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Abstract

Prenatal androgens are responsible for sex differences in behaviour and morphology in many primates and cause changes in neural structure and function that persist throughout the animal's life. Some of the variation in the expression of behaviour between individuals of the same sex can be attributed to individual differences in exposure to prenatal sex hormones. The phases in development when prenatal androgens have masculinising and defeminising effects on the brain, and consequently on behaviour, are also the phases when digit growth is influenced by androgen and oestrogen receptor activity. Thus, the ratio of the second and fourth digits (2D:4D ratio) is a proposed biomarker for prenatal androgen effects (PAE). Through assessment of 2D:4D ratios, this study aimed to investigate the relationship between inferred PAE and social behaviours in wild female chacma baboons (*Papio hamadryas ursinus*). 2D:4D ratios were measured indirectly for 20 adult and five adolescent females using digital photographs and computer-assisted image analysis software (ImageJ). Low 2D:4D ratios (high inferred PAE) were associated with high rank, lower rates of submission and with higher rates of non-contact and contact aggression among females. The 2D:4D ratio correlated positively with submission and negatively with dominance and aggression suggesting that PAE are linked to the expression of these behaviours in female baboons and likely in other cercopithecine primates. The 2D:4D ratio did not correlate with rate of behaviours indicating females' interest in infants or with rate of affiliation among females possibly because these behaviours are regulated by ovarian hormones in adult life rather than by PAE. Finally, mean 2D:4D ratios were positively correlated in six mother/infant pairs. These preliminary results suggest that the 2D:4D ratio may be heritable in baboons and other primates.

The 2D:4D ratio & social behaviour in female chacma baboons

Dominance, Aggression, Affiliation & Interest in Infants

Caroline Howlett

**A thesis submitted for the degree of
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Introduction

Behavioural differences between the sexes reflect in part the organisational effects of prenatal sex hormones on morphology and brain patterning. Behavioural predispositions that arise from these processes are then transformed into behaviour by the social environment in which the animal finds itself (Wallen 2005). Numerous studies have examined sex differences in behaviour (Adkins-Regan 2009; Hines 2010; Moore *et al.* 2005; Balthazart & Ball 1995; Johnston & File 1991; Eaton *et al.* 1985), but there is also marked variation in the expression of behaviour between individuals of the same sex. In some cases, this has been attributed to individual differences in exposure to prenatal sex hormones, such as androgens (Clipperton-Allen *et al.* 2011; Coleman *et al.* 2011; Nelson *et al.* 2010; Forstmeier *et al.* 2008). Manipulating sex hormones prenatally affects various morphological and behavioural characteristics in humans (Hines 2006; Brown *et al.* 2002b) and nonhuman primates such as the rhesus macaque (*Macaca mulatta*) (Thornton *et al.* 2009; Goy 1981; Goy & Resko 1972). Prenatal androgens are known to have masculinising and defeminising effects on morphology, brain and behaviour in primates and other mammals (Thornton *et al.* 2009; Bodo & Rissman 2008; Bailey & Hurd 2005), while oestrogens play important roles both pre- and postnatally in the regulation of sociality and affiliative behaviour (Ross & Young 2009). Prenatal sex hormones may therefore play important roles in the expression of behaviour in female baboons.

1.1 Sex hormones: effects on physiology, brain and behaviour

1.1.1 The developmental role of sex hormones

Male and female sex determination has two major temporal phases. The first occurs *in utero* during embryo organogenesis, while the second occurs at puberty (Gilbert 2003). Primary sex determination involves the development of either male or female sexual organs from the bipotential gonad. The 'default' pattern during sexual differentiation is female in mammals (Wallen 2005) and male sex hormones

are required for the development of the male phenotype (Thornton *et al.* 2009). In males, genes on the Y chromosome initiate a series of events that have sexually differentiating effects (Arnold & Breedlove 1985), without which, the gonad differentiates into an ovary.

Sex hormones are central to the regulation of gene expression during development (Kondo *et al.* 1997) and are involved in sexual differentiation and the development of sexual dimorphisms (Chang 2008). Testosterone and dihydrotestosterone (DHT) are the two main masculinising and defeminising androgen hormones. Masculinisation describes enhancement of male-typical structures or behaviours while defeminisation describes the suppression of female-typical structures or behaviours (Thornton *et al.* 2009). Testosterone is involved in the formation of internal male reproductive structures and 5 α -DHT is responsible for the formation of external genitalia. Oestrogen is responsible for the development of female reproductive structures (Gilbert 2003).

1.1.2 Sex hormone patterns during prenatal development

The potential effects of prenatal sex hormones on the expression of baboon behaviour are best understood through the rhesus macaque, an Old World monkey. Rhesus macaques are born with their internal and external reproductive organs fully differentiated (Wallen 2005). Gestation lasts between 168-185 days (Thornton *et al.* 2009) and the testes differentiate between gestation days 35-40 in males and begin secreting androgens at this time (Wallen & Hassett 2009). During gestation, androgen levels in males rise at around day 40, decline at around day 75 and increase once again at day 140 until birth (Resko *et al.* 1987). The testes continue to secrete androgens throughout gestation and as a result males are exposed to higher levels of prenatal androgens than females (Thornton *et al.* 2009; Wallen & Hassett 2009). Females are exposed to low but quantifiable testosterone levels, possibly of maternal origin, as fetal ovaries are inactive at this time (Wallen 2005).

1.1.3 The androgen receptor gene (AR)

Variation in the structure of the androgen receptor gene (AR) determines an organism's sensitivity to prenatal testosterone (Manning *et al.* 2002). The AR is X-

linked and thus is maternally determined in males. It codes for a receptor protein with three functional domains. The terminal domain has a polymorphic CAG microsatellite and encodes glutamine repeats of varying length (Chang *et al.* 1988). The number of CAG repeats influences the binding of the hormone receptor complex to DNA and so CAG length is negatively associated with testosterone sensitivity (Manning *et al.* 2003). Alleles with low numbers of CAG repeats are more sensitive to testosterone than alleles with high numbers of CAG triplets and low CAG repeat length is indicative of high sensitivity to testosterone (Manning *et al.* 2003). Humans tend to have between 11-31 CAG repeats, chimpanzees (*Pan troglodytes*) 8-14 CAG repeats, gorillas 6-17 CAG repeats and gibbons 6 CAG repeats (Djian *et al.* 1996). Mice and rats have fewer (2) CAG repeats suggesting a high sensitivity to testosterone in rodents compared to humans and nonhuman primates (Djian *et al.* 1996).

1.1.4 Sex hormone effects on physiology and behaviour

Prenatal androgen effects (PAE) are responsible for sex differences in behaviour and morphology in many animal species (Wallen 2005; Saino *et al.* 2007; Brown *et al.* 2002a). Sex hormone effects cause changes in neural structure and function which persist throughout life (Tomaszycki *et al.* 2005). An example of this is the female spotted hyena (*Crocuta crocuta*). Females of this species are dominant to males and have highly masculinised external genitalia (Dloniak *et al.* 2006). Offspring of hyena mothers whose faecal androgen levels were high late in pregnancy were more aggressive and mounted peers at higher rates than offspring from mothers with low faecal androgen levels (Dloniak *et al.* 2006). Manipulating the prenatal hormone environment can have significant effects on anatomy and behaviour. Female spotted hyenas treated with an anti-androgen give birth to offspring showing reduced sibling aggression in early postnatal life (Drea 2007). Regular administration of testosterone to sheep influences the development of lambs, causing them to be behaviourally and physically masculinised (Lilley *et al.* 2010). Exposing developing females to high prenatal androgens increases the expression of male-typical structures and behaviours (Hines 2006).

The timing of prenatal exposure to androgens is important in affecting the masculinisation/defeminisation of anatomy and behaviour in rhesus macaques (Thornton *et al.* 2009). The external genitalia are most responsive to the masculinising influence of androgens during the second quarter of gestation, roughly between days 42-84 post-conception. Early and sufficient increases in prenatal androgens can result in the genital masculinisation of female rhesus macaques and both testosterone and DHT, are capable of masculinising female reproductive organs (Thornton *et al.* 2009). As little as 15 days of androgen treatment are necessary during the second quarter of gestation to produce significant masculinisation of female genitalia (Goy 1981) but treatment during the third and fourth quarters (after gestation day 100) has no effect on the appearance of female genitalia (Goy *et al.* 1988). Females treated with testosterone propionate had a regular but empty scrotum, lacked a vaginal opening and possessed a small but fully formed penis. These females still had ovaries suggesting the external genitalia are more sensitive to testosterone manipulation than the internal organs (Thornton *et al.* 2009).

Androgen treatment of rhesus macaque females from gestation day 35 through to 75 altered both their reproductive organs and behaviour in a masculine fashion (Wallen 2005). Only increasing prenatal androgen levels late in gestation (after gestation day 100) was found to cause behavioural masculinisation. However, late administration of androgens had no detectable effects on female-typical reproductive structures (Wallen 2005). This may be due to the fact that cortical neuron proliferation is not complete in the macaque brain until gestation day 100 (Rakic 1988) and so androgens can have masculinising and defeminising effects on the brain once genital differentiation is already complete (Herman *et al.* 2000). This suggests that behavioural sex differences are not governed by the appearance of the external genitalia but by differences in the brain that have developed *in utero* under the influence of PAE (Herman *et al.* 2000).

1.1.5 The role of postnatal sex hormones

In many primate species, males experience a postnatal surge in circulating testosterone levels shortly after birth which is not shared by females (Brown & Dixson 1999; Dixson 1986). Mostly, manipulation of this postnatal surge has not

been found to have significant effects on behaviour in primates, but it has been known to modify physical characteristics. Suppression of the surge in testosterone in male rhesus macaque infants has been found to delay their pubertal growth spurt (Mann *et al.* 1998), and retard penile growth and development (Brown & Dixson 1999). In females clitoris growth is increased by testosterone treatment and this indicates that the tissue of both male and female external genitalia is sensitive to testosterone in early postnatal life. However, the sexually dimorphic behaviours play and mounting were unaffected by manipulation of postnatal testosterone in male and female infants (Brown & Dixson 1999) suggesting that the root of the dimorphism of these behaviours originates in the prenatal stages of development (Knickmeyer *et al.* 2005).

1.1.6 Dominance behaviour

In many species, behaviours used to gain, maintain and improve individual social status are often noted among those high in testosterone (Josephs *et al.* 2006; Josephs *et al.* 2003; Kraus *et al.* 1999). Testosterone levels rise in the face of a confrontation, triggering behaviours which are effective for enhancing status and dominating opponents (Mazur & Booth 1998) and have been correlated with social dominance (Booth *et al.* 1989) and social assertiveness (Lindman *et al.* 1987). A typical dominance contest consists of a physical challenge from an opponent responded to through physical fighting, intimidation or fleeing. Testosterone increases muscle mass and metabolism and is therefore advantageous for maintaining current status or regaining lost status in the face of a challenge (Josephs *et al.* 2006). Circulating testosterone has been found to predict status-related behaviours only when higher status is available but not in hierarchies in which ranks are stable (Josephs *et al.* 2006). The likely winners in this type of dominance encounter are high testosterone individuals (Ostner *et al.* 2002; Morgan *et al.* 2000).

Testosterone levels in adult humans have been positively correlated with sensitivity to social dominance (Josephs *et al.* 2003), drives for social status and the tendency to create hierarchies (Mazur *et al.* 1997). Men and women with higher baseline testosterone levels are more responsive to references to their status than their lower baseline testosterone counterparts (Josephs *et al.* 2006;

Josephs *et al.* 2003). Testosterone is also related to selective attention to threatening faces, which can also be interpreted as individuals who may pose a status threat. Individuals with low testosterone were found to look away from threatening faces whereas high testosterone individuals were found to spend more time looking at angry or threatening faces (van Honk *et al.* 1999). Testosterone levels in adult humans are therefore associated with their inclination toward or aversion to high status (Josephs *et al.* 2006). Behaviours with the function of asserting social status in adolescent male rhesus macaques, such as stares, threats, displacements and non-sexual male mounting, are positively linked to their cerebrospinal fluid (CSF) free testosterone levels. These are low intensity dominating behaviours, unlikely to result in injury to either party (Higley 1996).

1.1.7 Aggressive behaviour

Dominance and aggression are linked through testosterone in humans and nonhuman primates (Higley *et al.* 1996). Animal studies implicate PAE as having some influence over the shaping of an individual's tendency to future aggressive behaviour (Mazur & Booth 1998; Christiansen & Knusmann 1987). Adult levels of testosterone are positively correlated with aggressiveness in humans (Mazur *et al.* 1997) and serum testosterone, free testosterone (T₃) and DHT levels are positively correlated with men's self-ratings of impulsive aggression (Christiansen & Knusmann 1987). In adult animals, testosterone not only affects an individual's aggressive behaviour but also responds to it and rises in the face of a challenge (Mazur & Booth 1998). Significant correlations are most often found between circulating testosterone and aggression when these are measured during competitive situations, social status challenges or in response to provocation or intimidation (Benderlioglu & Nelson 2007; McIntyre *et al.* 2007; Higley 1996). Congenital adrenal hyperplasia (CAH) is a condition in which the glucocorticoid synthesis pathway in the adrenal glands is disrupted and results in androgen production at unusually high levels (Yan *et al.* 2008). As a consequence, affected girls are exposed to PAE comparable to those seen in normal boys (Wallen & Hassett 2009) and typically have virilised external genitalia, display masculinized behavioural phenotypes, prefer male play partners and male-typical toys (Hines 2006; Berenbaum & Hines 1992). CAH females also have a masculine pattern of amygdala activation. This is an area of the brain associated with aggression and

CAH females show masculinised aggression patterns as a result (Nielssen *et al.* 2011). Findings in nonhuman primates convergent to those found in human studies suggest that sex hormones mould features of aggressive behaviour in nonhuman primates as they do in humans (Trainor *et al.* 2008; Anestis 2006; Beehner *et al.* 2005; Christiansen & Knusmann 1987).

1.1.8 Affiliative behaviour

In humans, high prenatal androgen levels have been associated with a lack of empathy (Chapman *et al.* 2006), less emotion recognition, reduced social sensitivity and less eye contact (Baron-Cohen *et al.* 2005). Additionally, higher prenatal testosterone is linked with a reduced ability to guess the thoughts and feelings of others and several disorders in which social behaviour is affected such as autism and Asperger's syndrome (Knickmeyer & Baron-Cohen 2006; Lim & Young 2006). Ovarian hormones and the hypothalamic neuropeptides oxytocin (OT) and vasopressin are involved in the regulation of social behaviour. Oestrogen is associated with the expression of social affiliative behaviours (Witt *et al.* 1992) and OT facilitates social motivation and approach behaviour (Lim & Young 2006). Both neuropeptides are necessary for the discrimination of familiar individuals and social bonding (Bielsky & Young 2004) and many of the behavioural effects of OT are brought about by oestrogen activity (Razzoli *et al.* 2003; Young *et al.* 1998). CSF OT levels are higher in the more affiliative bonnet macaque (*Macaca radiata*) than in the less social pigtail macaque (*Macaca nemestrina*) (Rosenblum *et al.* 2002). Ovariectomized female Japanese macaques (*Macaca fuscata*) exhibit a reduction in positive social behaviours and dominance behaviours when compared to tube-ligated females whose ovaries were still intact and as such were still able to receive steroid hormones. Successful navigation of the social environment by macaque females may depend upon ovarian hormones in adulthood and the predisposing effects of oestrogens on brain patterning during development (Coleman *et al.* 2011; Ross & Young, 2009).

1.1.9 Interest in infants

Interest in infants is a female biased sexually dimorphic behaviour in humans (Herman *et al.* 2003) and nonhuman primates (Lovejoy & Wallen 1988). As such it may be linked with higher prenatal oestrogens and/or reduced prenatal androgens

(Herman *et al.* 2003). Ovariectomized female rhesus macaques interacted with infants at higher rates after they had received oestrogen treatment (Maestripieri & Zehr 1998). Girls with CAH show less interest in infants than their unaffected female relatives (Leveroni & Berenbaum 1998) and masculinised juvenile female rhesus macaques show reduced interest in infants compared to controls (Wallen 2005). Sex differences in interest in infants among juveniles are of interest as its expression occurs at the quiescent period of the gonads. It is likely that this trait reflects prenatally determined behavioural predispositions which do not need circulating hormones for their expression before puberty (Wallen 2005).

1.1.10 Summary

Prenatal exposure to sex hormones influences sex differences in behaviour and behavioural differences within a single sex that do not require circulating hormones for their future expression (Knickmeyer *et al.* 2005). There are different temporal phases during development when the brain tissues that mediate various sexually dimorphic behaviours are sensitive to modification by prenatal sex hormones (Knickmeyer *et al.* 2005) in animal models. The critical period for sexual differentiation of the brain typically occurs when sex differences in serum testosterone are highest (Malas *et al.* 2006; van de Beek *et al.* 2004). The phases in development when the sex hormones have their masculinising or feminising effects on the brain, and consequently on behaviour, are also the phases when the growth of the digits are influenced by androgen and oestrogen receptor activity (Knoll *et al.* 2007; Zheng & Cohn 2011).

1.2 The 2D:4D ratio

As demonstrated in the previous section, early exposure to prenatal sex hormones has lasting organisational effects on the physiology, brain and behaviour of the adult animal (Groothuis *et al.* 2005). However, it is often difficult and risky for the subject to attempt to measure the prenatal hormonal environment directly, particularly in mammals, due to the close association between the mother and her developing offspring (Tabor *et al.* 2009). This has led to the search for a biomarker, a physical characteristic produced by prenatal sex hormones which can be safely measured postnatally (Berenbaum *et al.* 2009). The ratio of the lengths

of the second digit (2D) and fourth digit (4D) (2D:4D ratio) of the hands (Fig. 1.1) is proposed as one such biomarker (Manning *et al.*1998) and has received considerable attention with literature on the subject totalling over 300 publications (Voracek & Loibl 2009).

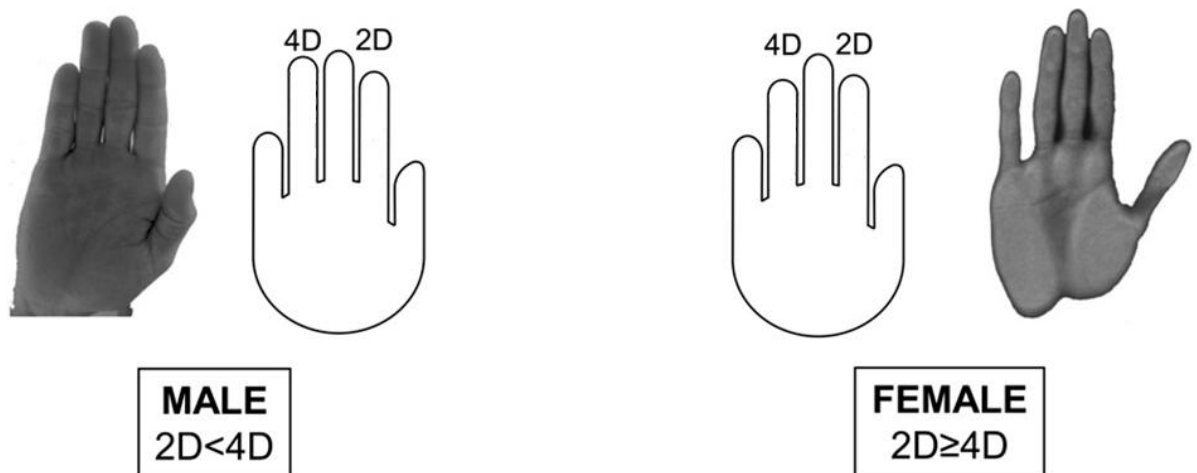


Figure 1.1: Diagram of 2D and 4D used to determine the 2D:4D ratio in human male and female hands. Adapted from Manning (2011).

1.2.2 Homeobox genes

The development of the urogenital system, limbs and digits is under the control of Homeobox genes, the functions of which are phylogenetically conserved among the vertebrates (Kondo *et al.* 1997; Zákány *et al.* 1997). *Hox* gene products are involved in the specification of where limbs form and the fate of mesenchymal cells as humerus, radius-ulna, or fingers in the forelimbs or their equivalents in the hind limbs of vertebrates (Gilbert 2003). The *Hox* family of genes is arranged into four clusters, *Hoxa* to *Hoxd* (Manning *et al.* 1998), which are heavily influenced by prenatal exposure to sex steroid hormones (Kondo *et al.* 1997). *Hox* genes are shared between the distal limb buds and the genital bud and the posterior-most *Hoxa* and *Hoxd* genes (groups 11-13) are needed for the growth and patterning of the digits and genital bud differentiation (Kondo *et al.* 1997; Zákány *et al.* 1997; Zákány & Duboule 1999). In humans mutations in the HOXA-13 gene can result in hand-foot-genital syndrome and in HOXD-13 in polysyndactyly (Gilbert 2003).

Sexual dimorphism of the 2D:4D ratio in humans was noted over a hundred years ago (Baker 1888) and to date the majority of studies have focussed on this trait and its correlates in humans. Only in the last decade have relationships begun to be investigated in other animal species (e.g. strawberry poison dart frog [*Oophaga pumilio*]: Chang 2008; green anolis lizard [*Anolis carolinensis*]: Lombardo & Thorpe 2008; Guinea baboon [*Papio hamadryas papio*]: Roney *et al.* 2004; zebra finch [*Taeniopygia guttata castanotis*]: Burley & Foster 2004; mouse [*Mus musculus*]: Brown *et al.* 2002a). The sex difference in 2D:4D ratio is not biased in the same direction in all species studied and varies among species and sometimes between populations of the same species (Chang 2008; Saino *et al.* 2007; Manning *et al.* 2004; Rubolini *et al.* 2006). Females usually have higher 2D:4D ratios than males among synapsid mammals (McIntyre *et al.* 2009; Brown *et al.* 2002a; Manning *et al.* 1998) and the opposite is usually the case in the diapsid birds and reptiles (Saino *et al.* 2007; Chang *et al.* 2006; Rubolini *et al.* 2006; Burley & Foster 2004) and in at least one anapsid anuran (Chang 2008). 2D:4D ratio in the strawberry poison dart frog was found to be higher in males than in females and as anurans are a basal group to the diapsids and synapsids, the diapsid species appear to express the sexually dimorphic trait in its ancestral form (Chang 2008). The relevance of applying findings from studies of human digit ratios to other diverse taxa stems from the ontogeny of tetrapod limbs and the aforementioned conserved nature of the *Hox* genes. Pentadactyly (five digits) is the ancestral condition in tetrapods and analogous associations between sex hormone-related traits and digit ratio have been documented across a diverse array of taxa. The evidence indicates that the trait is mediated by a common molecular mechanism, shared among the tetrapods, which arose more than 300 mya (Forstmeier *et al.* 2010).

1.2.3 Development of the 2D:4D ratio

In human men the 4D is typically longer than the 2D and in women 2D is either equal to or longer than the 4D (Fig. 1.1). There is substantial overlap between the sexes (Hönekopp *et al.* 2007), with female values averaging 0.25 standard deviations higher than male values (Manning *et al.* 2000). Human men have lower ratios of <1 and women have higher ratios of ≥ 1 (Manning *et al.* 2004; Manning *et*

al. 2000; Manning *et al.* 1998). This dimorphism can be explained by the fact that developing digits differ in their sensitivity to androgen and oestrogen hormones, the levels of which differ between the two sexes (Zheng & Cohn 2011). Both androgen and oestrogen receptor activities are higher in the 4D than in the 2D and nuclear androgen receptors remain present in higher numbers in the 4D throughout development (Zheng & Cohn 2011). Androgen receptors increase chondrocyte proliferation in the 4D and oestrogen receptors reduce chondrocyte proliferation in the 4D. In male mice androgen receptor activity increases in the 4D between embryonic day 12.5 and 14.5, but decreases in female mice during the same period. Males are exposed to higher prenatal androgen levels and this has the effect of promoting the growth of the 4D resulting in a lower (more masculine) 2D:4D ratio. Females, on the other hand, are exposed to higher prenatal oestrogen levels and this reduces growth in the 4D leading to a higher (more feminine) 2D:4D ratio. Therefore, sexual dimorphism of the 2D:4D ratio arises as a result of differential growth of the 4D in response to the different levels of sex hormones that the sexes are exposed to prenatally (Zheng & Cohn 2011). It is also likely that variation in prenatal sex hormones accounts for variation in digit ratio among individuals of the same sex (Manning 2002). Artificial addition of androgen in mice embryos mimics inactivation of oestrogen receptors and gives rise to a longer 4D whereas addition of oestrogen mimics inactivation of androgen receptors and means a shorter 4D (Zheng & Cohn 2011; Manning 2011). In mice, the 2D:4D ratio is generated by the balance of prenatal androgen to prenatal oestrogen signalling during a narrow window of fetal digit development and a similar process is likely to be occurring in other mammal species (Zheng & Cohn 2011). Consequently, lower (more masculine) 2D:4D ratios are indicative of higher PAE. The number of CAG repeats is positively associated with the 2D:4D ratio of the right hand in humans and low CAG repeat length is linked to low 2D:4D ratios, suggesting higher activation of the AR in individuals with more masculine 2D:4D ratios (Manning *et al.* 2003). Recently, secreted modular calcium-binding protein 1 (SMOC1) has been implicated as having roles in limb development, in the sexually dimorphic development of the gonads and in influencing digit ratio in humans (Lawrance-Owen *et al.* 2013). This gene product is secreted by the SMOC1 gene during osteoblast differentiation and acts as an antagonist of bone morphogenetic proteins (BMPs). Expression of the SMOC1 gene is increased by androgen (Love

et al. 2009) and decreased by oestrogen (Coleman *et al.* 2006) in prostate tissue and variation in digit ratio has been linked to variation upstream of SMOC1. Therefore, the SMOC1 gene could be acting as a mediator between prenatal sex hormone exposure and digit ratio (Lawrance-Owen *et al.* 2013).

Sex hormone effects on digit ratio happen during the early stages of fetal development and the trait remains relatively stable thereafter (Lombardo & Thorpe 2008; McIntyre *et al.* 2005; Brown *et al.* 2002b). Dimorphism in 2D:4D ratio is present as early as nine weeks of gestation in humans (Malas *et al.* 2006), is not altered palpably by the increase in steroid hormones experienced at puberty and is relatively stable over growth (Manning *et al.* 2004; 2003). Although a slight increase in 2D:4D ratio with age was reported in very young children (Trivers *et al.* 2006), this is not supported in studies with larger sample sizes (Manning *et al.* 2004; 1998) and appears to be stable after two years of age (Knickmeyer *et al.* 2011; Manning 2002). There are notable ethnic and population differences in 2D:4D ratio. Among European Americans 2D:4D ratios were higher than those seen in African Americans (Manning *et al.* 2002). Higher age stability was observed in right hand 2D:4D ratio (Trivers *et al.* 2006) and this has been attributed to the right hand being more sensitive to PAE and more robust to postnatal environmental effects (Flegr *et al.* 2008; Gobrogge *et al.* 2008).

1.2.4 Lateral asymmetry of 2D:4D ratio

The 2D:4D ratio shows lateral asymmetry (Rizwan *et al.* 2007; Manning *et al.* 1998) with right hand 2D:4D showing stronger associations with sexually dimorphic traits (humans – Flegr *et al.* 2008 but see Putz *et al.* 2004; zebra finches - Burley & Foster 2004; baboons – McFadden & Bracht 2003; mice - Brown *et al.* 2002a). Sexual dimorphism is greater for the right hand than the left in humans (McFadden & Shubel 2002) and in general sexually dimorphic traits tend to be displayed in the more masculine form on the right side of the body e.g. testes size larger on the right (Tanner 1990). This asymmetry may be a result of increased sensitivity to sex hormones on the right side of the body (Dreiss *et al.* 2008). Infection with the protozoan parasite, *Toxoplasma gondii*, is believed to increase testosterone and dopamine levels in the host (Flegr 2007) and induces behavioural and neurophysiological changes in humans and other animals (Flegr

et al. 2008). Human males infected with the parasite are taller, perceived as more dominant and masculine (Hodková *et al.* 2007) and have lower left hand 2D:4D ratios (Flegr *et al.* 2005). Parasitized human females give birth to more male than female offspring (Kaňková *et al.* 2007a), as is also the case in lab infected female mice (Kaňková *et al.* 2007b). High testosterone levels have immunosuppressive effects so we cannot be sure that the association between low left 2D:4D ratios and infection with the parasite is due to the higher susceptibility of these individuals to parasitic infection or whether it is a result of host modification by the effects the parasite has on the host's testosterone levels (Flegr *et al.* 2008). In addition to this evidence for postnatal sex hormones having greater influence on the left hand 2D:4D ratio, inconsistencies in 2D:4D ratios of the front left legs were recorded in two different laboratory populations of anole lizards (Chang *et al.* 2006). This suggests that the mean of the right and left 2D:4D ratios or right hand 2D:4D ratio should be used when investigating traits associated with the prenatal hormonal environment in preference to the left hand 2D:4D ratio.

1.2.5 The source of the hormones influencing digit ratio

Knowledge concerning the source of the prenatal steroid hormones that affect the expression of digit ratio is incomplete. Although the main source of prenatal sex steroids in mammals are the gonads, the adrenal glands have also been known to influence digit ratio as is seen in females with CAH (Hönekopp & Watson 2010). CAH girls have been observed to have lower, more male-typical 2D:4D ratios (Brown *et al.* 2002b) suggesting that steroid hormones originating in the fetal adrenal glands may also affect digit development in certain situations and supporting the 2D:4D ratio as an androgen sensitive trait.

Exposure to maternal testosterone during gestation was not found to impact 2D:4D ratio of field vole (*Microtus agrestis*) offspring (Lilley *et al.* 2010) and amniotic testosterone levels are not correlated with maternal testosterone levels in humans (van de Beek *et al.* 2004). This suggests that the sex hormones influencing the development of the digit ratio originate from the foetus itself in mammals (Lilley *et al.* 2010). A possible explanation for this is the nature of the mammalian placenta, in which the enzyme aromatase acts to buffer the foetus

from high levels of testosterone (Cohen-Bendahan *et al.* 2005). In the case of mammals, maternal sex hormones may have a limited ability to influence fetal hormone levels (Lilley *et al.* 2010). This is in agreement with the generally low and non-significant correlations reported between amniotic fluid and maternal plasma androgen levels (van de Beek *et al.* 2004).

Another steroid hormone, cortisol, commonly known as the 'stress hormone', has been known to affect the physiology and behaviour of individuals (Lilley *et al.* 2010). Maternal stress can influence the development of gestating embryos (Hines *et al.* 2002). High corticosterone levels during pregnancy can be detrimental to the masculinisation of male foetuses in rats and cause increased masculinisation of female behaviour in guinea pigs and prairie voles (Lilley *et al.* 2010; Thornton *et al.* 2009). There is evidence for some influence of corticosterone on the development of the 2D:4D ratio. Maternal pre-pregnancy stress (corticosterone) levels were associated with lower 2D:4D ratio in the right paw of male and female field vole offspring but not in the left paw (Lilley *et al.* 2010). Corticosterone may also affect the degree of lateral asymmetry between the 2D:4D ratios of the right and left hands, causing a reduction in symmetry (Lilley *et al.* 2010).

The cleidoic eggs of reptiles and birds provide an enclosed environment in which it is possible to test the effects of prenatal sex hormones without the confounding factors presented by the internal gestation in mammals (e.g. maternal hormones) (Saino *et al.* 2007). Evidence exists for a maternal influence on the sex hormone environment encountered by bird species through variation of sex hormone allocation to egg yolk (Burley & Foster 2004). This adaptation may enhance maternal fitness by regulating patterns of competition within broods as yolk androgens are known to have some bearing on hatchling performance (Schwabl & Lipar 2002). In several bird species yolk androgen levels increase with position in the laying order (American Coot [*Fulica americana*]: Reed & Vleck 2001; Canary [*Serinus canaria*]: Schwabl 1993) and this is proposed to increase the competitive ability of younger and smaller offspring, improving the chances that later-hatching individuals will survive (Burley & Foster 2004). In other species, yolk androgen levels decrease over the laying period and this is a common pattern in species that experience unpredictable food supplies (Gil *et al.* 1999) or in which siblicide is a common occurrence (Schwabl *et al.* 1997). In zebra finches the 4D is longer in

birds hatched from earlier laid eggs which are higher in yolk androgen levels and 2D:4D ratio increases with position in the laying order. This is in keeping with greater sensitivity of the 4D to androgens as is seen in humans and mice (Zheng & Cohn 2011). Injecting ring-necked pheasant eggs with testosterone produced females with more masculinised digit ratios than control birds (Romano *et al.* 2005). Increasing oestrogen levels in yolk by injecting eggs with estradiol feminized digit ratios in the right foot of male ring-necked pheasants so that they were not significantly different from digit ratios of female controls (Saino *et al.* 2007; Romano *et al.* 2005). Testosterone can be converted into estradiol by aromatase locally in the brain and in the bone growth plates and oestrogens are known to affect bone growth (Forstmeier *et al.* 2010). Genetic variation in oestrogen receptors was associated with digit ratio in zebra finches but variation in androgen receptors was not (Forstmeier *et al.* 2010). Therefore, androgen hormones may be more important for the expression of the 2D:4D ratio and sexually dimorphic traits in mammals and oestrogen hormones may be more important in birds (Forstmeier *et al.* 2010).

1.2.6 The 2D:4D ratio and reproductive success

The 2D:4D ratio is a sexually dimorphic trait and correlates with several other sexual dimorphisms which act as signals of an individual's prenatal hormonal environment. These traits are often determined by sex hormones and are important for reproductive success in humans and other species (Dreiss *et al.* 2008; Saino *et al.* 2006b). Men are primed to choose women with high fertility and the 2D:4D ratio in women is positively associated with oestrogen and luteinizing hormone levels (Manning *et al.* 1998). Women with low (masculine) 2D:4D ratios tend to have lower reproductive success and have a higher susceptibility to parasitic infection (Saino *et al.* 2006b; Flegr *et al.* 2008) which comes from developing in a prenatal environment high in testosterone. Masculine 2D:4D ratios have also been associated with conditions causing infertility in women such as polycystic ovary syndrome (Cattrall *et al.* 2005). Evolutionarily, women may have been selected to prefer men displaying high testosterone-dependent traits (Saino *et al.* 2006b). Male facial characteristics are structured prenatally by testosterone and shaped during puberty (Neave *et al.* 2003; Kasperk *et al.* 1997). Higher levels

of prenatal testosterone likely produce more typically masculine faces in humans (e.g. lengthened lower facial bone, forward growth of eyebrow ridge bones and lateral growth of the cheekbones), and lower levels produce male faces with more typically feminine characteristics (Burriss *et al.* 2007; Neave *et al.* 2003). The 2D:4D ratio has been observed to correlate negatively with how dominant and masculine a man's face is perceived. More masculine faces were rated as more dominant but not more attractive by women (Neave *et al.* 2003; Swaddle & Reiersen 2002) and women with more masculine faces were rated as more dominant by other women (Watkins *et al.* 2012). There is also support for 2D:4D ratio correlating with sexual dimorphisms that have a role in reproductive success in bird species. Right foot 2D:4D ratio in barn swallows (*Hirundo rustica*) is negatively linked to a secondary sexual characteristic in this species, tail length, in both sexes (Dreiss *et al.* 2008). This implies that early sex hormone levels simultaneously affect the future expression of two sexually dimorphic traits in this bird; tail length and digit ratio (Dreiss *et al.* 2008).

1.2.7 The 2D:4D ratio and behaviour

The 2D:4D ratio correlates with several behavioural measures across a variety of species and in humans correlates with numerous behavioural and physiological sexual dimorphisms (Zheng & Cohn 2011; Fisher *et al.* 2010). Human participants scoring high on a test for behaviours associated with testosterone had longer 4Ds and lower 2D:4D ratios and participants who scored high on behaviours associated with oestrogen/OT had longer 2D and higher 2D:4D ratios (Fisher *et al.* 2010). The 2D:4D ratio has also been found to be lower in humans with autism and Asperger's syndrome, disorders associated with elevated PAE (Manning *et al.* 2001). Further evidence that the 2D:4D ratio correlates with PAE on behaviour comes from studies on humans with the X-linked disorder complete androgen insensitivity syndrome (CAIS). These are XY individuals who lack functioning androgen receptors and so are unable to respond to the hormones *in utero*. As a result, although genetically male, they develop as sterile females (Hines 2006). These people have a female-typical appearance, psychosexual development, gender identity and behaviour and as such are treated as female (Hines *et al.* 2003). Interestingly, they also display feminised 2D:4D ratios (Berenbaum *et al.*

2009). Higher 2D:4D ratios which were closer to human female population norms were found in human men with Klinefelter's Syndrome (KS; 47 XXY). This is a condition in which the endocrine system is affected and results in low testosterone levels being present in fetuses, new-borns and adults affected with the syndrome (Manning *et al.* 2013) lending further support to the 2D:4D ratio acting as a biomarker for prenatal androgen exposure.

In humans, low 2D:4D ratios are correlated with higher dominance-related behaviours in both sexes and higher drives for social status (Millet & Dewitte 2007; 2009). Additionally, individuals with low 2D:4D ratios are perceived as more dominant (Neave *et al.* 2003) and show higher reactive aggression (Benderlioglu & Nelson 2004). The 2D:4D ratio is also related to sperm count (Manning *et al.* 1998), fecundity (Manning *et al.* 2002), sporting ability (Manning & Taylor 2001), strength (Fink *et al.* 2006), intelligence (Luxen & Buunk 2005), agreeableness and cooperativeness (Millet & Dewitte 2006) in humans.

1.2.8 Heritability of the 2D:4D ratio

Heritability studies in rhesus macaques, humans and zebra finches point towards considerable genetic contributions to the expression of the 2D:4D ratio (Nelson & Voracek 2010; Forstmeier *et al.* 2008; Paul *et al.* 2006a; Forstmeier 2005) and testosterone production is highly heritable in humans (Hines 2006). Heritability was found to be higher in the right hand than the left in rhesus macaque mother/offspring pairs (Nelson & Voracek 2010), a result paralleled in human twin studies (Paul *et al.* 2006a). Heritability of the 2D:4D ratio in a human twin study was moderate to high and unsurprisingly similarity was higher between monozygotic than dizygotic twins (Gobrogge *et al.* 2008). Females with male co-twins are masculinised in their expression of sensation seeking (Resnick *et al.* 1993) and have lower 2D:4D ratios than females with same-sex twins (van Anders *et al.* 2006). As fetal skin is permeable to fluid and some dissolved solutes up to the 18th week of gestation and amniotic fluid passes through the entire foetoplacental unit this is likely to be due to transfer of their brother's androgens having masculinising effects on the female foetus (Knickmeyer *et al.* 2005). A similar effect is also seen in female rats, with those gestated between two males

being more masculinised and aggressive and showing masculinised 2D:4D ratios (Hurd *et al.* 2008).

1.2.9 The 2D:4D ratio in nonhuman primates

In general, nonhuman primates have more masculinised digit ratios than humans (Nelson & Shultz 2010; Manning *et al.* 2003). Polygynous primates tend to have lower 2D:4D ratios (high PAE) and pair-bonded species tend to have higher 2D:4D ratios (low PAE) (Nelson & Shultz 2010). The 2D:4D is sexually dimorphic in chimpanzees and bonobos (*Pan paniscus*) with males exhibiting lower 2D:4D ratios than females in both species. Chimpanzees displayed 2D:4D ratios which were lower and more masculine than found in human populations (McIntyre *et al.* 2009). However, bonobos were found to have considerably higher 2D:4D ratios than chimpanzees, closer to human population means (McIntyre *et al.* 2009; Manning *et al.* 2000). This was attributed to their relatively female-dominated social system compared with the male-dominated system of their chimpanzee cousins. Behavioural differences between the two closely related species include increased tolerance and a greater potential for cooperating with conspecifics in bonobos (Hare *et al.* 2007) and are speculated to reflect differences in exposure to PAE causing reduced masculinisation in bonobos compared to chimpanzees. This is supported by adult male chimpanzees having higher testosterone levels than adult male bonobos and reduced sexual dimorphism between male and female bonobos. Male chimpanzees have larger canine teeth and body size than females, a difference which arises during puberty (McIntyre *et al.* 2009). Chimpanzees also show a marked increase in the sex difference in 2D:4D ratio with age with male 2D:4D ratio decreasing during puberty (McIntyre *et al.* 2009). This is akin to evidence in human populations and other primates that differences 2D:4D ratio are linked to the level of polygyny and intra-sexual competition among males (Nelson & Shultz 2010; McIntyre *et al.* 2009; Manning & Fink 2008).

In a study of Guinea baboons, adult males had higher 2D:4D ratios than adult female baboons, the opposite of the human pattern (Roney *et al.* 2004). Western lowland gorillas (*Gorilla gorilla gorilla*) display moderate-high sex differences in ratios of metacarpals and metatarsals that are not attributable to differences in body size between males and females (McFadden & Bracht 2003). As in Guinea

baboons, male gorillas had higher length ratios than females between the second and fourth metacarpals but female gorillas had higher length ratios between the second and fourth metatarsals (McFadden & Bracht 2003). Several studies have reported correlations between the 2D:4D ratio and behaviours linked to dominance and aggression (Hurd *et al.* 2011; McIntyre *et al.* 2009; Bailey & Hurd 2005; Neave *et al.* 2003). The 2D:4D ratio correlated negatively with dominance rank in free-ranging adult female rhesus macaques (Nelson *et al.* 2010) and right hand 2D:4D ratio also negatively correlated with rank in captive adult female Hamadryas baboons (*Papio hamadryas hamadryas*) and in orphaned juvenile female chacma baboons (*Papio hamadryas ursinus*) (Howlett *et al.* 2012). This negative correlation between 2D:4D ratio and female dominance rank appears to be universal across Old World monkeys and perhaps may apply more widely to primates in general (Howlett *et al.* 2012; Nelson *et al.* 2010). The evidence suggests that, in addition to its use in humans, the 2D:4D ratio is capable of acting as a biomarker for PAE on behaviour of nonhuman primates, both between and within sexes.

1.2.10 The 2D:4D ratio as a biomarker

Postnatal sex hormone levels fluctuate extensively over seasons, the time of day and in response to various stimuli (Bernhardt *et al.* 1998) making attempting to use them as a reflection of the prenatal hormonal environment challenging if not impractical. Adult serum sex hormones do not appear to correlate with 2D:4D ratio (Muller *et al.* 2011; Neave *et al.* 2003) and the onset of sexual maturity does not alter the sex difference in 2D:4D ratio in humans (Manning *et al.* 1998; McIntyre *et al.* 2005; Hönekopp *et al.* 2007). Postnatal hormonal manipulation, between the 1st and 3rd days of life, had no effect on the 2D:4D ratio of mice (Zheng & Cohn 2011). Malas *et al.* (2006) found no significant change in 2D:4D ratio over gestational age and no correlation between 2D:4D ratio and gestational age in humans reinforcing the suggestion that, in the absence of direct measurements, the 2D:4D ratio can be used as a valid indicator of an individual's prenatal sex hormone environment.

1.3 Competition and female relationships

Dominance, aggression and competition are all important behaviours governing social life in primates (Sterck *et al.* 1997). The basic assumption of socioecological theory is that females compete for access to nutritional resources and males compete for access to females (Kappeler & van Schaik 2002). Predation risk and feeding competition are among the ecological factors that contributed to the evolution of female social relationships. Predation risk led diurnal female primates to form groups for safety (van Schaik 1989; 1983). Female-female relationships are therefore influenced by the style and strength of the feeding competition that they face within their social group, which is sculpted by the distribution of resources (Kappeler & van Schaik 2002; Koenig 2002; Sterck *et al.* 1997; Chapman *et al.* 1995). When resources are evenly distributed or plentiful then indirect (scramble) competition is the norm (Kappeler & van Schaik 2002). However, when resources are clumped and monopolisable then direct (contest) competition is expected to occur. This brings about agonistic interactions between females and results in the formation of hierarchical relationships (Sterck *et al.* 1997).

1.3.1 Female baboons

Social relationships among gregarious females can be categorised as dispersal-egalitarian, resident-egalitarian, resident-nepotistic and resident-nepotistic-tolerant (Sterck *et al.* 1997). One of the most common forms of social system is resident-nepotistic, and is the system seen in female baboons. Female baboons live in strongly female bonded societies within matrilineal societies consisting of a matriarch and her close female kin (Silk *et al.* 2010). A stable linear dominance hierarchy exists between the various matrilineal societies in a troop and also between female kin within each matriline (Silk *et al.* 2006; Samuels *et al.* 1987; Hausfater *et al.* 1982). A female's rank is inherited from her mother and dominance relationships among females follow younger daughter ascendancy, so that younger daughters displace their older sisters to gain the rank position below their mother (Silk *et al.* 2010; Engh *et al.* 2009; Altmann 2001). Close kin often occupy adjacent ranks and kinship is important in the formation and maintenance of social bonds (Dunbar 1988). Rank reversals are uncommon and the hierarchy in female baboons is remarkably

stable over time (Cheney & Seyfarth 2007; Engh *et al.* 2006). In most species, male baboons emigrate out of their natal troops once they reach maturity (Cheney & Seyfarth 2007) but are dominant to all females years before they emigrate (Engh *et al.* 2009). In contrast to the relative stability of the female hierarchy, the dominance hierarchy in males is unstable and rank changes occur often (Kitchen *et al.* 2003). A male may occupy several rank positions over his lifetime and tenures as dominant male tend to be short (Cheney & Seyfarth 2007).

Female baboons are permanently gregarious, intensely social, female-bonded primates and form stable, linear dominance hierarchies in which dominance relations are despotic. They are therefore ideal subjects for investigating the correlation between the 2D:4D ratio (inferred PAE) and female social behaviour, in particular dominance, and to explore how these may apply to primates in general. The social processes behind rank acquisition in female baboons, such as maternal support and alliances with kin have been well studied and social factors contributing to the maintenance of hierarchies are well understood (Silk *et al.* 2006; 2010). The part that physiological development plays in affecting female social behaviour, however, has not received the same detailed attention. Thus, this thesis aims to explore correlations between PAE (using the 2D:4D ratio as a marker) and social behaviour in adult female chacma baboons focussing on dominance, aggression, interest in infants and affiliation.

1.4 Summary of aims

The primary aims of this study are:

- 1) To validate an indirect photographic and computer software method for measuring 2D:4D ratios in wild baboons.
- 2) To determine whether a potential prenatal androgen marker (2D:4D ratio) correlates with a female's position in the dominance hierarchy in wild adult female baboons.
- 3) To examine the relationship between prenatal sex hormones (inferred from 2D:4D ratios) and social interactions among females.
- 4) To assess indirect evidence for heritability of the 2D:4D ratio by testing for a correlation between mother/infant pairs.

- 5) To assess indirect evidence for effects of maternal rank on offspring 2D:4D ratio.

1.5 Hypotheses & Predictions

Hypothesis 1: PAE are related to dominance and submission.

Individuals with lower 2D:4D ratios have been exposed to higher PAE (Zheng & Cohn 2011) and their behaviour is likely to be more masculinised and dominant than those exposed to lower PAE.

1a: I predict that all 2D:4D ratio measures will correlate negatively with dominance rank with females with lower 2D:4D ratios having higher positions in the dominance hierarchy than females with higher 2D:4D ratios.

1b: I predict that all measures of 2D:4D ratio will correlate positively with rate of submission. Females with lower 2D:4D ratios will show lower rates of submission.

Hypothesis 2: PAE are related to aggression.

Animal studies implicate PAE as having some influence over the shaping of an individual's tendency toward aggressive behaviour in adulthood (Mazur & Booth 1998; Christiansen & Knussmann 1987) and PAE also shape an individual's 2D:4D ratio.

2a: I predict that all measures of 2D:4D ratio will correlate negatively with rates of aggression. Females with lower 2D:4D ratios will display higher rates of both non-contact and contact aggression.

2b: I predict that only highly masculinised (low 2D:4D) individuals will show physical aggression at high rates and predict that the correlation between 2D:4D ratio measures and rate of contact aggression will be higher than between 2D:4D ratio measures and rate of non-contact aggression.

2c: I predict that the rate at which a female receives aggression will correlate positively with all 2D:4D ratio measures. Females with lower 2D:4D ratios will receive aggression from other group members at lower rates than females with higher 2D:4D ratios.

Hypothesis 3: PAE are related to interest in infants.

Interest in infants is more prevalent in females and hence hypothesised to be oestrogen-dependent and is reduced in androgenised female humans and rhesus macaques (Leveroni & Berenbuam 1998; Herman *et al.* 2003).

3a: I predict that all 2D:4D ratio measures will correlate positively with interest in infants. Females with lower (more masculine) 2D:4D ratios will show lower rates of interest in infants than females with higher (more feminine) 2D:4D ratios.

Hypothesis 4: PAE are related to affiliation.

Oestrogens are associated with the expression of affiliative social behaviours and, in humans, high PAE are associated with disorders in which sociality is impaired (Manning *et al.* 2001). OT and vasopressin are regulated by oestrogen and are necessary for discrimination of familiar individuals and social bonding (Bielsky & Young 2004). Females exposed to higher prenatal oestrogens may be more motivated to form social bonds and seek social contact than females exposed to higher PAE (Lim & Young 2006).

4a: I predict that all 2D:4D ratio measures will correlate positively with rate of affiliation. Females with lower 2D:4D ratios will show lower rates of affiliation than females with higher 2D:4D ratios.

4b: I predict that all 2D:4D ratio measures will correlate positively with number of grooming partners and number of social partners. Females with lower 2D:4D ratios will have fewer grooming and social partners than those with higher 2D:4D ratios.

4c: I predict that all 2D:4D ratio measures will correlate positively with rate of grooming given. Females with lower 2D:4D ratios will groom others at lower rates than females with higher 2D:4D ratios.

4d: I predict all 2D:4D ratio measures will correlate negatively with rate of grooming received. Females with lower 2D:4D ratios will receive grooming at higher rates than those with higher 2D:4D ratios.

Hypothesis 5: Dr-I is related to social behaviour.

Like the 2D:4D ratio, right hand 2D:4D minus left hand 2D:4D (Dr-I) is unrelated to adult sex hormone levels (Hönekopp *et al.* 2007) and may be a negative correlate of PAE in humans (Manning *et al.* 2003; Manning 2002). Therefore, in addition to examining the relationship between behaviours and 2D:4D ratio measures, I will also look into the relationship between Dr-I and behaviours.

5a: I predict Dr-I and dominance rank will correlate negatively. Females with lower Dr-I will be higher-ranked than those with higher Dr-I.

5b: Dr-I will also show a negative relationship with rate of non-contact aggression and rate of contact aggression. Females with lower Dr-I will show higher rates of both types of aggressive behaviour.

5c: There will be a positive association between Dr-I and rate of submission. Females with lower Dr-I will show lower rates of submission than those with higher Dr-I.

Hypothesis 6: The 2D:4D ratio is heritable.

There is evidence that genetic contributions have substantial involvement in the expression of the 2D:4D ratio (Nelson & Voracek 2010; Paul *et al.* 2006a; Forstmeier *et al.* 2008) and heritability of the 2D:4D ratio is higher in the right hand than the left in rhesus macaque mother/offspring pairs (Nelson & Voracek 2010).

6a: I predict that there will be a high positive correlation between mother's mean, right and left 2D:4D ratios and the corresponding 2D:4D ratio measures in her infant.

6b: I predict that correlation between maternal right 2D:4D ratio and infant right 2D:4D ratio will be stronger than between all other combinations.

6c: I predict maternal rank will correlate negatively with offspring 2D:4D ratio. Higher-ranked females will produce offspring with lower 2D:4D ratios.

Pilot experiments

2.1 Overview

Various methods have been used to measure 2D:4D ratio, some more widely than others. Popular methods include direct measurements with callipers (Scutt & Manning 1996), photocopies (Manning *et al.* 2005) and measurement of scanned images of hands (Bailey & Hurd 2005). Scaled tubes (Nicholls *et al.* 2008), radiographs (Paul *et al.* 2006b) and digital photographs (Pokrywka *et al.* 2005) have been used less often. To date very few studies have used high definition (HD) video as a method to measure length of objects. Mostly this method has been employed by those interested in studies that require non-destructive observation methods (Pelletier *et al.* 2011) such as in marine and plant studies, for example to measure fish length (Harvey *et al.* 2004) or to predict crop yield (Novaro *et al.* 2001). More recently, researchers have begun to explore the use of computer-assisted analysis in 2D:4D research. Allaway *et al.* (2009) found computer-assisted measurement to be more accurate than direct measurements with callipers and measurements from photocopies and scans, with greater intra- and inter-observer reliability, and recommend the use of computer-assisted measurements in the place of other known methods whenever possible.

The majority of the 2D:4D ratio literature has focussed on human behaviour and the studies cited above used humans or the model organism for mammalian development, the mouse. A few studies have investigated digit ratios in nonhuman primates, most of which used the direct calliper measurement method (Nelson *et al.* 2010; Roney *et al.* 2004) or measurements from scanned images (McIntyre *et al.* 2009). The problem with measuring digit ratios in non-anaesthetised nonhuman primates is their unpredictable behaviour. Further issues arise from the study of wild populations, which cannot be trained to hold their limbs in certain positions or anaesthetised to obtain direct measurements of digits.

The vast majority of the 2D:4D literature on humans has focused on ratios of finger lengths and only one study that I am aware of investigated the 2D:4D ratio in human toes (McFadden & Shubel 2002). Measurement difficulties arise with using toes as opposed to fingers due to the natural curvature of toes (McFadden & Shubel 2002) but the hind feet/paws are regularly used in literature involving other animal species such as mice (Hurd *et al.* 2008), amphibians (Chang 2008) and birds (Burley & Foster 2004; Saino *et al.* 2007). My aim here was to obtain finger length ratios as the chacma baboon walks on its palms with its fingers held straight and so I was more likely to obtain photographs with digits held in good positions from hands than from feet. Thus, I needed to determine whether it was possible to get accurate 2D:4D ratios when measuring from the dorsal side of the hand, as such photographs of baboon hands were easiest to attain. I needed to establish whether the distance a photograph was taken from and camera zoom setting had an effect on 2D:4D ratio obtained from digital photographs. I also needed to determine which angles of the hand produced accurate 2D:4D ratio measurements and which did not in order to establish which photographs to use in analyses. Therefore I tested the abilities of the digital photographic method and HD video method to provide accurate 2D:4D ratio measurements in humans with the intention of employing this method on wild baboons. I then tested the accuracy of the digital photographic method on chacma baboons. I aimed to assess the validity of using digital photographic and HD video methods to measure 2D:4D ratios in a troop of wild baboons and to understand the limitations of each in order to obtain realistic digit measurements using computer-assisted analysis. To do so, I conducted a stepwise series of pilot experiments, first using human subjects and then progressing onto captive baboon subjects. Testing methods intended for research on nonhuman primates on human subjects has limitations due to morphological differences between humans and nonhuman primates. However, human behaviour is more predictable, and it is easier to control the environment for data collection and I wanted to ensure that the methods were successful under controlled conditions with cooperative human subjects before moving on to baboon subjects. Next, I tested the accuracy of the measurement methods on captive baboon subjects in an environment more controlled than in the wild to validate the methods for use on wild baboons.

2.2 Using digital photographs to measure 2D:4D ratios in human hands

2.2.1 Study subjects

The study cohort comprised 12 human volunteers, recruited from my family, and included six males and six females between the ages of eight years and 79 years. I explained the purpose of the study to participants and allowed them to ask questions prior to data collection.

2.2.2 Data collection

I measured the 2D and 4D on each hand of each subject from the crease where the finger joins the palm (ventral side) to the tip of the extended digit (nearest mm) using Draper callipers (Manning, *et al.* 1998). I measured the 2D of the left hand first, followed by the 4D and repeated the same order for the right hand. I took measurements three times for each digit and used the mean in analyses. I calculated the 'true' 2D:4D ratio of each participant using these direct calliper measurements by dividing the length of the 2D by the length of the 4D for comparison with 2D:4D ratios obtained from images.

Next, I assessed whether the distance the photograph was taken from had an effect on the ratios obtained. A photograph was taken from close to the participant's hand and then from 3 m away without adjusting the camera settings. Also, the effect of camera zoom was investigated by photographing hands with the camera set at 0 %, 50 % and 100 % zoom. In both cases I used five images of a randomly chosen hand (in ventral view with hand flat and fingers straight as seen in Fig. 2.1: position I) from five different subjects.

I invited volunteers to place their hand on a flat surface in 10 different positions without applying pressure (Fig. 2.1). I took one photograph of both the left and right hand in each position and stored these in a computer for later analysis. I analysed these digital images using computer-assisted image analysis software (Image Processing and Analysis in Java, ImageJ) using mouse-controlled callipers to measure digit lengths from the images in pixels. I measured digits from both dorsal and ventral surfaces. When measuring from the ventral surface, I took measurements from the basal crease of each digit to its tip. When measuring from

the dorsal surface the crease is not visible so I took measurements from the webbing between the digits (which is in line with the basal crease on the ventral surface) or an equivalent landmark to the tip of the digit. I took measurements five times for each digit and used the mean of these for analyses. As above, I calculated 2D:4D ratios obtained for each image by dividing the length of the 2D by the length of the 4D. I chose the hand positions based on poses often seen in baboons (personal observation) when resting, walking and foraging that may be useful for measuring 2D:4D ratios in wild baboons (Fig. 2.2).

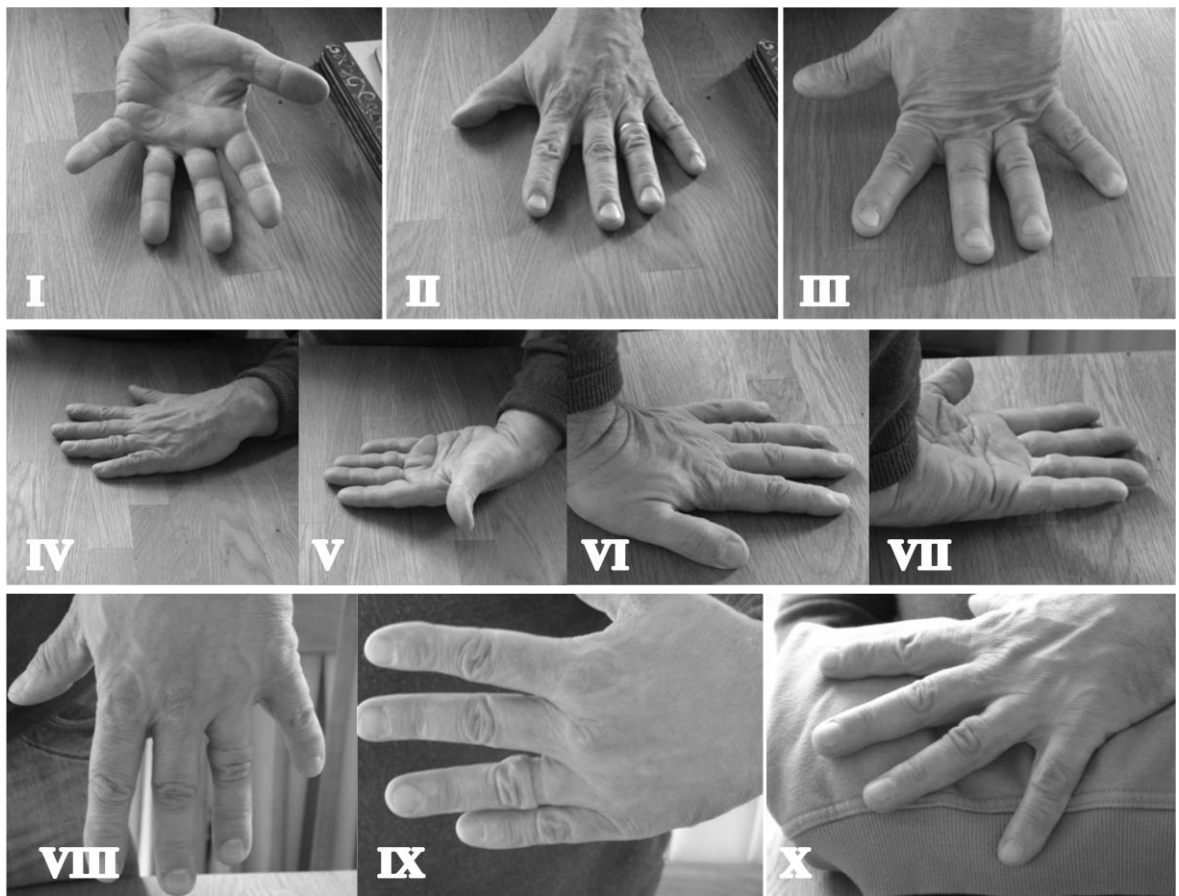


Figure 2.1: Ten different hand positions investigated to determine which give accurate 2D:4D ratios in humans. I – ventral view hand flat fingers straight; II – dorsal view hand flat fingers straight; III – dorsal view hand bent fingers flat and straight; IV –dorsal view hand flat fingers sideways (facing out); V – ventral view hand flat fingers sideways (facing out); VI – dorsal view hand flat fingers sideways (facing in); VII – ventral view hand flat fingers sideways (facing in); VIII – dorsal view fingers free hanging downwards; IX – dorsal view fingers free hanging sideways; X – dorsal view relaxed hand resting on surface with fingers at different elevations.

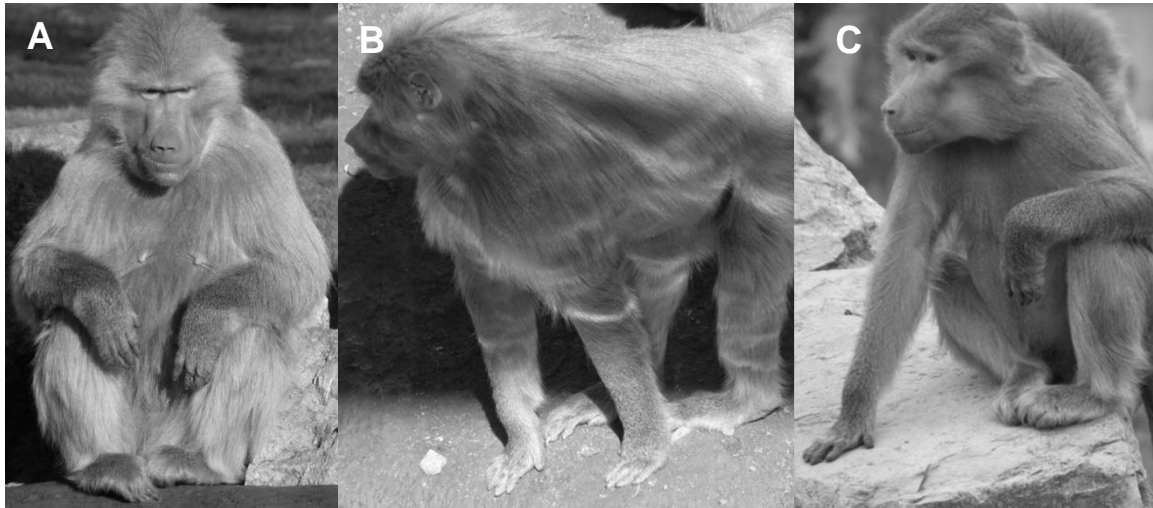


Figure 2.2: Examples of postures commonly observed in baboons. A – a resting pose in which the animal has its hands relaxed and hanging freely downwards (analogous to position VIII); B – walking stance, where the baboon bends its hand maintaining straight fingers (analogous to position III); C – another position frequently seen with animals resting their hands on a surface on which their fingers are at different elevations (analogous to position X).

2.2.3 Statistical analyses

I used Kolmogorov-Smirnov tests throughout these pilots to assess normality of data. The relationship between distance, zoom and image 2D:4D ratios were first analysed using general linear models (ANOVA) with distance and zoom as factors. Correlations between image 2D:4D ratios and true 2D:4D ratios were investigated for each hand position using Pearson's correlations for both the left and right hands of each subject. Correlations between image 2D:4D ratios obtained from ventral and dorsal views were also tested using Pearson's correlations.

2.2.4 Results

Data were normally distributed for true 2D:4D ratios ($P = 0.129$), image 2D:4D ratios ($P = 0.119$), distance ($P = 0.197$) and zoom ($P = 0.197$). The distance the photograph was taken from had no significant effect on the 2D:4D ratio in the images ($F_{1, 8} = 0.000$, $P = 1.000$). In fact, the same 2D:4D ratio was obtained at each distance regardless of how close the object being photographed was. No significant differences were found between percentage of zoom on the camera and 2D:4D ratios obtained from images ($F_{2, 12} = 0.000$, $P = 1.000$), and the same 2D:4D ratio was obtained at each zoom setting for each photograph.

Positions V and VI produced image 2D:4D ratios higher than true 2D:4D ratios (overestimation), and produced the correct ratio in only four of 24 measurements for position V and one of 24 measurements for position VI. 2D:4D ratios obtained from images with the hand in these positions exhibited non-significant moderate to low correlation with true 2D:4D ratios (Table 2.1). Other positions (IV, VII, VIII, IX and X) caused substantial underestimation of true 2D:4D ratios. Image 2D:4D ratios obtained from position IV were correct in two of 12 cases in the left hand and in one of 12 cases in the right hand. Image 2D:4D ratios showed a significant and high correlation with true 2D:4D ratios for the left hand but not for the right hand (Table 2.1).

Positions VII, VIII and IX produced image 2D:4D ratios corresponding exactly to true 2D:4D ratios in only one of the 24 measures. Image 2D:4D ratios were less than true 2D:4D ratios in the majority of cases and displayed low to negligible correlation with true 2D:4D ratios (Table 2.1). Image 2D:4D ratios from position X did not correlate with true 2D:4D ratios and image 2D:4D ratios corresponding exactly to true 2D:4D ratios were never obtained from this position for either hand (Table 2.1).

True 2D:4D ratios and image 2D:4D ratios were tightly correlated for hand positions I, II and III in both left and right hands of subjects (Table 2.1). Position I yielded image 2D:4D ratios corresponding exactly to true 2D:4D ratios in 19 out of 24 measurements and position II and III in 20 out of the 24 measurements. Where correct 2D:4D ratios were not obtained from digital images they deviated only by 0.01 - 0.02, with positions I and II resulting in very slight overestimations and position 3 in very slight underestimations of true 2D:4D ratios.

No significant difference was found between image 2D:4D ratios obtained in position I (ventral view) and position II (dorsal view) ($F_{1, 22} = 0.022$, $P = 0.882$). The image 2D:4D ratios for each view were also tightly correlated ($r = 0.974$, $df 12$, $P < 0.001$).

Table 2.1: Correlation coefficients (r) between true 2D:4D ratio and image 2D:4D ratio and P-values for the left and right hand in each position. Significant correlations are marked with *.

	Left hand		Right hand	
Position	r	P-value	r	P-value
I	0.972	0.001*	0.944	0.001*
II	1.000	0.001*	0.972	0.001*
III	0.956	0.001*	0.932	0.001*
IV	0.834	0.001*	0.169	0.598
V	0.410	0.186	0.497	0.101
VI	0.480	0.114	0.014*	0.965
VII	0.232	0.467	0.603	0.038*
VIII	0.082	0.800	0.024	0.941
IX	0.364	0.245	0.372	0.234
X	0.072	0.824	-0.005	0.989

2.2.5 Discussion

These results indicate that it is possible to gain accurate 2D:4D ratio measurements from digital photographs but the method is more accurate for some hand positions than others. The most accurate 2D:4D ratios are obtained from digital photographs in which the fingers are flat and straight and the entire digit visible (positions I, II and III). There was no significant difference between 2D:4D ratios obtained from the ventral view or from the dorsal view suggesting that calculating 2D:4D ratio from the dorsal side of the hand is a valid option. Only one photograph of each hand in each position was taken and minor inconsistencies in the data for I, II and III are most likely due to measurement error or an image not showing digits in optimum positions. This could be overcome by averaging across multiple photographs and choosing those in which hands are in the most favourable position possible. The very high correlation observed between true ratios and image ratios for the left hand in position IV suggest this position as a potential candidate for 2D:4D measurements. It produced the same ratio as the true 2D:4D ratio in only two of the 12 measurements, however, so it cannot be considered a suitable position for accurately measuring 2D:4D ratios with this

method in the field. The moderate significant correlation for the right hand in position VII is most likely due to the entire ventral surface of the digits being visible. However, the correlation was not significant for the same position in the left hand and it is also an unlikely position for a baboon to hold its hand in.

Unsurprisingly, curved fingers, as represented by positions VIII and IX, resulted in underestimation and lower 2D:4D ratios than expected, even when the curvature was slight. Also, fingers viewed from the side at different elevations (position X) yielded 2D:4D ratios that differed substantially from true ratios obtained from calliper measurements, most likely due to the area at the base of the 2D or 4D being obscured by the knuckle of the middle finger making knowing where to measure from difficult. This suggests that being able to see the entire digit is important for obtaining valid 2D:4D ratios from digital photographs.

2.3 Using HD video to measure 2D:4D ratio in human hands

2.3.1 Study subjects

The cohort comprised three human volunteers (two males and one female) between the ages of 22 and 57 years who had taken part in the previous experiment. Prior to data collection, I showed each individual a short three minute video of baboon behaviour so that they were aware of the type of movement they were attempting to emulate. They could watch this video as many times as they liked and I invited them to ask any questions.

2.3.2 Data collection

I taped a 2x2 m square box onto the floor using masking tape and asked participants to stay within this area and to walk quadrupedally if they wished to move around. I placed several objects inside the box and invited individuals to interact with these as they wished in order to create a more naturalistic scene. I set up a Panasonic FZ150 digital HD video recorder and recorded one minute of footage per individual. I watched each one minute movie for its full duration three times and identified suitable hand positions. I then converted videos into frames (JPG format) for every second of footage using VideotoJPG converter software.

This resulted in 200 JPG frames per video for each individual (Procaccini *et al.* 2011). I isolated five frames per hand for each subject in which hands were in favourable positions (as identified in the previous experiment) for analysis using ImageJ.

2.3.3 Results

Blurring sometimes occurred in frames during rapid movement of the subject, although enough frames can be obtained from a sequence (up to 1000) to make this a minor issue as a large number of good quality frames can be achieved. However, when zooming in on frames to measure digits the image quality was severely degraded making measuring digit lengths difficult and inaccurate.

2.3.4 Discussion

It was not possible to gain sufficient resolution on images to measure 2D:4D ratios with any accuracy despite HD quality of the footage and increasing the fine quality of JPG frames. This would likely not be the case with taking still photographs thanks to the camera's various 'sports settings' which reduce blurring when photographing fast moving objects by freezing the action. 'Burst shooting mode' allows the photographer to capture a number of images simultaneously with one click (suitable for fast action such as moving cars and flying birds) and allows for focussing the camera before capturing the image. I conclude that HD video does not produce images of sufficient quality to be applied to measuring 2D:4D ratios in wild nonhuman primates. It would be most beneficial to use digital photographic methods when attempting to determine 2D:4D ratios without the aid of direct measurements.

2.4 Using digital photographs to measure digit ratios in chacma baboons

2.4.1 Study site

I collected data from a captive troop of juvenile chacma baboons from 7th – 21st February 2012 at the Centre for Animal Rehabilitation and Education (C.A.R.E),

Phalaborwa, South Africa. Animals were housed in outdoor enclosures enriched with tyres, nets, ropes, tree branches and other play toys. The study troop contained 21 individuals of both sexes all approximately 18 months old and one older male juvenile at approximately three years of age.

2.4.2 Study subjects

Study subjects comprised 12 members of this troop (three females and nine males). These individuals had all been orphaned and were raised by human surrogates from a very early age and engaged in daily contact with several carers for up to 12 hours a day after weaning. As a result these individuals were comfortable being handled and photographed.

2.4.3 Data collection

The animals were habituated to my presence over four days. I then spent time sitting with the baboons initially accompanied by a member of staff for help in identifying individuals and so as to become familiar enough to be tolerated spending time in the baboon's enclosure unaccompanied for subsequent data collection. I obtained digit measurements over three days in one hour long periods. I encouraged animals to come close through use of their own communicative behaviours (lipsmacking and grunting) and groomed or embraced them while taking measurements. I permitted them to investigate the callipers used prior to measuring so they were not subjected to undue stress caused by fear of a foreign object. I measured the 2D and 4D of each hand of each animal directly from the basal crease to the tip of the extended digit (nearest mm) using Draper callipers and calculated 2D:4D ratios. For four of the male baboons it was only possible to gain direct measurements of their left hands as they became difficult to handle during the procedure and were released to avoid them becoming unnecessarily stressed. Ratios from calliper measurements were considered the 'true' 2D:4D ratios and were used to compare the accuracy of 2D:4D ratios obtained from digital photographs.

2.4.4 Digital photographs

I left the troop for 24 hours after direct calliper measurements to avoid any effects this process might have on their behaviour interfering with capturing photographic images. Over several observation days I sat in the enclosure with the animals for a period of one hour in order to photograph individual's hands. I made no contact with the baboons during this time in order to prevent them soliciting grooming or play or causing other distractions. I took five photographs each of the right and left hands of each baboon from the dorsal view in which the hand was in an optimal position and analysed these using ImageJ (Fig. 2.3). I measured the 2D and 4D 10 times for each photograph and used the mean of these measurements as the lengths of the digits. I used mean digits lengths to calculate the 2D:4D ratio for that image. I recorded image 2D:4D ratios obtained from each photograph and used the mean of the five as the overall image 2D:4D ratio for a particular subject's hand.



Figure 2.3: Examples of digital photographs of captive juvenile chacma baboons used to attain image ratios using ImageJ image analysis software.

2.4.5 Statistical analyses

Data for true 2D:4D ratios ($P = 0.906$) and image 2D:4D ratios ($P = 0.966$) were normally distributed and so I used Pearson's correlations to determine how closely the two variables correlated with one another.

2.4.6 Results

True ratios and image ratios obtained from photographs correlated strongly and positively ($r = 0.999$, $df = 20$, $P = 0.01$). When true and image ratios of each hand were analysed separately a very high, significant, positive correlation was also found (right hand: $r = 0.999$, $df = 8$, $P = 0.01$; left hand: $r = 0.999$, $df = 12$, $P = 0.01$). In terms of accuracy, in only three out of 20 cases did the mean image 2D:4D ratio differ from the true 2D:4D ratio, in each case by less than 0.008 (Table 2.2).

Table 2.2: True 2D:4D ratio and image 2D:4D ratio for each hand for each study subject (abbreviated to age/sex class). RH = right hand, LH = left hand. Image ratios that did not correspond exactly to true ratios are marked with *.

Subject	True ratio RH	Mean Image ratio RH	True ratio LH	Mean Image ratio LH
Juvfem1	0.82	0.82	0.84	0.84
Juvfem2	0.85	0.85	0.91	0.91
Juvfem3	0.84	0.84	0.88	0.88
Juvmale1	0.95	0.95	0.93	0.93
Juvmale2	/		0.87	0.87
Juvmale3	/		0.89	0.89
Juvmale4	0.91	0.91	0.85	0.85
Juvmale5	/		0.83	0.83
Juvmale6	0.89	0.89	0.95	*0.94
Juvmale7	/		0.88	0.88
Juvmale8	0.86	*0.87	0.84	*0.85
Juvmale9	0.77	0.77	0.80	0.8

2.4.7 Discussion

The results indicate that accurate 2D:4D ratio measurements of baboon species can be obtained with use of digital photographs and computer software. A minimum of five photographs per hand per individual appears to be sufficient to

gain image 2D:4D ratios corresponding exactly to true 2D:4D ratios. The small discrepancies between image 2D:4D ratios and true 2D:4D ratios are most likely due to measurement error as opposed to inaccuracy in the method itself and may be overcome by averaging across more photographs.

2.5 Conclusions

The outcome of this series of pilot experiments suggests that using HD video is not a valid option for measuring 2D:4D ratios due to the low quality images produced making measuring digits difficult. I conclude that using digital photographs and the computer software ImageJ to measure 2D:4D ratios in wild chacma baboons without the aid of direct measurements is a valid option.

Methods

3.1 Study Species

Baboons are widely distributed across Africa and display morphological and behavioural variations in response to their local environment and evolutionary history (Barrett 2009). Older classifications recognise five species; the chacma (*Papio ursinus*; Kerr 1792), olive (*P. anubis*; Lesson 1827), yellow (*P. cynocephalus*; Linnaeus 1766), Guinea (*P. papio*; Desmarest 1820) and Hamadryas (*P. hamadryas*; Linnaeus 1758) (Barrett 2009; Sithaldeen *et al.* 2009). More recently it has been suggested that the Kinda baboon (*P. kindae*; Jolly 1993) also warrants the same taxonomic status as the five listed above (Jolly *et al.* 2011; Zinner *et al.* 2009; Frost *et al.* 2003; but see Groves 2001). These have since been grouped together as a single superspecies under the name *P. hamadryas* (Barrett 2009), though the taxonomy of *Papio* baboons is still under debate (Zinner *et al.* 2013). The six subspecies are capable of hybridisation along contact zones and this occurs among northern yellow baboons and olive baboons, hamadryas and olive baboons (Kummer 1995), northern chacma and southern yellow baboons (Barrett 2009) and northern chacma and kinda baboons (Jolly *et al.* 2011). Chacma, olive, yellow, kinda and Guinea baboons display typical baboon sociality, living in troops with multiple males, multiple females and their offspring with female philopatry and male dispersal (Cheney & Seyfarth 2007; Jolly *et al.* 2011). Hamadryas baboons, in contrast, show a unique social structure among *Papio* baboons in that they live in one-male, multi-female groups (OMUs) (Kummer 1995), in which a dominant male herds and guards a group of females. The pattern among Hamadryas baboons is usually male philopatry and female dispersal, although both sexes may migrate out of their natal groups (Dunbar 1988; Kummer 1968).

The focal subspecies in this study is the chacma baboon, which emerged as an independent lineage approximately 1.84 mya (Sithaldeen *et al.* 2009). The chacma baboon is widely distributed across southern Africa and occupies a broad range of habitats within this area including savannah, grassland, montane, woodland, shrubland, semi-desert and swamp environments (Sithaldeen *et al.* 2009). Chacma baboons live in permanent groups of between four and 177 individuals depending on their local environment (Barton *et al.* 1996). Populations occupying the cold, barren slopes of the Drakensburg Mountains live in small groups with a mean of 22 individuals (Barton *et al.* 1996), whereas in the fertile Okavango Delta of Botswana (an area considered to have higher densities of baboons than other parts of Africa) chacma baboons live in larger groups of up to and exceeding 75 individuals (Cheney *et al.* 2004). The chacma baboon is widespread and abundant over the majority of its range and is classified as least concern on the IUCN red list (International Union for Conservation of Nature, September 2012). Among chacma baboons there is large phenotypic diversity but in general it is agreed that three main morphs are present within modern chacmas. These include Cape chacmas (*Papio ursinus ursinus*: Kerr 1792), Ruacana chacmas (*Papio ursinus ruacana*: Groves 2005 but see Grubb *et al.* 2003) and Grayfoot chacmas (*Papio ursinus griseipes*: Pocock, 1911). Cape chacmas are large and spread over much of South Africa. Those of the Ruacana form are not as large as Cape chacmas, have darker coloured fur and are found throughout Namibia and southern Angola (Burrell 2008). The Grayfoot form is lighter coloured and also smaller than the Cape form with grey hands and feet and is distributed over much of the north-eastern portion of the chacma range (Sithaldeen *et al.* 2009). Based on the Sithaldeen *et al.* (2009) estimate, the baboons of my study group fall just within the Grayfoot area of distribution (Figs. 3.1 & 3.2). However, as there is considerable overlap in ranges and interbreeding at contact zones between different lineages is common it is not possible to be certain of this. The authors also caution that, as a result of these factors, it is difficult to specifically identify the boundaries of the different morphotypes. Consequently, study animals will be referred to by their common name, chacma baboons.

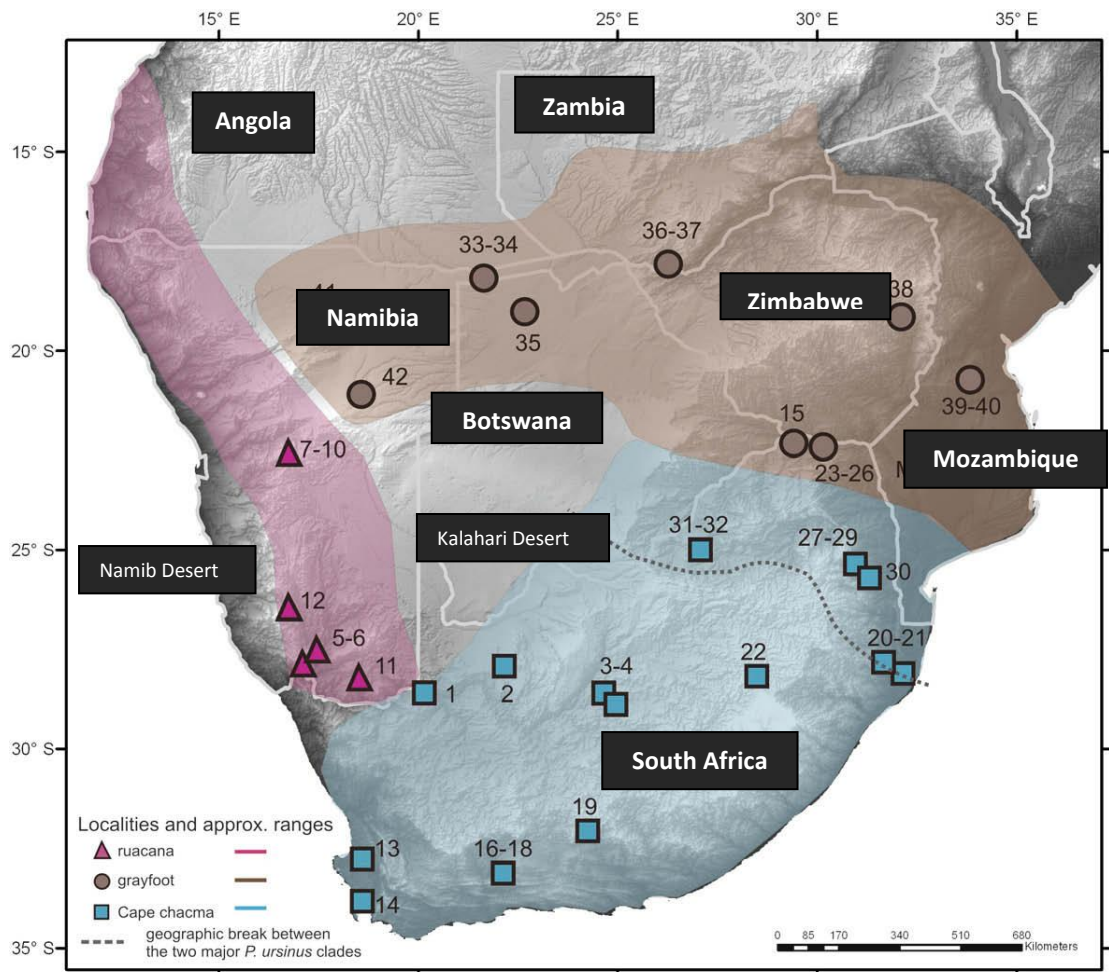


Figure 3.1: Estimated distribution of different chacma baboon lineages across southern Africa. Ruacana chacma (pink area), grayfoot chacma (brown area) and cape chacma (blue area). Adapted from Sithaldeen *et al.* (2009).

Chacma baboon home range size and daily travel distance have been related to group size (Barton *et al.* 1992). Other factors that affect home range size and travel distance in chacma baboons include climate (Hill 1999), resource availability (Barton *et al.* 1992) and the availability of sleeping sites (Anderson 2000; Barton *et al.* 1992). Chacma baboons are opportunistic feeders, eating a mainly vegetarian diet of leaves, fruits, shoots, seeds, bulbs, grass roots, and other underground storage organs (Whiten *et al.* 1991; Byrne *et al.* 1993; Barton & Whiten 1993). They supplement their diet with animal material such as insect prey (Isoptera, Orthoptera and Lepidoptera), lagomorphs and bushbuck young (personal observation) and chacma baboons have also been observed to prey on vervet monkeys (Willems 2007).

3.2 Study area

I conducted research in the northernmost mountain range of South Africa, the Soutpansberg or “mountains of salt”. The range is a narrow ridge set in the Limpopo Province and varies from between 15-60 km north to south and extends 250 km east to west (lying from 23° 05' S & 29° 17' E and 22° 25' S & 31° 20' E) (Berger *et al.* 2003). The location of this study, the Lajuma Research Centre, spans an area of 430ha and is located in the western side of the Soutpansberg mountain range between Louis Trichardt (Makhado) and Vivo. The Lajuma Research Centre (Fig. 3.2), a Natural History Site since 1997, also became part of a private wilderness area in UNESCO’s Vhembe Biosphere Reserve in 2009. This is in acknowledgement of the area’s biodiversity and ecological significance in the region.



Figure 3.2: Map of South Africa (dark grey) and its bordering countries (light grey). The Soutpansberg mountain range is shown (red) with the location of the study site (white arrow) (Willems 2007).

3.2.1 Climate

The climate in the Soutpansberg Mountains is affected by the east-west orientation of the range and the local climate at the Lajuma Research Centre can be best described as temperate/mesothermal. The region has cool dry winters

between April and September and hot wet summers between October and March (de Raad 2011). This study encompassed both late summer and early winter months. Data on the climate and weather conditions over the study period were collected from an automated weather station located on the property. Temperatures over the study period ranged from a mean of 17.6 °C in April, to 17 °C in May and 13.5 °C in June. At the time of this study the area was experiencing an uncharacteristic period of drought. Rainfall was variable over the study months, with 11.6 mm in April, dropping to 0.8 mm in May and only 0.2 mm in June. Usually, the driest month is August and has a minimum mean rainfall of 4 mm with the wettest weather occurring in January with a mean rainfall of 158 mm (Willem, 2007). Rainfall during the study period was well below average for the time of year but as the Soutpansberg Mountain range falls within a mist-belt zone in which mist makes up 40% of annual precipitation (South African Department of Environmental Affairs, 1988), moisture levels are under represented by rainfall alone (Willems 2007).

3.2.2 Flora

The Soutpansberg region is very diverse and boasts plant species belonging to 1066 genera and 240 families (Hahn 1997). Vegetation across the study area varied extensively and vegetation types of Forest, Grassland, and Savannah Biomes are represented, along with azonal plant communities and some endemic species. Nine main vegetation types have been described for the Soutpansberg region, five of which are found in the study area (Mostert *et al.* 2008). These include 'arid northern bushveld' which consists of open woodland with a sparse field layer. Also, 'moist mountain thickets' which describe an assortment of plant communities in which there is no gap between tree and shrub layers. 'Leached sandveld' is also present which is composed of a homogenous mixture of woody and grass species and is found in dry areas of the mountains. 'Cool mistbelt' vegetation type is made up of a diverse array of peatlands, low open grasslands, and small island thickets and is found 1200+ m above sea level. Lastly, 'forest' vegetation type is made up of evergreen high forests and deciduous shrub forests and is located mostly on the southern-most slopes of the mountains (Mostert *et al.* 2008).

3.2.3 Fauna

Animal life is also very diverse, with 36% of reptile, 56% of bird and 60% of mammal species found in South Africa occurring in the region (Berger *et al.* 2003; Gaigher & Stuart 2003). The Lajuma Research Centre is home to all five species of South African nonhuman primate: the vervet monkey (*Cercopithecus aethiops*), samango monkey (*Cercopithecus mitis erythrarchus*), thick-tailed bushbaby (*Otolemur crassicaudatus*), lesser bushbaby (*Galago moholi*) and chacma baboon. The region supports a variety of antelope species including bushbuck (*Tragelaphus scriptus*), klipspringer (*Oreotragus oreotragus*), kudu (*Tragelaphus strepsiceros*), common duiker (*Sylvicapra grimmia*), and red duiker (*Cephalophus natalensis*). Many other mammal species thrive in the area including aardvark (*Orycteropus afer*), cape porcupine (*Hystrix africaeaustralis*), and dwarf mongoose (*Helogale parvula*). There are also several predator species present including the leopard (*Panthera pardus*), brown hyena (*Hyaena brunnea*), serval (*Lepatailurus serval*), and caracal (*Felis caracal*), some of which pose a potential threat to baboons. Broad scale faecal dietary analysis from the study area found primate species made up 15.8% of leopards' intake and 4.3% of this was baboon (Chase-Grey 2011). I suspect the disappearance of one adult female during the study to be the result of leopard predation, since she had been healthy and was pregnant at the time.

3.3 Study group

3.3.1 Troop composition

House Troop comprised approximately 80 individuals. Thick vegetative cover causing low visibility means that this value is estimated based on known individuals. The troop consisted of 12 adult males, four adolescent males, 17 juvenile males, 20 adult females, five adolescent females, seven juvenile females, four infant females and eight infant males. The 20 adult and five adolescent females in the troop were the focus of this thesis. I used six mother/infant pairs in the troop (two male infants and four female infants) to assess heritability of the 2D:4D ratio.

I recorded the reproductive status of each female in the study group on a daily census. Females were classified as pregnant, lactating, or cycling. Those females who were cycling were further sub classified with regards to the size of their perineal swelling as either 'flat', 'swelling small', 'swelling medium', 'swelling large' or 'swelling going down'. Lactating females were those who were nursing dependent offspring and had not resumed sexual cycling. I considered females adolescent once they had had their first sexual swelling but had not yet conceived and as adult once they had become pregnant for the first time. The number of adult females varied over the study period from 20 to 19 individuals due to the disappearance of one adult female likely the victim of predation as mentioned previously.

3.4 Data collection

3.4.1 Behavioural data

At the time of this research House Troop were also the subjects of a PhD study and had been followed and observed almost daily for several months prior to the start data collection. As such the animals were fully habituated to human observers on foot. I identified females from 1st March – 1st April. I followed the troop for full days from their morning sleeping site to their evening sleeping site on an almost daily basis in order to learn the study subjects on an individual basis for subsequent collection of behavioural data. Data collection commenced on the 3rd April 2012 and lasted until the 20th June 2012.

I conducted 10 minute focal samples of each adult and adolescent female troop member in random order and recorded behavioural interactions on a continuous basis on a Psion Walkabout Pro PDA device equipped with Observer XT 10 software package. I recorded both interactions initiated by the focal individual and those directed toward the focal individual by another troop member along with the identity of the social partner for adult and adolescent females or age/sex class for other troop members (e.g., Subject A gives threat to Subject B - Subject A receives fear grimace from Subject B). Behavioural categories were affiliation, dominance, submission, contact aggression, non-contact aggression, and interest in infants. These categories had within them several behaviours aimed at

addressing the particular questions of interest (Table 3.1). Also, I recorded the number of grooming partners a female had and the number of social partners. Grooming partners were those who I observed the focal female grooming or receiving grooming from. I defined a social partner as any female who I saw the focal female interact with in an affiliative manner that was not grooming.

I collected data over three sample periods to ensure an equal spread of samples across the day: early morning (6 - 10am), midday (10am – 2pm) and late afternoon (2 – 6pm) for the duration of the study. I balanced focals for each female across these periods which amounted to two hours per female for each observation period and a total of six hours focal observation time per female (Table 3.2). One female disappeared during the study period and so I was only able to achieve three hours and 40 minutes of focal data on her. Data for this female were almost balanced with 70 minutes in observation periods one and two and 80 minutes in observation period three.

Table 3.1: Ethogram of behaviours and behavioural categories used when collecting focal data.

Behaviour	Description
Affiliative	
Present	Present rear, tail up to muzzle of other animal
Muzzle inspection	Presses face into muzzle of other animal
Rear inspection	Places hand/face to rear of other animal
Lipsmack	Rapid tongue over lip movement repeated
Grunt	Series of short grunts to communicate actor's friendly intentions
Embrace	'Hugging' or placing arm over back/shoulders of another individual
Groomer	Grooming the fur of another individual
Groomed	Being groomed by another individual
Contact Aggression	
Bite	Biting a body part of the victim
Slap	Slapping at another individual
Tug	Takes hold of victim's fur and pulls
Pin	Holding another individual to the ground with hands and/or mouth
Non-contact aggression	
Threaten	Includes eye flashing, threatening vocalisations, head bobbing, ground drumming (no physical contact)
Lunge	Lunge toward another individual without making physical contact
Silent chase	Rapidly running toward target, unaccompanied by gestures of fear or submission without vocalisation
Scream and chase	Rapidly running toward target, unaccompanied by gestures of fear or submission whilst making screaming vocalisations
Threat ignored	Individual shows no response to antagonism received
Dominant behaviours	
Mount	Non-sexual mounting behaviours, where individual stands on hind legs and presses ventral surface to rear of the other animal
Supplant	One individual's actions cause another to move away without any direct interaction occurring between the two
Displace	One individual actively causes another individual to move location where the first individual may take over the action of the other
Submissive behaviours	
Flee	Run away from an individual at speed and/or while being chased
Move away	Leaves area occupied by aggressor at normal pace
Fear grimace	Lips pulled apart wide to show teeth gritted in a grimace
Fear keck	Series of short staccato grunts directed at another individual

Cower	Crouch low to ground in submissive posture
Scream	Loud 'eeeeee' scream of fear in response to antagonism from another individual
Interest in Infants	
Infant kidnapping	An individual attempts/succeeds in taking another females infant against her will
Infant carrying	Individual carries an infant in dorsal or ventral position (when not the infant's mother)
Infant inspections	Individual attempts to visually inspect and/or make physical contact with another female's infant, often accompanied with grunting

Table 3.2: Breakdown of focal data, with time (in minutes) each female was observed in each reproductive state and total observation time (in minutes). Female names are abbreviated to two letters in the first column.

Female	Cycling flat	Cycling swelling small	Cycling swelling medium	Cycling swelling large	Cycling swelling going down	Pregnant	Lactating	Total
No	0	0	0	0	0	360	0	360
Ma	0	0	0	0	0	360	0	360
En	0	110	10	0	10	0	230	360
El	0	0	0	0	0	0	360	360
Ni	0	0	0	0	0	0	360	360
Fr	220	90	10	0	40	0	0	360
Si	150	0	10	110	40	50	0	360
Pi	150	180	0	0	30	0	0	360
Me	0	140	0	0	0	0	220	360
Ju	0	0	0	0	0	220	0	220
Lo	0	0	0	0	0	0	360	360
Pe	0	0	0	0	0	0	360	360
Tu	0	30	130	130	70	0	0	360
Ri	0	0	0	0	0	0	360	360
Sl	80	50	130	70	30	0	0	360
Sc	260	0	0	30	20	50	0	360
He	0	100	0	0	0	0	260	360
Ht	0	0	0	0	0	0	360	360
Tr	170	10	50	80	50	0	0	360
Br	0	0	0	0	0	0	360	360
Bo	80	140	90	50	0	0	0	360
Yo	0	0	0	0	0	0	360	360
St	270	0	0	40	0	50	0	360
Te	0	0	0	0	0	0	360	360
Sh	250	20	20	10	0	60	0	360

3.4.2 Dominance hierarchy

Using focal data I ascertained female rank via the direction of supplant and displacement interactions occurring between females (Nelson *et al.* 2010; Altmann 1974). Also, I recorded the direction of submissive behaviours (fear grimace, fear keck, cower, etc). I also recorded the direction of submissive behaviours opportunistically on an *ad libitum* basis both within focal periods (for interactions involving group members other than the focal individual) and between focal periods to supplement focal data for the construction of the dominance hierarchy (Martin & Bateson 2007). I assigned a female's dominance rank based on these observations ranging from 1 (highest-ranked) to 25 (lowest-ranked).

3.4.3 2D:4D ratio measurements

To obtain 2D:4D ratio measurements of House Troop females and infants I used a Panasonic FZ150 digital camera in 'burst shooting' mode in which the camera was set to take 12 frames per shot allowing for high quality images to be obtained despite the fast and unpredictable movement of the baboons. I took multiple photographs of the dorsal view of each individual's right and left hands and identified 10 photographs per hand per individual in which hands were in optimum positions for digit measurements (based on the pilot experiments). These were photographs in which the hand and digits were in a flat and straight position, digits were fully extended and the entire lengths of both digits were visible (Fig. 3.3). I used 20 digital photographs for each individual, 10 for the right hand and 10 for the left hand. I analysed photographs with ImageJ using mouse-controlled callipers to measure digit lengths from the photographs. I measured the 2D and 4D 10 times each per photograph and used the mean of these measurements as the digit lengths for that photograph. I calculated 2D:4D ratios for each photograph, giving 10 ratios for the hand. I used the mean of these as the 2D:4D ratio of the hand. I repeated the process for both right and left hands to give 2D:4D ratios for each hand and determined an individual's mean 2D:4D ratio by taking the mean of the right and left hand 2D:4D ratios.



Figure 3.3: Examples of digital photographs used to measure digit lengths with ImageJ.

3.5 Statistical analyses

I used Kolmogorov-Smirnov tests throughout when assessing normality of data. I used two tests to measure the repeatability of my 2D:4D ratio measurements. I used repeated measures ANOVA to compare the error mean squares (i.e. differences between the repeated measurements) and group mean squares (i.e. differences between the subjects). I then used the F ratio to determine whether the differences between subjects were significantly larger than measurement error. I used the intraclass correlation coefficient (ICC) set to the 'absolute agreement' definition to test intra-observer reliability. I investigated differences in left and right 2D:4D ratios of females and infants using a paired *t*-test (two-tailed).

2D:4D ratio data are classified as the independent variable and dominance rank and behavioural data as the dependent variables. I used Pearson's correlations to assess the relationship between a female's dominance rank and her mean, right, left 2D:4D ratios and Dr-I. I used a multiple regression model to compare the contributions of left, right and mean 2D:4D ratios on dominance rank. The two predictor variables were highly correlated in this model. While this does not reduce the predictive power or reliability of the model as a whole it may affect the validity of results with regards to the individual predictors themselves. I used Pearson's correlations to investigate the relationship between Dr-I and mean, right and left 2D:4D ratios.

I converted all behavioural data into rates per hour of observation time prior to analysis. I used Pearson's correlations to analyse the relationship between rate of submission, rate at which individuals received aggression, rate of interest in

infants and rate of affiliation and mean, right and left 2D:4D ratios. I also employed Pearson's correlations to assess the relationships between the different 2D:4D ratio data and rate of grooming given and rate of grooming received, number of grooming partners and number of social partners.

Data for rate of non-contact aggression and rate of contact aggression were not normally distributed and were robust to attempts at transformation due to the data containing a number of zero scores. I therefore used non-parametric Spearman Rank correlations when investigating relationships between these variables and 2D:4D ratio data. Infant mean, left, and right 2D:4D ratios were all normally distributed but due to the small sample size of six mother/infant pairs I used Spearman Rank tests to examine the relationship between 2D:4D ratios in mother/infant pairs and to assess the relationship between infant 2D:4D ratio measures and the dominance rank of their mothers. I used a multiple regression model to compare the contributions of mother's left and right 2D:4D ratios on R/L 2D:4D ratios of infants.

I conducted all data analyses using IBM SPSS statistics for Windows version 19 (2010).

Results

4.1 Normality tests

Mean, right, left 2D:4D ratios and Dr-I were all normally distributed for females (mean: $P = 0.155$; right: $P = 0.135$; left: $P = 0.126$; Dr-I: $P = 0.200$), as were data for dominance rank ($P = 0.387$). Additionally, infant left ($P = 0.200$), right ($P = 0.200$) and mean ($P = 0.200$) 2D:4D ratios were all normally distributed. Rate of submission ($P = 0.200$), rate at which individuals received aggression ($P = 0.200$), rate of interest in infants ($P = 0.200$), rate of affiliation ($P = 0.200$), rate of grooming given ($P = 0.186$), rate of grooming received ($P = 0.095$), number of grooming partners ($P = 0.183$) and number of social partners ($P = 0.103$) were normally distributed. Data for rate of non-contact aggression and rate of contact aggression were not normally distributed ($P < 0.001$ and $P = 0.011$ respectively).

4.2 Reliability

Repeated measures of 2D:4D ratio from photographs showed no significant difference within females (repeated measures ANOVA, right hand: $F_{9, 216} = 0.673$, $P = 0.733$; left hand: $F_{9, 216} = 0.851$, $P = 0.570$). Repeated measures of 2D:4D ratio from photographs showed no significant difference within females (repeated measures ANOVA, right hand: $F_{9, 216} = .673$, $P = 0.733$; left hand: $F_{9, 216} = .851$, $P = 0.570$). Thus, there was no significant difference between repeated measurements for either hand, suggesting that measurements were highly repeatable (Fig. 4.1). The intra-class correlation coefficient (ICC) also showed that 2D:4D ratio measurements for females were highly repeatable for the right (ICC = 0.968, $F_{24, 216} = 299.062$, $P < 0.001$) and left (ICC = 0.969, $F_{24, 216} = 309.784$, $P < 0.001$) hands, indicating a high level of intra-observer reliability. Left and right 2D:4D ratios in females were not significantly different ($t_{24} = 0.842$, $P = 0.408$) and were tightly correlated ($r = 0.919$, $df = 25$, $P < 0.001$). Dr-I in females did not correlate

significantly with any of the 2D:4D ratio measures (mean: $r = 0.092$, $df = 25$, $P = 0.661$; right: $r = -0.114$, $df = 25$, $P = 0.588$; left: $r = 0.288$, $df = 25$, $P = 0.163$). Repeated measures of 2D:4D ratio from photographs in infants showed no significant difference within individuals (repeated measures ANOVA, right hand: $F_{1,5} = 3.971$, $P = 0.103$; left hand: $F_{1,5} = 0.600$, $P = 0.474$) and ICC indicated a fair agreement in 2D:4D measurements of the right hand (ICC = 0.362, $F_{5,45} = 6.662$, $P < 0.001$) and moderate agreement in the left hand (ICC = 0.559, $F_{5,45} = 12.613$, $P < 0.001$). Left and right 2D:4D ratios in infants were not significantly different ($t_6 = 0.650$, $P = 0.544$) and were tightly correlated ($r = 0.829$, $df = 6$, $P = 0.042$) so I also used the mean 2D:4D ratio of both hands for females and infants in subsequent analyses.

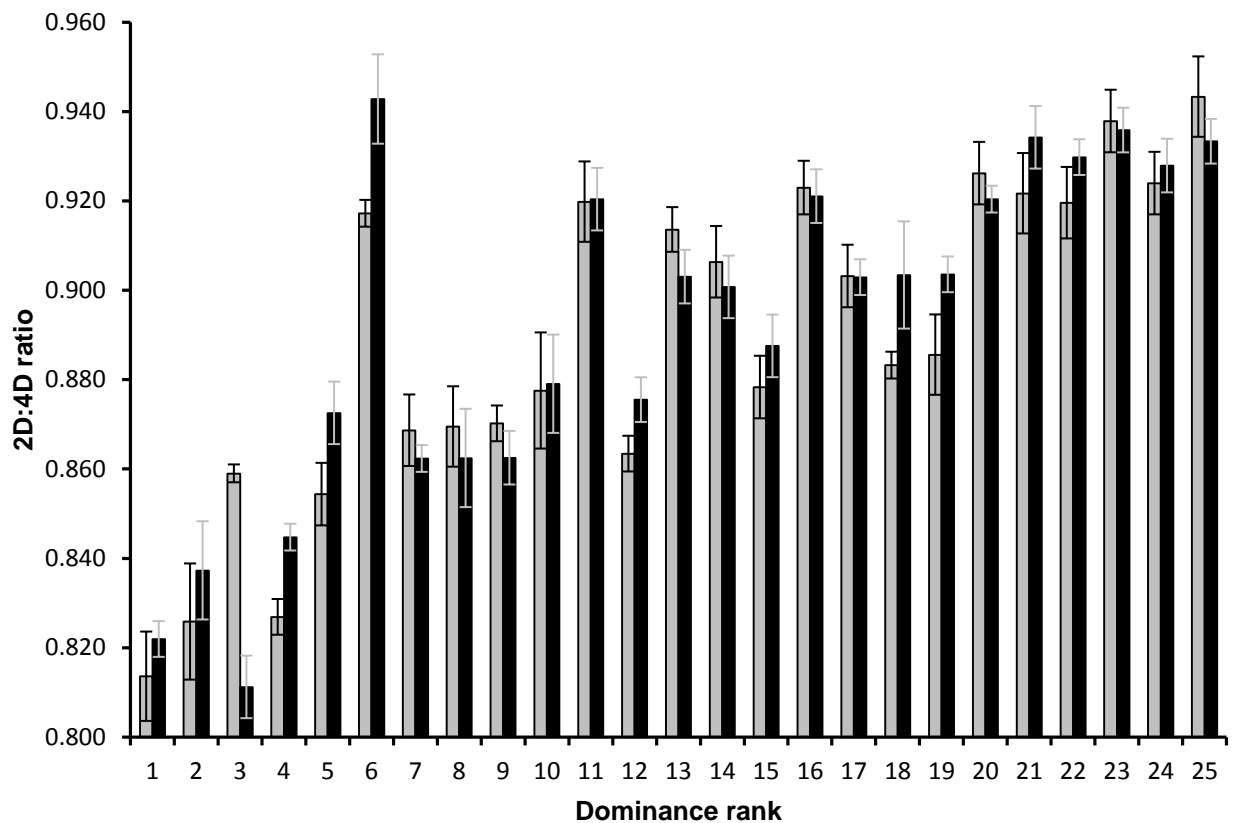


Figure 4.1: Mean \pm standard deviation of right (grey bars) and left (black bars) 2D:4D ratios for each female vs. dominance rank. Rank is in descending order from highest (1) to lowest (25).

4.3 Digit ratios and dominance rank

House Troop females formed a linear, transitive dominance hierarchy typical of female baboons (Table 4.1). High-ranking females have lower 2D:4D ratios in both hands and lower mean 2D:4D ratios than low-ranking females (Fig. 4.1). Mean

2D:4D ratio and dominance rank were highly negatively correlated ($r = 0.833$, $df = 25$, $P < 0.001$) (Fig. 4.2). Right 2D:4D ratio and dominance rank were significantly negatively correlated ($r = 0.820$, $df = 25$, $P < 0.001$), as were left 2D:4D ratio and dominance rank ($r = 0.810$, $df = 25$, $P < 0.001$) (Fig. 4.3). Dr-I, however, did not correlate significantly with dominance rank ($r = 0.049$, $df = 25$, $P = 0.818$) (Fig. 4.4).

Table 4.1: Dominance matrix for adult and adolescent females in House Troop with frequency of decided dominance interactions. Names are abbreviated to two letters; winners are represented in rows and losers in columns and show females in descending rank order from highest (No) to lowest (Sh).

	No	Ma	En	El	Ni	Fr	Si	Pi	Me	Ju	Lo	Pe	Tu	Ri	Sl	Sc	He	Ht	Tr	Br	Bo	Yo	St	Te	Sh	Total
No		6	5	4	4	2	1	4	3	0	1	3	2	3	1	5	1	5	0	3	0	0	1	1	0	55
Ma	0		2	2	9	1	0	1	2	2	3	2	2	1	1	3	0	2	1	4	0	2	0	3	0	43
En	0	0		8	4	2	1	0	5	0	3	5	2	1	1	1	2	6	5	1	1	3	0	4	1	56
El	0	0	0		3	1	4	4	4	0	2	6	6	2	2	0	1	9	1	1	1	1	2	2	0	52
Ni	0	0	0	0		2	3	3	7	1	8	9	0	2	3	2	3	4	3	3	1	4	3	0	2	63
Fr	0	0	0	0	0		3	1	1	3	0	3	0	1	8	1	0	1	2	1	2	2	1	7	2	39
Si	0	0	0	0	0	0		3	1	1	4	3	3	4	4	3	6	3	7	7	6	1	3	1	0	60
Pi	0	0	0	0	0	0	0		11	0	4	0	4	3	3	5	3	1	1	8	5	4	6	1	1	60
Me	0	0	0	0	0	0	0	0		4	1	2	2	0	2	5	1	1	2	7	1	4	3	1	3	39
Ju	0	0	0	0	0	0	0	0	0		2	3	1	0	2	1	2	0	2	1	0	1	2	1	0	18
Lo	0	0	0	0	0	0	0	0	0	0		13	1	9	10	2	3	3	1	0	5	2	4	1	2	56
Pe	0	0	0	0	0	0	0	0	0	0	0		1	7	1	3	4	1	1	7	3	1	1	1	0	31
Tu	0	0	0	0	0	0	0	0	0	0	0	0		3	0	3	0	1	0	3	3	0	3	3	2	21
Ri	0	0	0	0	0	0	0	0	0	0	0	0	0		1	4	3	4	1	3	1	4	1	2	2	26
Sl	0	0	0	0	0	0	0	0	0	0	0	0	0	0		2	2	4	3	0	3	1	3	1	4	23
Sc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		7	6	3	3	5	2	4	6	1	37
He	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		5	1	4	2	2	7	1	1	23
Ht	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		2	2	1	0	2	2	4	13
Tr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		2	4	4	4	1	2	17
Br	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		1	4	5	4	1	15
Bo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		1	6	2	1	10
Yo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		1	1	0	2
St	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		1	0	1
Te	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		4	4
Sh	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0

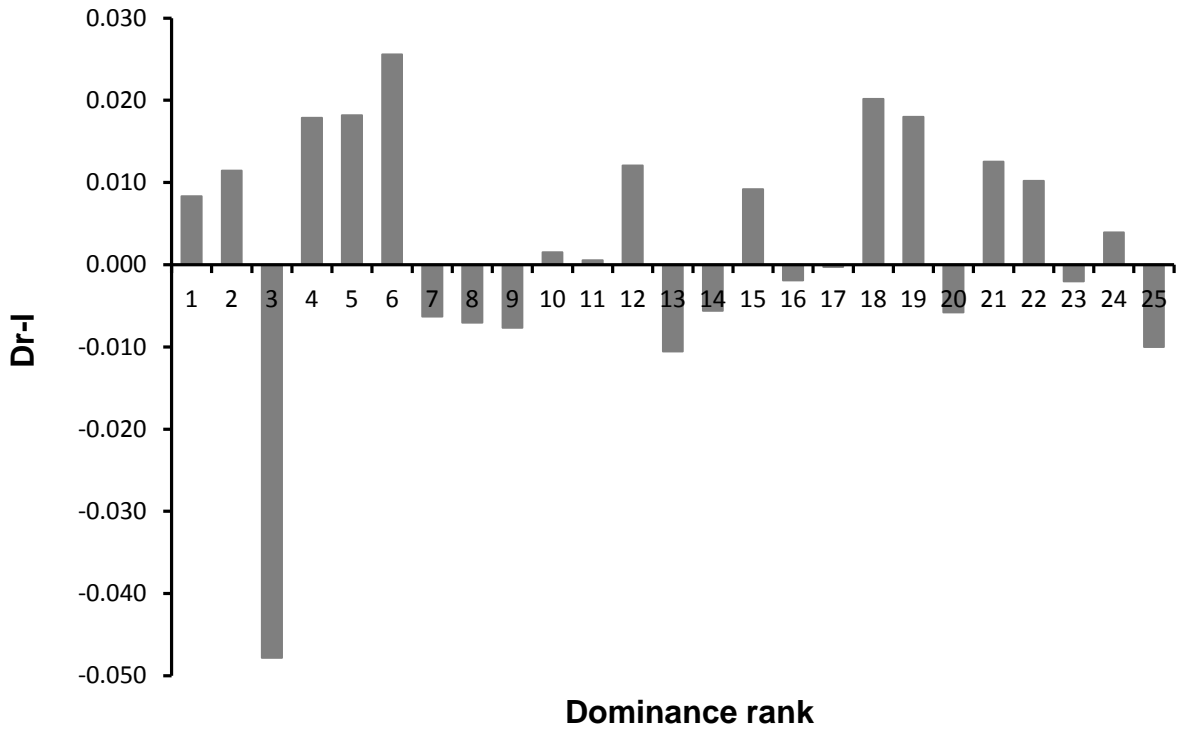


Figure 4.4: Relationship between Dr-I and dominance rank in females.

The rate of submission was positively correlated with mean 2D:4D ratio ($r = 0.594$, $df = 25$, $P = 0.002$), right 2D:4D ratio ($r = 0.568$, $df = 25$, $P = 0.003$) and left 2D:4D ratio ($r = 0.595$, $df = 25$, $P = 0.002$) (Fig. 4.5). However, Dr-I was uncorrelated with rate of submission ($r = 0.110$, $df = 25$, $P = 0.601$).

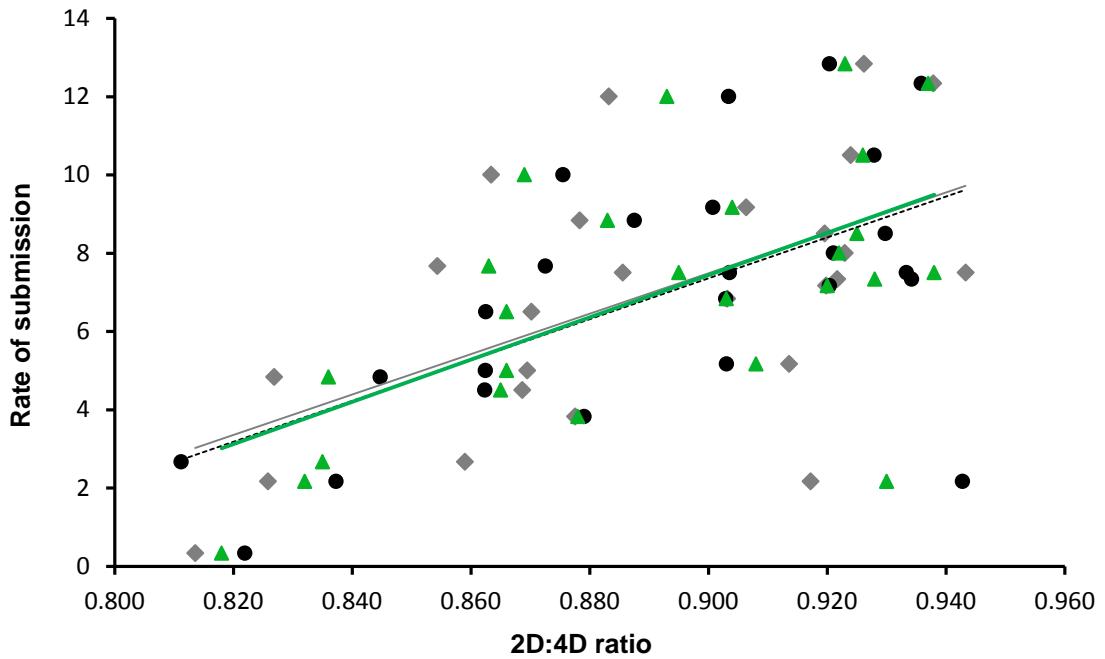


Figure 4.5: The relationship between mean 2D:4D ratio (green triangles, solid green line), right 2D:4D (grey diamonds, grey solid line) and left 2D:4D (black circles, black dotted line) and rate of submission.

A multiple regression analysis of the relationship between dominance rank and right 2D:4D ratio and left 2D:4D ratio found that 66.5 % of variance in dominance rank could be predicted by the contribution of right and left 2D:4D ratios (adjusted R squared = 0.665; $F_{2, 22} = 24.826$, $P < 0.001$ [using enter method]). Individually these were not significant: Right 2D:4D, Beta = 0.481, $P = 0.122$; Left 2D:4D, Beta = 0.384, $P = 0.231$. Mean 2D:4D ratio when regressed with dominance rank predicted 68 % of the variance in dominance rank (Adjusted R squared = 0.680; $F_{1, 23} = 51.935$, $P < 0.001$) and was significant: mean 2D:4D, Beta = 0.833, $P < 0.001$.

4.4 Digit ratios and aggression

Mean, right and left 2D:4D ratios all correlated significantly and negatively with rate of non-contact aggression (Mean: $r = - 0.490$, $df 25$, $P = 0.013$; right: $r = - 0.418$, $df 25$, $P = 0.037$; left: $r = - 0.483$, $df 25$, $P = 0.014$). Females with lower left, right and mean 2D:4D ratios displayed higher rates of non-contact aggression than those with higher 2D:4D ratios (Fig. 4.6). Dr-I was not significantly correlated with either rate of non-contact aggression ($r = - 0.169$, $df 25$, $P = 0.418$) or contact aggression ($r = - 0.372$, $df 25$, $P = 0.067$). Contact aggression significantly negatively correlated with mean 2D:4D ratio ($r = - 0.449$, $df 25$, $P = 0.024$) and left 2D:4D ratio ($r = - 0.499$, $df 25$, $P = 0.011$) but not with right 2D:4D ratio ($r = - 0.369$, $df 25$, $P = 0.070$) (Fig. 4.7).

The rate at which a female received aggression from other group members was moderately positively correlated with her mean, right and left 2D:4D ratios (mean: $r = 0.630$, $df 25$, $P = 0.001$; right: $r = 0.660$, $df 25$, $P < 0.001$; left: $r = 0.574$, $df 25$, $P = 0.003$), with females with higher 2D:4D ratios receiving aggression at higher rates (Fig. 4.8).

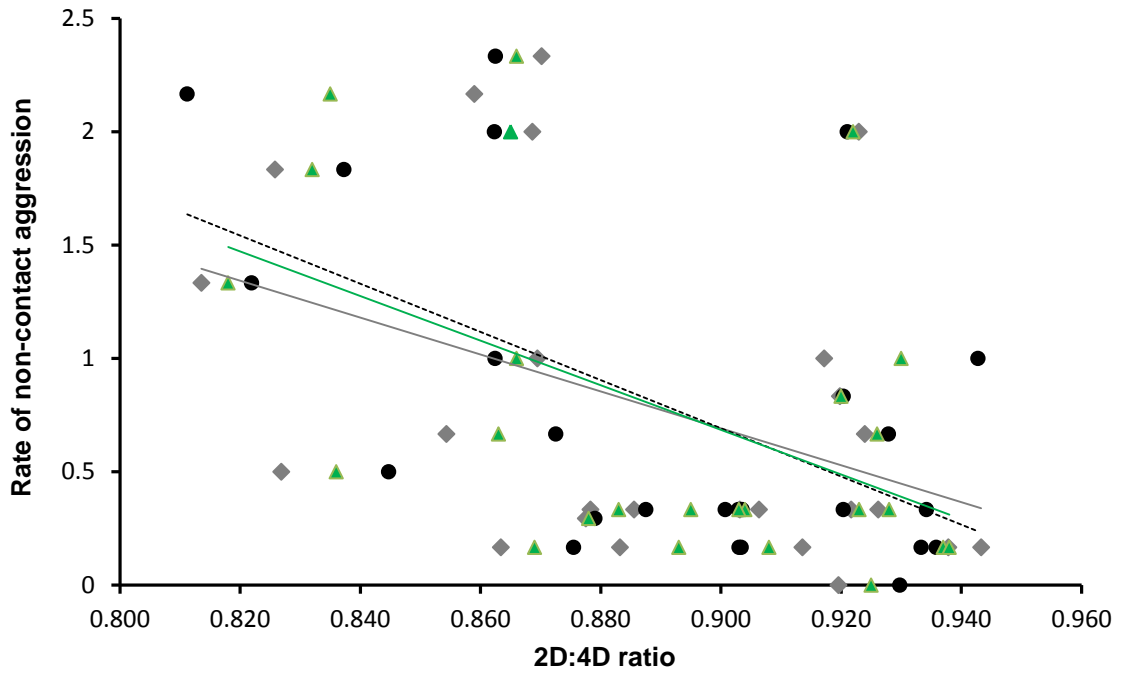


Figure 4.6: Relationship between mean 2D:4D ratio (green triangles, solid green line), right 2D:4D (grey diamonds, grey solid line) and left 2D:4D (black circles, black dotted line) and rate of non-contact aggression.

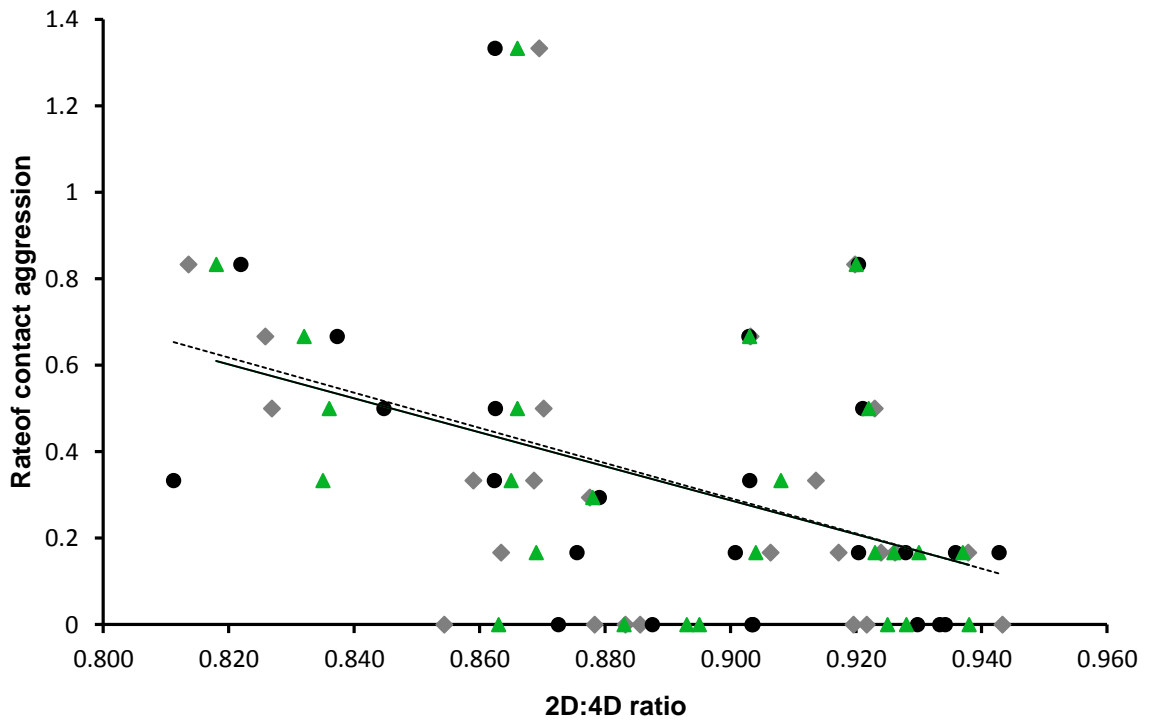


Figure 4.7: Relationship between mean 2D:4D ratio (green triangles, solid green line), right 2D:4D (grey diamonds) and left 2D:4D (black circles, black dotted line) and rate of contact aggression.

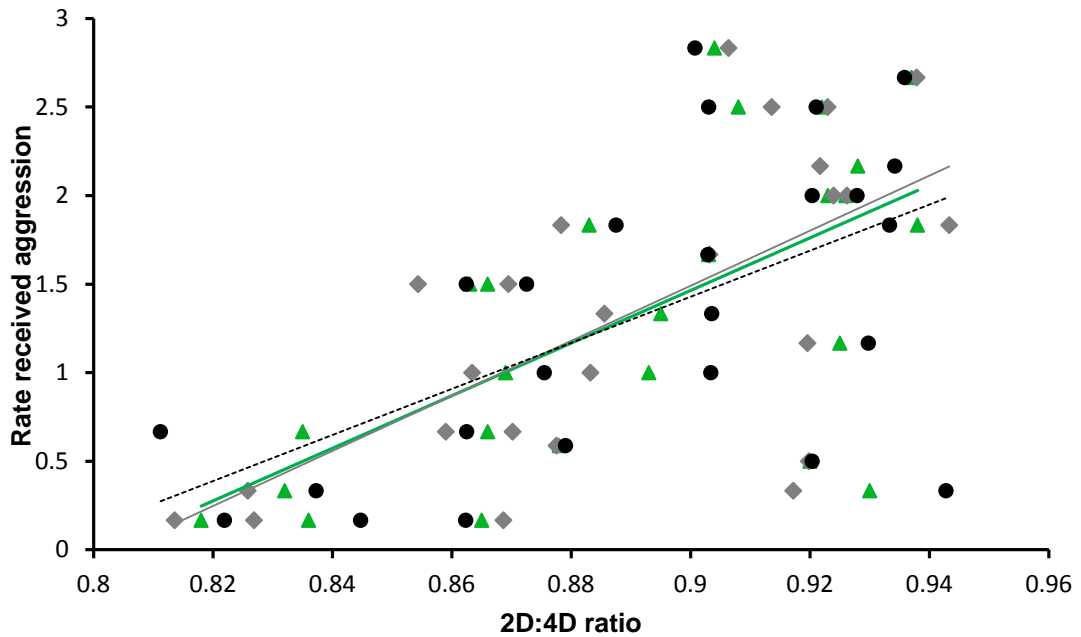


Figure 4.8: Relationship between mean 2D:4D ratio (green triangles, solid green line), right 2D:4D (grey diamonds, grey solid line) and left 2D:4D (black circles, black dotted line) and rate at which a female received aggression from another group member.

4.5 Digit ratios and interest in infants

There was no significant correlation between a female's interest in infants and her mean 2D:4D ratio ($r = 0.190$, $df = 25$, $P = 0.364$) (Fig. 4.9). Nor were there significant correlations between a female's right ($r = 0.197$, $df = 25$, $P = 0.344$) or left ($r = 0.178$, $df = 25$, $P = 0.395$) 2D:4D ratios and her rate of interest in infants.

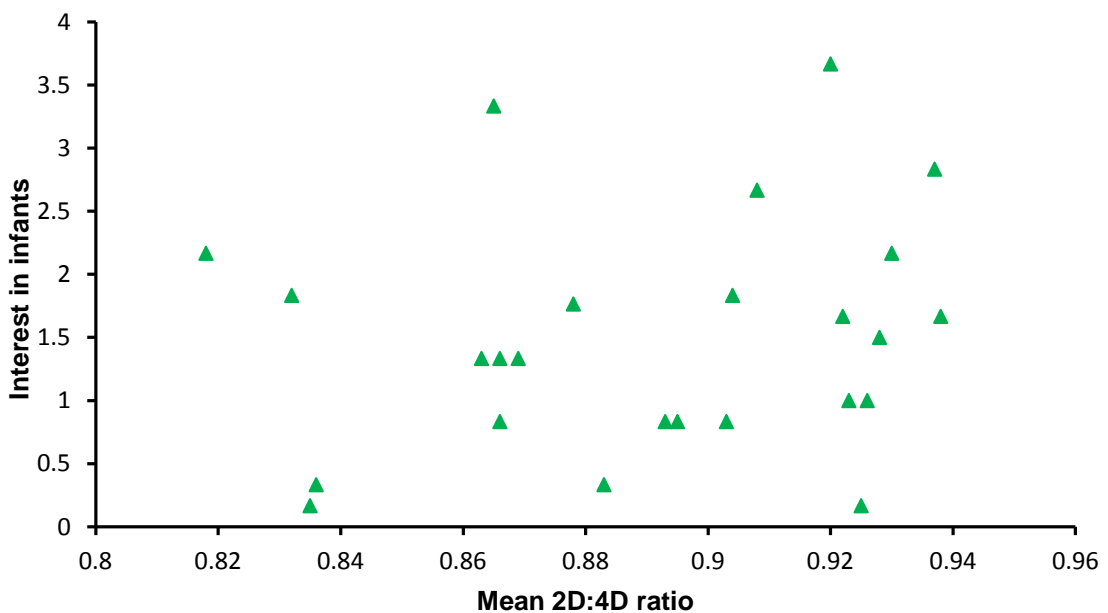


Figure 4.9: The relationship between mean 2D:4D ratio and rate of interest in infants among females.

4.6 Digit ratios and affiliation

No significant correlations were found between a female's rate of affiliation and her mean ($r = 0.086$, $df = 25$, $P = 0.682$), right ($r = 0.165$, $df = 25$, $P = 0.430$) and left ($r = 0.007$, $df = 25$, $P = 0.974$) 2D:4D ratios (Fig. 4.10). The mean number of grooming partners was 4.68 (± 1.99) and the mean number of social partners was 7.68 (± 3.28) in this population. A female's mean 2D:4D ratio was not significantly correlated with her number of grooming partners ($r = 0.206$, $df = 25$, $P = 0.324$) or with her number of social partners ($r = 0.112$, $df = 25$, $P = 0.593$). No significant correlations were found between the rate at which a female groomed another female or was groomed by another female and her mean, right or left 2D:4D ratios (mean: grooming given – $r = 0.164$, $df = 25$, $P = 0.433$ and grooming received – $r = 0.261$, $df = 25$, $P = 0.207$; right: grooming given – $r = 0.157$, $df = 25$, $P = 0.454$ and grooming received – $r = 0.260$, $df = 25$, $P = 0.209$; left: grooming given – $r = 0.164$, $df = 25$, $P = 0.435$ and grooming received – $r = 0.253$, $df = 25$, $P = 0.223$).

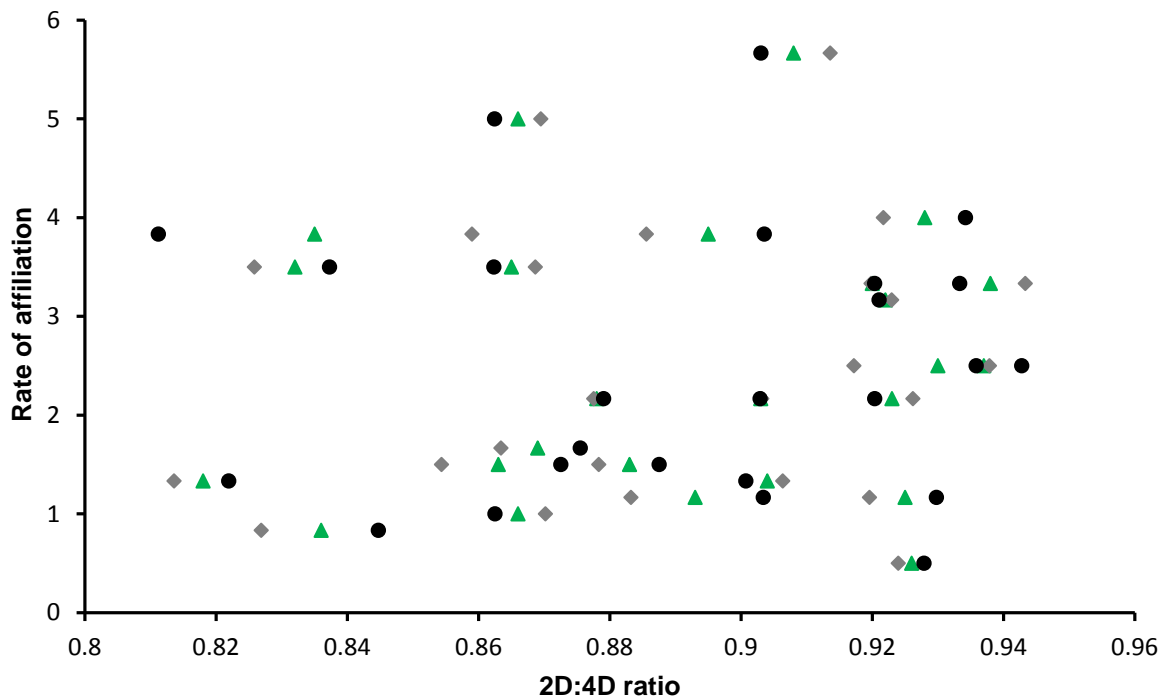


Figure 4.10: The relationship between mean 2D:4D ratio (green triangles, solid green line), right 2D:4D ratio (grey diamonds, grey solid line) and left 2D:4D ratio (black circles, black dotted line) and rate of affiliation.

4.7 Heritability of the 2D:4D ratio

The correlation between female's mean 2D:4D ratio and her infant's mean 2D:4D ratio was both strong and significant ($r = 0.829$, $df = 6$, $P = 0.042$) (Fig. 4.11). Maternal right 2D:4D ratio and infant right 2D:4D ratio were not significantly correlated ($r = 0.257$, $df = 6$, $P = 0.623$), nor were maternal left 2D:4D ratio and infant left 2D:4D ratio ($r = 0.771$, $df = 6$, $P = 0.072$). Maternal right 2D:4D ratio and infant left 2D:4D ratio were not significantly correlated ($r = 0.429$, $df = 6$, $P = 0.397$). However, maternal left 2D:4D ratio and infant right 2D:4D ratio did show a strong significant correlation ($r = 0.943$, $df = 6$, $P = 0.005$) (Fig. 4.12). In the mother/infant pairs analysed here, mothers held a range of dominance ranks (9, 15, 17, 20, 22 and 24). Infant mean 2D:4D ratio showed significant negative correlation with maternal dominance rank ($r = 0.829$, $df = 6$, $P = 0.042$) (Fig. 4.13) but neither infant right 2D:4D ratio ($r = 0.771$, $df = 6$, $P = 0.072$) nor left 2D:4D ratio ($r = 0.714$, $df = 6$, $P = 0.111$) correlated significantly with maternal dominance rank.

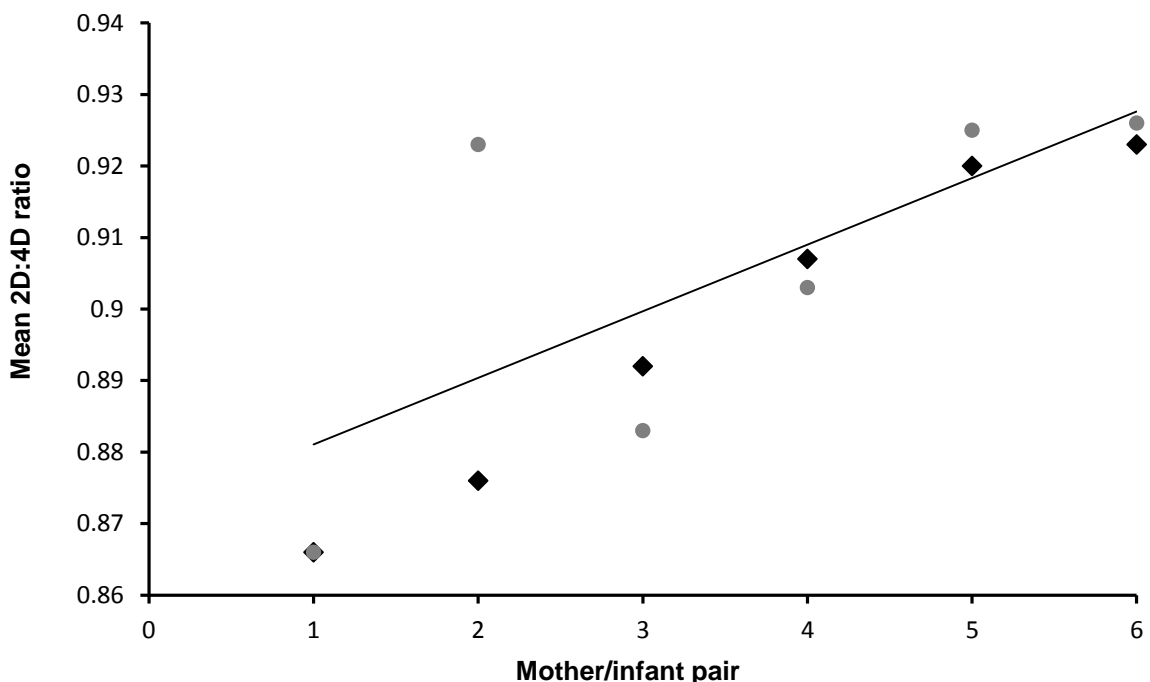


Figure 4.11: Relationship between mother's mean 2D:4D ratio (grey circles) and her infant's mean 2D:4D ratio (black diamonds).

A significant model was not produced in a multiple regression between infant mean and maternal right and left 2D:4D ratios (adjusted R squared = 0.651, $F_{2,3} = 5.663$, $P = 0.096$). Neither a maternal right 2D:4D ratio nor left 2D:4D ratio were significant predictors of infant mean 2D:4D ratio in this model (right: Beta = -1.585, $P = 0.182$; left: Beta = 2.280, $P = 0.089$).

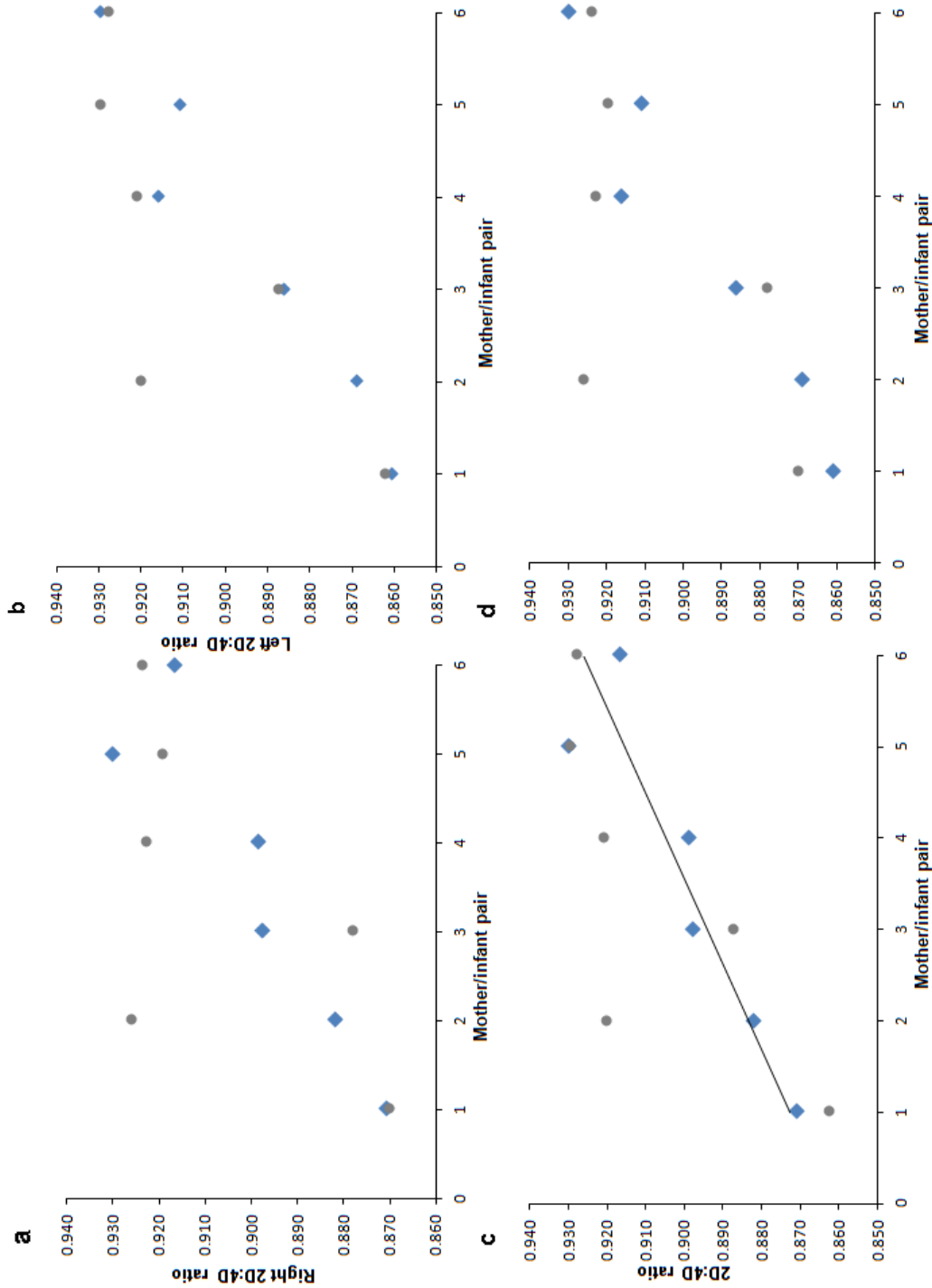


Figure 4.12: Relationship between (a) maternal right 2D:4D ratio (grey circles) and infant right 2D:4D ratio (Blue diamonds), (b) maternal left 2D:4D ratio and infant left 2D:4D ratio, (c) maternal left and infant right 2D:4D ratio and (d) maternal right and infant left 2D:4D ratio.

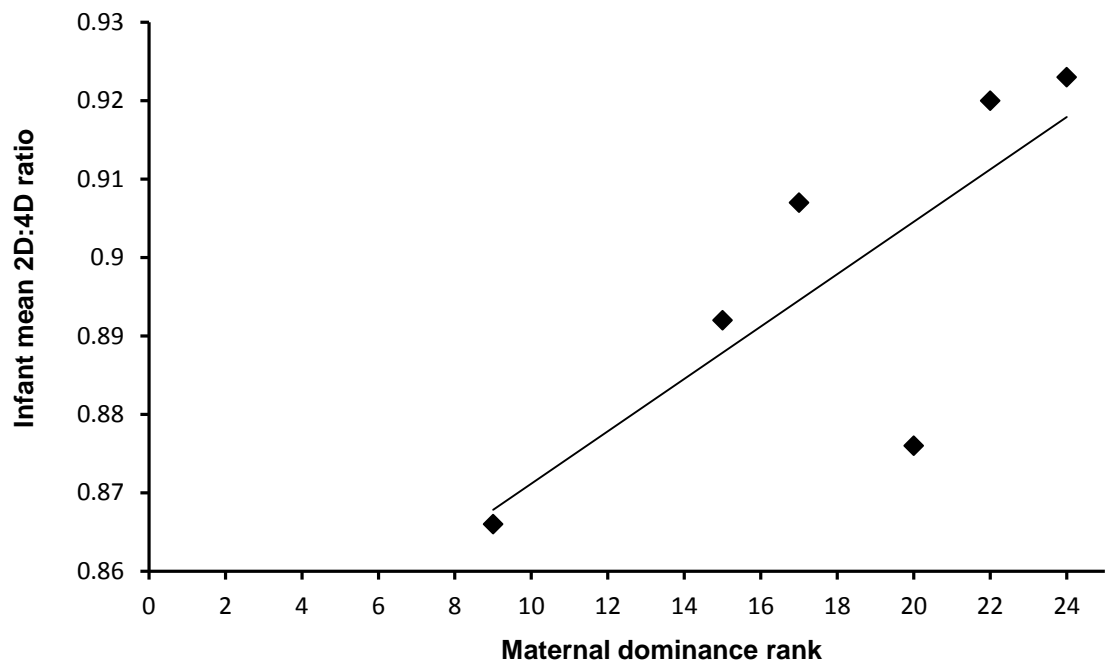


Figure 4.13: Relationship between maternal dominance rank and the infant mean 2D:4D ratio.

Discussion

This study demonstrates that PAE, as inferred from 2D:4D ratios, correlate with the dominance hierarchy in wild female chacma baboons. Higher-ranked females had lower 2D:4D ratios in both hands and lower mean 2D:4D ratios than lower-ranked females. The negative correlation between 2D:4D ratio and dominance rank suggests that, as predicted, prenatal androgens influence a female's position in the dominance hierarchy in natural groups. The effects of higher PAE may predispose behaviour in low 2D:4D ratio individuals to be more masculinised and, in this case, dominant (Thornton *et al.* 2009; Wallen 2005). This is consistent with other research in cercopithecine primates, in which female dominance rank was negatively correlated with their 2D:4D ratio (Howlett *et al.* 2012; Nelson *et al.* 2010). Alternatively, maternal experience within the social group with respects to her rank could influence gestational processes, such as PAE, which in turn could contribute to the maintenance of rank inheritance. However, no birth order effects on 2D:4D ratios were observed within matriline in rhesus macaques, suggesting PAE may not be involved in younger daughter ascendancy in cercopithecine primates (Nelson *et al.* 2010). All 2D:4D ratio measures showed a positive association with rate of submission. Females with lower 2D:4D ratios showed lower rates of submission than females with higher 2D:4D ratios suggesting that females exposed to higher PAE are less submissive than those exposed to lower levels of PAE. Androgenised female rhesus macaques were observed to withdraw less often from the approaches of other animals after they had been treated with testosterone propionate during prenatal development supporting hypothesis 1 (Thornton *et al.* 2009). As in the macaque females, higher PAE may affect the behaviour of baboon females toward being less submissive.

Variance in mean 2D:4D ratios predicted 68 % of variance in dominance rank but the right and left 2D:4D ratios individually were not found to be significant predictors suggesting that effects for the two hands cannot be separated and both are subject to PAE. However, co-linear variables were used in the model and this

must be acknowledged as a potential confounding factor in interpreting the contributions of the individual predictors. The relationship between 2D:4D ratio and dominance rank in females did not display a perfect, linear pattern with the highest ranked female having the lowest 2D:4D ratio, the second highest-ranked female having the next lowest and so on down the hierarchy. This may be because contingencies in social processes and rank inheritance mean that some females occupy higher or lower positions in the hierarchy than their PAE, inferred from their 2D:4D ratios, would suggest.

Regulation of a female's tendency toward future aggressive behaviour is another way in which PAE may affect a female's dominance rank (Higley *et al.* 1996). All 2D:4D ratio measures correlated negatively with rate of non-contact aggression. Females with lower 2D:4D ratios display non-contact aggression at higher rates than those with higher 2D:4D ratios. The same pattern was observed between 2D:4D ratio measures and contact aggression, although correlation was not significant for the right 2D:4D ratio. The right 2D:4D ratio is suggested to be a better marker for the prenatal hormonal environment than the left hand 2D:4D ratio so this comes as a surprise as it should reflect more strongly the organisational effects of prenatal androgens. This lack of relationship may be a result of sample size. Larger sample sizes could confirm a significant correlation between right 2D:4D ratio and rate of contact aggression but this requires further study. However, females with lower mean and left 2D:4D ratios displayed contact aggressive behaviours at higher rates than those with higher mean and left 2D:4D ratios. Prediction 2b that correlation between 2D:4D ratio measures would be higher for contact aggressive behaviours than non-contact aggressive behaviours was not supported. Correlations were consistently higher for non-contact aggression than contact aggression, except for the left 2D:4D ratio which showed a slightly higher correlation with contact aggression. This is possibly due to generally low rates of contact aggression among the females in the study group and seven of the 25 females were never observed to engage in any contact aggressive behaviours.

Mean, right and left 2D:4D ratios all showed a positive association with the rate at which a female received aggression from other group members, so females with lower 2D:4D ratios suffered less aggression than females with higher 2D:4D ratios.

Women with low 2D:4D ratios show higher reactive aggression under provocation (Zeynep & Nelson 2004) and female nonhuman primates with low 2D:4D ratios may have a similar disposition. Female baboons exposed to high PAE (low 2D:4D ratios) may have a greater tendency to retaliate to any aggression they receive than those exposed to low PAE (high 2D:4D ratios) who may be more likely to submit to any aggression they receive. For this reason other group members may target high 2D:4D ratio females in preference to low 2D:4D ratio females as they are less likely to be faced with repercussions from these females or their allies. Also, as individuals with higher 2D:4D ratios in this group are also those lower in rank, it is likely to be a reflection of individuals being targeted based on their social rank. PAE may create different personality types according to rank and may promote rank appropriate behaviours (Nelson *et al.* 2010). It would not be adaptive for a low-ranked female, after receiving aggression, to retaliate toward a higher-ranked female as she is likely to be faced with dangerous ramifications for transcending the rank boundaries. Therefore, PAE may increase the potential for confrontational behaviour in high-ranked (low 2D:4D) animals and promote submissive behaviour in low-ranked (high 2D:4D) animals (Nelson *et al.* 2010).

Dr-I did not correlate with any of the behaviours examined nor with any of the 2D:4D ratio measures. This suggests that right hand 2D:4D ratio minus left hand 2D:4D ratio has no relationship with female behaviour whether this involves aspects of dominance, submission, or aggression. In this study Dr-I did not act as a useful negative correlate for PAE in baboons, as it does in humans (Manning 2002).

Contrary to prediction 3a, the 2D:4D ratio was not correlated with rate of interest in infants. Females with lower 2D:4D ratios did not show less interest in infants than those with higher 2D:4D ratios. None of the females in this study had been artificially androgenised and it is likely that they developed in a prenatal environment where steroid hormone levels were within the normal range for their sex. Consequently, they are likely to display normal female-typical behavioural patterns. PAE may have low ability to affect female-typical behaviours which rely on female sex hormones for their expression unless present at unusually high levels as is seen in flutamide treated female rhesus macaques (Wallen 2005) and in girls with CAH (Leveroni & Berenbaum 1998), both of which show reduced

interest in infants. This would explain the lack of association between 2D:4D ratios and interest in infants among the females of my study group.

Rate of affiliation and 2D:4D ratio measures were not significantly correlated suggesting that PAE are not involved in the expression of affiliative behaviour in female baboons. In adult females, affiliative social behaviour is regulated by ovarian hormones, specifically oestrogen (Witt *et al.* 1992). It is likely that adult and adolescent females' affiliative social behaviours were influenced by oestrogen originating in their ovaries and not PAE. Thus, a female's 2D:4D ratio did not, as predicted (4a), correlate positively with her rate of affiliation. Higher OT levels increase social contact time between adult rats (Witt *et al.* 1992) and OT facilitates social motivation (Lim & Young 2006). However, there was no association between the number of grooming partners and social partners a female had and her mean 2D:4D ratio. Hypothesis 4, that PAE would be related to affiliative behaviours, was not supported as females with lower 2D:4D ratios are not less social and females with higher 2D:4D ratios are not more social. The number of grooming partners a female had was positively correlated with the number of social partners she had suggesting that females with larger social networks had more grooming partners or vice versa.

Contradictory to expectations outlined in predictions 4c and 4d, I found no relationship between a female's mean, right and left 2D:4D ratios and the rate of grooming she gave or rate of grooming she received. The results indicate that females with higher 2D:4D ratios did not groom other females at higher rates and females with lower 2D:4D ratios were not groomed at higher rates. There was also no correlation between the rate at which a female groomed other individuals and the rate at which she received grooming. Grooming interactions are likely to be far more complicated than just a female's motivation to engage in social contact with others. Grooming has both hygienic and social value (Saunders & Hausfater 1988) and is used as 'currency' by females, for example to obtain tolerance at feeding sights from higher-ranked females or to gain access to another female's infant (Barrett *et al.* 1999; 2002). Therefore, the rate of grooming a female gives and receives is unlikely to be a simple reflection of prenatal sex hormones predisposing her motivation to seek or avoid social interaction with other females. Normal levels of PAE may not affect the expression of female-typical behavioural

patterns, such as affiliation and interest in infants, which are governed by ovarian hormones in adult life (Lim & Young 2006; Witt *et al.* 1992). Prenatal androgens may have the largest effects on behaviours that are mediated by male sex hormones such as dominance and aggression in female baboons.

Mean 2D:4D ratios of mothers and their infants were positively correlated suggesting high similarity in mean 2D:4D ratio between mother/infant pairs. This may be evidence for a genetic contribution to the expression of the mean 2D:4D ratio in chacma baboons. However, neither variance in mother's left or right 2D:4D ratios were found to predict variance in the mean 2D:4D ratio of her infant. Heritability in rhesus macaques was significant in mother/son pairs but not in mother/daughter pairs (Nelson & Voracek 2010). The androgen receptor gene is maternally determined in males and this could go some way to explaining this significant relationship but with a limited sample size I was not able to test for differences in similarity between mothers with male and female infants. Heritability of the 2D:4D ratio was higher in the right hand than the left in human twin studies (Paul *et al.* 2006a) and in rhesus macaques mother/infant dyads (Nelson & Voracek 2010) but the correlation was not higher between 2D:4D ratios of the right hand in baboon mother/infant pairs. When all mother/infant 2D:4D ratio combinations were analysed separately, only the right 2D:4D ratio of infants and left 2D:4D ratio of mothers were significantly correlated. This may be due to effects of stress levels in females which may affect the postnatal growth of their left 2D:4D ratio which is postulated to be more sensitive to early postnatal environmental factors. Maternal stress during pregnancy could affect the prenatal hormone environment of her developing offspring. Right 2D:4D ratio is more robust to early postnatal influences than left 2D:4D ratio and so is more likely to show any possible gestational effects on infant digit ratios (Nelson *et al.* 2010). This could explain the association between a mother's left 2D:4D ratio and her offspring's right 2D:4D ratio. The fact that mother mean and infant mean 2D:4D ratios were positively correlated suggests perhaps both genetic influences and shared environmental influences are important in the expression of similarity of the 2D:4D ratio in mother/infant pairs (Nelson & Voracek 2010). No association was found between maternal rank and the right or left 2D:4D ratio of offspring. However, in support of prediction 6c, mean 2D:4D ratio was highly negatively correlated with

maternal rank, suggesting that higher-ranked mothers produce infants with lower mean 2D:4D ratios.

This was a mixed sex group of infants and infant age was not uniform across the group with some being close to weaning age with completely yellow pelage and others being much younger with completely dark pelage. The 2D:4D ratio is known to increase over age in very young human children (McIntyre *et al.* 2005) but to remain stable in adulthood (Manning 2002). It is possible therefore that 2D:4D ratios may change as infants age suggesting that older offspring should be used when comparing mother/offspring 2D:4D ratios, although this could potentially increase the affects of non-shared environmental influences on 2D:4D ratios. Additionally, my sample consisted of only six mother/infant pairs and the positive correlation between mother and infant mean 2D:4D ratios can only be considered a preliminary observation.

5.1 Methodological issues

Although the digital photographic and computer software method was useful as a non-invasive technique for measuring 2D:4D ratios in wild animals it was very time consuming. Measuring digits from photographs with ImageJ took over 90 hours. Further issues with this method arise from the environment. I found it very difficult to obtain photographs of baboon hands due to the dense vegetation in which they spent the majority of their time and photographing opportunities were restricted to times when the baboons came out into the open onto flat rocks or onto the road. This method may be more suited to studies of baboons living in more open habitats or of captive animals. For the latter, routine veterinary check-ups often make direct measurements of digits just as feasible as using indirect digital photographic methods.

I found that it was more difficult to get close enough to infants to take photographs as they were not as used to being observed as were the older baboons. Their hands were also smaller than those of adult and adolescent females and most of the time they were clinging to their mothers which made getting hand photographs difficult. When not on their mothers, infants displayed much more rapid movement (e.g. when playing) than adult and adolescent females adding to the difficulty of obtaining photographs when hands were in optimum positions. These issues may

have contributed to the lower ICC value for infant hands compared to that of adult and adolescent female hands suggesting that intra-observer reliability was lower for 2D:4D ratio measurements in infants.

Due to the time consuming nature of this method and its restricted use in densely vegetated environments I would recommend more direct methods of digit measurement be used where ever possible. However, despite the limitations raised in this section, I believe the issues above detract little from the methodological validity and the results I obtained.

5.2 Directions for future research

The 2D:4D ratios of the right and left hands were significantly tightly correlated in this study. This result differs from data on human right and left 2D:4D ratios where the correlation is much lower (Manning *et al.* 2000; Manning 2002). My sample size was small and represents data from a single baboon troop and one baboon subspecies. The 2D:4D ratio varies widely between human populations (Manning 2002) and this may also be the pattern among baboons and is a topic worthy of further study. Also, it is worth noting that my sample consisted solely of female study subjects. Sexually dimorphic traits, including 2D:4D ratio (Hönekopp & Watson 2010), tend to be displayed in the masculine form more strongly on the right side of the body in humans (Tanner 1990; Kimura 1994) and it is possible the difference between right and left 2D:4D ratios may be greater among male than female baboons. Research into the developmental mechanisms which may contribute to the observed differences human and baboon 2D:4D ratios would be interesting, particularly from an evolutionary perspective.

Further studies into correlations between 2D:4D ratios and behaviour in nonhuman primate species would be useful to assess how the trait generalises with behaviour across the Order. Future heritability research should aim for larger, multigenerational samples, and should take into account paternity. Unfortunately, relatedness among House Troop females was not known and research into similarities in 2D:4D ratios among related female baboons would be useful for further assessment of the heritability of this trait. In humans, 2D:4D ratio varies with birth order and sex of older siblings (Saino *et al.* 2006a). Exploring 2D:4D ratios within matrilineal groups could perhaps test the hypothesis that prenatal sex

hormones are linked to younger daughter ascendancy pattern in baboons. Finally, research as to whether there is any relationship between the 2D:4D ratio and dominance rank among female social strepsirrhines could provide insight into the evolutionary history of this association within the primate Order.

5.3 Conclusions

I conclude that PAE, indexed by 2D:4D ratios, play a significant role in the dominance hierarchy in wild female baboons living in a troop with a natural social structure. PAE may contribute to the maintenance of female rank through their effects on the future expression of a female's behaviour such as her tendencies toward submission and aggression or may even be linked to maternal effects. In hierarchical social systems, small differences in an individual's ability to dominate others are likely to impact an individual's fitness and so PAE could have positive effects on the fitness of primates living in despotic groups. PAE do not have significant involvement in the expression of interest in infants and affiliation in female baboons and may have limited power to affect behaviours regulated by female sex hormones in non-hormonally manipulated female primates. Although results for heritability (estimates based on correlations) are preliminary due to a small sample size, they hint at possible genetic and gestational contributions to the expression of the 2D:4D ratio in baboons. In addition to social learning, the effect that prenatal sex hormones have on brain patterning and personality, may be involved in shaping certain aspects of social behaviour in wild female baboons.

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