	0.04	0.01
	Left 4Mc:5Mc	10	1.13	0.04	13	1.12	0.04	0.01
	Right 4Mc:5Mc	15	1.13	0.05	15	1.12	0.03	0.01
Aotus azarae (Type 1)	Left 2Mc:4Mc	3	1.01	0.02	5	0.99	0.03	0.02
	Right 2Mc:4Mc	3	1.03	0.02	6	0.99	0.03	0.04
	Average 2Mc:4Mc	5	1.02	0.02	6	0.99	0.03	0.03
	Left 2Mt:4Mt	4	0.94	0.00	7	0.93	0.01	0.01
	Right 2Mt:4Mt	5	0.95	0.01	7	0.93	0.02	0.02
	Average 2Mt:4Mt	7	0.94	0.00	10	0.93	0.01	0.01
	Left 2Mc:3Mc	3	0.94	0.01	5	0.92	0.02	0.02
	Right 2Mc:3Mc	3	0.94	0.01	6	0.93	0.02	0.01
	Left 2Mc:5Mc	3	1.33	0.08	5	1.29	0.04	0.04
	Right 2Mc:5Mc	3	1.36	0.03	6	1.32	0.04	0.04
	Left 3Mc:4Mc	5	1.08	0.01	5	1.07	0.02	0.01
	Right 3Mc:4Mc	3	1.09	0.01	7	1.07	0.03	0.02
	Left 3Mc:5Mc	3	1.43	0.05	5	1.40	0.05	0.03
	Right 3Mc:5Mc	3	1.44	0.05	7	1.43	0.03	0.01
	Left 4Mc:5Mc	5	1.31	0.04	5	1.31	0.03	0.00
	Right 4Mc:5Mc	4	1.32	0.04	7	1.34	0.03	-0.02
Hylobates lar (Type 1)	Left 2Mc:4Mc	36	1.16	0.02	38	1.15	0.02	0.01
	Right 2Mc:4Mc	39	1.16	0.02	38	1.15	0.02	0.01
	Average 2Mc:4Mc	41	1.16	0.02	48	1.15	0.02	0.01
	Left 2Mt:4Mt	32	1.11	0.02	41	1.10	0.03	0.01
	Right 2Mt:4Mt	35	1.11	0.03	31	1.11	0.02	0.00
	Average 2Mt:4Mt	40	1.11	0.02	45	1.10	0.03	0.01
	Left 2Mc:3Mc	39	1.06	0.02	38	1.06	0.02	0.00
	Right 2Mc:3Mc	38	1.06	0.02	38	1.06	0.02	0.00

(table cont'd)

	Descriptive Statistics of Ratios						
		Female			Male		
	Ratio	N	Mean	Std. Dev.	N	Mean	Std. Dev.	Female-Male
	Left 2Mc:5Mc	34	1.31	0.03	37	1.30	0.04	0.01
	Right 2Mc:5Mc	37	1.31	0.03	37	1.30	0.03	0.01
	Left 3Mc:4Mc	37	1.09	0.02	38	1.09	0.02	0.00
	Right 3Mc:4Mc	39	1.09	0.01	39	1.06	0.17	0.03
	Left 3Mc:5Mc	35	1.23	0.03	37	1.22	0.03	0.01
	Right 3Mc:5Mc	38	1.23	0.03	39	1.19	0.20	0.04
	Left 4Mc:5Mc	37	1.13	0.02	38	1.12	0.02	0.01
	Right 4Mc:5Mc	39	1.13	0.02	39	1.12	0.02	0.01
Macaca fascicularis (Type 4)	Left 2Mc:4Mc	3	1.07	0.03	1	1.13		-0.06
	Right 2Mc:4Mc	16	1.08	0.03	15	1.09	0.03	-0.01
	Average 2Mc:4Mc	16	1.08	0.03	15	1.09	0.03	-0.01
	Left 2Mt:4Mt	4	0.95	0.02	1	0.95		0.00
	Right 2Mt:4Mt	18	0.95	0.02	12	0.98	0.09	-0.03
	Average 2Mt:4Mt	18	0.95	0.02	13	0.97	0.08	-0.02
	Left 2Mc:3Mc	3	1.02	0.01	2	1.02	0.01	0.00
	Right 2Mc:3Mc	17	1.04	0.02	14	1.04	0.02	0.00
	Left 2Mc:5Mc	3	1.17	0.02	0			
	Right 2Mc:5Mc	13	1.18	0.04	14	1.18	0.04	0.00
	Left 3Mc:4Mc	4	1.05	0.02	1	1.10		-0.05
	Right 3Mc:4Mc	17	1.04	0.02	14	1.05	0.02	-0.01
	Left 3Mc:5Mc	4	1.15	0.01	0			
	Right 3Mc:5Mc	14	1.14	0.03	14	1.14	0.04	0.00
	Left 4Mc:5Mc	4	1.10	0.01	1	1.10		0.00
	Right 4Mc:5Mc	13	1.09	0.02	14	1.08	0.03	0.01
Presbytis rubicunda (Type 3)	Left 2Mc:4Mc	2	1.00	0.01	0			
	Right 2Mc:4Mc	16	1.02	0.01	18	1.03	0.01	-0.01
	Average 2Mc:4Mc	17	1.02	0.01	18	1.03	0.01	-0.01
	Left 2Mt:4Mt	2	0.90	0.01	0			
	Right 2Mt:4Mt	16	0.89	0.01	17	0.89	0.01	0.00
	Average 2Mt:4Mt	16	0.92	0.01	17	0.91	0.02	0.01
	Left 2Mc:3Mc	2	0.97	0.01	0			
	Right 2Mc:3Mc	15	0.97	0.01	17	0.98	0.01	-0.01
	Left 2Mc:5Mc	2	1.04	0.01	0			

(table cont'd)

		Descriptive Statistics of Ratios						
		Female			Male			
	Ratio	N	Mean	Std. Dev.	N	Mean	Std. Dev.	Female-Male
	Right 2Mc:5Mc	17	1.06	0.02	17	1.07	0.02	-0.01
	Left 3Mc:4Mc	2	1.04	0.01	0			
	Right 3Mc:4Mc	16	1.06	0.01	17	1.05	0.01	0.01
	Left 3Mc:5Mc	2	1.07	0.03	0			
	Right 3Mc:5Mc	16	1.09	0.02	16	1.07	0.02	0.02
	Left 4Mc:5Mc	2	1.03	0.02	0			
	Right 4Mc:5Mc	17	1.04	0.01	17	1.04	0.02	0.00
Trachypithecus cristatus (Type 3)	Left 2Mc:4Mc	8	1.02	0.02	3	1.03	0.02	-0.01
	Right 2Mc:4Mc	27	1.02	0.02	15	1.00	0.02	0.02
	Average 2Mc:4Mc	29	1.02	0.02	16	1.01	0.02	0.01
	Left 2Mt:4Mt	8	0.92	0.03	3	0.91	0.01	0.01
	Right 2Mt:4Mt	24	0.91	0.01	17	0.91	0.01	0.00
	Average 2Mt:4Mt	26	0.90	0.01	17	0.89	0.01	0.01
	Left 2Mc:3Mc	9	0.99	0.01	3	0.98	0.02	0.01
	Right 2Mc:3Mc	28	0.99	0.01	16	0.98	0.01	0.01
	Left 2Mc:5Mc	8	1.06	0.03	3	1.06	0.01	0.00
	Right 2Mc:5Mc	27	1.07	0.02	16	1.05	0.02	0.02
	Left 3Mc:4Mc	9	1.03	0.02	4	1.05	0.01	-0.02
	Right 3Mc:4Mc	29	1.03	0.01	15	1.02	0.01	0.01
	Left 3Mc:5Mc	9	1.08	0.02	4	1.08	0.02	0.00
	Right 3Mc:5Mc	29	1.08	0.02	16	1.07	0.02	0.01
	Left 4Mc:5Mc	9	1.05	0.02	4	1.03	0.02	0.02
	Right 4Mc:5Mc	28	1.05	0.02	15	1.05	0.02	0.00

CHAPTER 5. DISCUSSION AND CONCLUSIONS

The results fail to reject the Null Hypothesis 1 that the sexes do not differ in their 2Mc:4Mc ratio within the species. The only species with a statistically significant difference were *A. azarae* on their right side, *P. rubicunda* on their right side and the average of both sides, and *T. cristata* on their right and the average of both sides. This result is consistent with findings on the fourth digit in Manning (2002) and Howlett et al. (2015) that, in the fourth digit, the androgen receptors would increase the length while estrogen receptors decrease the length. The results from comparing other ratios between sex within species deemed meaningful in other research were also generally not significant. Despite McFadden and Bracht (2002; 2003) and Tague (2002) finding results that were statistically significant, the Mann-Whitney U test results showed no significant difference between sexes of the species and sexes of the competition level in the same ratios found in their studies. Therefore, other ratio differences are not consistent and cannot be used as a proxy for sexual dimorphism in the 2Mc:4Mc ratio.

Null Hypothesis 2 predicted that the average 2Mc:4Mc ratios of the species are the same averaged over sex among the competition levels. Species with Competition Level Type 3 would be intermediate between levels one and four. Since testosterone levels are an influencer of the 2D:4D ratio, the hypothesis is that species with high aggression, and therefore high testosterone, would have lower ratios because of the increased length in fourth digit. This research does not consider interfemale aggression as a variable. Using the two-way factorial ANOVA, the relationship between competition level and 2Mc:4Mc ratios and 2Mt:4Mt regardless of sex was not significant. However, the main effect of competition level on the 2Mc:4Mc ratios and 2Mt:4Mt was significant, although the interaction of competition level and sex on the ratio was generally not significant. Therefore, competition level influences the dimorphic trait of the

metacarpals more than the variable sex influences the 2Mc:4Mc ratio. This significant difference was expected as the variation in testosterone levels would influence the fourth digit/metapodial (Manning, 2002; Howlett et al., 2015). However, the results show that neither the Competition Level Type 1 nor the Competition Level Type 4 species have a statistically significant difference which fails to reject the Null Hypothesis 2. Using the Mann-Whitney U test, the Alternative Hypothesis 2 was that the Competition Level Type 4 species would be the only ones with a significant difference between sexes, but Competition Level Type 1 species will still have more testosterone exposure to males than females. As previously stated, the only species with a significant difference on either side were *A. azarae, T. cristata*, and *P. rubicunda*. None of these species is ascribed to Competition Level Type 4 with one species from Competition Level Type 1 and two from Competition Level Type 3. Therefore, there is not enough evidence to reject the Null Hypothesis 2 that the Competition Level Type 4 would have the greatest statistical difference.

A significant finding from McFadden and Bracht (2005) is that the sex differences in the digits are not evident in the metacarpals. A hypothesized explanation for these results was that the metapodials developed before the exposure to androgens (McFadden and Bracht, 2009). Given the results from this research and other research mentioned throughout this study (McFadden and Bracht, 2003, 2005; Nelson and Shultz, 2010) examining the sexual differences in metacarpals, this is most likely the reason as to why there was no significant difference detected. As stated earlier, *Hox* genes affect the overall pattern of development by regulating the structures that directly control cellular processes based on different extents of androgen sensitivity in the *Hox* gene clusters (Manning et al., 1998; Manning, 2002; Reno et al., 2008). The distal zeugopod module is assumed to include both the metacarpals and the phalanges, but

inferring from this study, the metacarpals are influenced by androgens to a different extent than results found for 2D:4D. Since there is still much to learn about the effects of *Hox* genes, the modules may be incorrect. The modules in the limbs could be smaller to include the bones that are affected the same way by the same hormones. The zeugopod and the autopod are modules existing in the distal aspect of the limbs (Reno et al., 2008). The digits and the metacarpals are thought to be part of the same module meaning they are influenced by the same stimulus; however, the results from this research indicate that the metacarpals are not influenced in the same way as the digits. The findings in this research contradict the concept of modularity (Callebaut and Rasskin-Gutman, 2005).

The differences in the lengths of the male and female ratios in metapodials are not significant nor as large as the differences found in phalanges. Tables 4.4 and 4.6 show that the differences are not what would be expected since pair-bonded species with low intermale competition have larger differences than the polygynous species with high intermale competition. This finding could also indicate a potential interfemale competition of the species that could affect the results. Further research would need to be conducted to examine the correlations of interfemale competition on PNAE and the 2D:4D ratio.

Another cause for the differences could be from locomotion use. Tague (2002) found that differences in the metapodial lengths corresponded with differences in locomotion which could be produced by homeobox gene fluctuations. In addition, Harris et al. (1992) found that the sexual dimorphism in human hands changes from 11.7 percent at a young age to 12.2 percent at an older age which was attributed to males changing more than females in adulthood. They also found that hand changes were more pronounced in males with stronger grip strengths (Harris et al., 1992). If grip strength is associated with change in hand dimensions, then metacarpal and

phalangeal lengths among other primate species may be influenced by grip strength and mode of locomotion. For example, Shultz (1933) measured gibbons and siamangs, which are brachiators, and found a pattern in the finger length with the second digit to be longer than the fourth digit, but he found the opposite in Old World Monkeys whose locomotion behavior is terrestrial and arboreal quadrupedalism (i.e. *M. fascricularis, P. rubicunda,* and *T. cristatus*) (Fleagle, 1988). The difference in length of the second digit and second metacarpal for Hylobatidae as discussed in Shultz (1933; 1936) could explain why there was no significant difference in comparing 2Mc:4Mc among competition levels. Future studies should include locomotion as a factor as the locomotion behavior can change the hand and the corresponding ratios.

The results from this study could be due to a biased sample. As discussed in McFadden and Bracht (2005), specimens available in a museum may not be a random sample from the wild population. Essentially, the specimens collected for the museums may not be a representative sample of the dominance hierarchy in a species as certain hierarchical levels could be more prominent in the sample population (McFadden and Bracht, 2005). Therefore, the sex differences may not be representative of the species. However, it should not influence the results for the Competition Level Type 1 species because these individuals should not have as much of a sex difference in androgen levels.

5.1 Conclusions and future research

In conclusion, the results from this research have found that the 2Mc:4Mc ratio is not influenced by intermale competition to the same extent and in the same direction as measured in the 2D:4D ratios. However, competition level has a consistently significant effect on the 2Mc:4Mc ratio while sex and the interaction between sex and competition level does not. There was no statistical difference between the sexes with the Competition Level Type 1 and Type 4

species, but there was a statistically significant difference in the Competition Level Type 3 species which could be attributed to factors not included in this research. The results also show that the levels of intermale competition have more of an influential effect on the ratios than sex indicating the importance in further studies on intrasexual competition in species.

For future research, the cause of the significant difference between the Competition Level Type 3 species should be explored. Several factors not controlled for in this research could explain the results, such as body size and geographic region. In addition, locomotion may be a relevant factor in comparing ratios in metacarpals and phalanges between species. Other research measuring the factors influencing 2D:4D and 2Mc:4Mc ratios should consider the influence of interfemale aggression or maternal behavior within species as they can affect testosterone and estrogen levels. The variation could then stimulate or inhibit either the growth of the second digit or the growth of the fourth digit.

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VITA

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