The expression of the 2D:4D ratio across the Order Primates

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Declaration

This is to certify that:

1. The thesis contains only my original work towards the fulfilment of the degree of Doctor of Philosophy at the University of Kent, except where stated otherwise.
2. Acknowledgement has been made in the text to all other material used.

C. Howlett

Caroline Howlett, February 2019

Abstract

The ultimate causes of variation in primate behaviour and social systems have been well studied, but less attention has been paid to the underlying role of proximate mechanisms. Using the second-to-fourth digit ratio (2D:4D ratio) as a biomarker for prenatal androgen effects (PAE) and phylogenetic comparative methods where appropriate, this thesis aims to complement the ultimate perspective by assessing the degree to which variation in PAE may provide a proximate explanation for the observed variation in primate behaviour. Specifically, this study examines 1) the role of PAE in male intrasexual competition and mating behaviour in non-human primates, 2) the relationship between PAE and human marriage systems, 3) the role of PAE in female intrasexual competition and social relationships in non-human primates and 4) the role of PAE in the expression of aspects of human and non-human primate personality.

In study 1, a cross-species analysis investigating the relationship between PAE and aspects of intrasexual competition in male non-human primates revealed no relationships between 2D:4D ratios and anatomical traits associated with male intrasexual competition (male canine crown height and canine crown height dimorphism) or male reproductive skew and mating skew. Male digit ratios did, however, vary across species characterised by different types of mating systems; males of species characterised by monogamous mating had the highest 2D:4D ratios, followed closely by polyandrous males (low inferred PAE), while polygynandrous and polygynous males had the lowest 2D:4D ratios (high inferred PAE). Male 2D:4D ratios also varied with the form of polygyny and polygynandry corresponding to the need for males to display competitive over cooperative behaviours in each mating system. Higher PAE may therefore be adaptive for male non-human primates which experience high levels of direct intrasexual competition. This pattern was also evident in female non-human primates (Study 3), but was not mirrored in analysis of humans, where no associations were found between male or female 2D:4D ratios and marriage system (Study 2). As males are the competing sex among humans, there is likely strong selective pressure for high PAE regardless of the marriage system. Likewise, due to its negative impact on female fertility, sexual selection may favour low PAE in human females regardless of the marriage system. However, as the sample was biased in favour of monogamous populations, a more balanced dataset encompassing a wider range of marriage systems may provide further insights.

PAE were also implicated in the maintenance of intersexual dominance relationships, particularly female dominance, as evidenced by lower female 2D:4D ratios in species characterised by female dominance than in species characterised by male dominance or codominance (Study 3). There was no evidence that variation in female-female dominance interactions is associated with variation in PAE across the primate order as evidenced by the lack of relationships between 2D:4D ratio and rates of female-female agonism or the directional consistency of agonistic interactions among females (argued to be a measure of the extent to which dominance relationships are despotic vs egalitarian), although these analyses were based on small sample sizes. Likewise, relationships between 2D:4D ratios and degree of frugivory and group size were nonsignificant, possibly because these variables are not good measures of direct intrasexual competition among females. However, in a more taxonomically-narrow analysis conducted with macaque species (*Macaca* spp.)*,* female 2D:4D ratio varied according to social style, with more "tolerant" species having higher 2D:4D ratios than less tolerant species, suggesting that PAE may contribute to this variation. Results indicate that PAE may act as a proximate mechanism underlying behavioural expression in male and female non-human primates in ways that are ultimately adaptive to their social system.

In study 4, PAE on behavioural variation within species was explored using personality traits (boldness, exploration tendency/curiousness, persistency, competitiveness) in three species: ring-tailed lemurs (*Lemur catta*), robust capuchins (*Sapajus* spp.) and human children (*Homo sapiens*). 2D:4D ratios were not associated with any trait in ring-tailed lemurs or with persistency in any species, suggesting that expression of this trait may not be influenced by PAE. Boldness and exploration tendency in boys correlated negatively with 2D:4D ratios, as did competitiveness in robust capuchins, suggesting that PAE play a role in the expression of these traits in these and perhaps also in other haplorhine primates. In addition to broad cross-species influences, PAE thus appear to underlie inter-individual differences in the expression of some adaptive behavioural traits, highlighting the importance of considering proximate as well as ultimate causes in studies of primate behaviour.

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- Chapter 1 -

General Introduction

1.1: Introduction

The evolutionary underpinnings of social structure and behaviour in humans and non-human primates remains a contentious issue (Thierry 2008; Koenig & Borries 2009; Sussman *et al.* 2005; Sussman & Garber 2004). While ultimate explanations concerning adaptations to ecological conditions have been central in these debates (Koenig *et al.* 2013; Przybyta 2013; Kappeler & van Schaik 2004; van Schaik 1989; Sterck *et al*. 1997; Trivers 1972), the roles of underlying proximate mechanisms (e.g. hormones, physiology, genetics) have received less attention. Consequently, the effects that proximate mechanisms may have on primate behaviour, sociality and mating systems are still poorly understood. By examining one such proximate mechanism, prenatal androgen effects (PAE), alongside the ultimate mechanisms attributed to variation in behaviour, this thesis aims to provide a more complete understanding of the factors that contribute to the variation in social systems and individual behaviour across the Order Primates.

1.1.1: Prenatal sex hormones

Prenatal sex hormones (androgens and oestrogens) have organisational effects on morphology and brain patterning, and the behavioural predispositions that arise from these processes are mediated by the social environment in which the animal finds itself (Wallen 2005). Variation in prenatal exposure to sex hormones brings about behavioural differences between the sexes (Knickmeyer *et al.* 2005; Wallen 2005) and numerous studies have examined the resulting sex differences in behaviour (Hines 2010; Adkins-Regan 2009; Moore *et al*. 2005; Balthazart & Ball 1995; Johnston & File 1991; Eaton *et al.* 1985). There is also marked variation in the expression of behaviour between individuals of the same sex which can, in part, be attributed to individual differences in exposure to prenatal sex hormones (Clipperton-Allen *et al.* 2011; Coleman *et al*. 2011).

1.1.2: The developmental role of prenatal sex hormones

Prenatal sex hormones play vital roles in regulating gene expression during development (Kondo *et al*. 1997) and are necessary for male and female sex determination (Tomaszycki *et al*. 2005). Prenatal androgens are vital for the development of the male phenotype in mammals and have masculinising and defeminising effects on anatomy and behaviour in both sexes (Thornton *et al*. 2009), while prenatal oestrogens are behind the development of female reproductive structures (Gilbert 2003). Prenatal androgens have lasting effects on the physiology and behaviour of individuals and play a key role in shaping an individual's competitive behaviours (Josephs *et al*. 2006; Josephs *et al*. 2003; Kraus *et al*. 1999). Conversely, oestrogens have pre- and postnatal roles in the regulation of sociality and social bonding, including enhancing cooperative, affiliative and prosocial behaviours (Trumble *et al*. 2015; Coleman *et al.* 2011; Ross & Young 2009; Bielsky & Young 2004). In humans, high PAE are associated with reduced empathy (Chapman *et al*. 2006), reduced social sensitivity (Baron-Cohen *et al*. 2005) and several disorders in which social behaviour is affected, such as Asperger's syndrome (Knickmeyer & Baron-Cohen 2006; Lim & Young 2006). Due to the role that PAE play in organising sexually selected traits, in addition to social behaviour, it is reasonable to assume that the phase in development when sex hormones exert their influence, is under strong selective pressure in humans and non-human primates.

1.1.3: Prenatal sex hormones and intrasexual competition

Intrasexual competition facilitates the evolution of physical and behavioural adaptations which are necessary for attracting mates and/or obtaining the resources necessary for reproduction and offspring care (Darwin 1871). The nature and intensity of intrasexual competition selects for variation in behaviour, and in the developmental and neurobiological processes that regulate and reinforce behavioural phenotypes. Dominance, aggression and competition are all important factors governing social life in primates and PAE play an important role in shaping an individual's competitive and aggressive behaviours (Higley *et al.* 1996). Feeding competition is thought to be a key factor contributing to the evolution of female social relationships, with despotic relationships being favoured under certain ecological conditions (Koenig 2002). In such cases, increases in the expression of dominant and aggressive behaviour would be advantageous to group-living female primates, as these behaviours enable the individuals expressing them to gain greater access to essential resources (Koenig 2002).

Similarly, competition for access to receptive females is considered to be a strong selective force in males, contributing to the evolution of male mating strategies (Trivers 1972; Kappeler & van Schaik 2004). For male primates (including humans), high PAE during development could be advantageous in terms of outcompeting sexual rivals at both the pre- and post-copulatory levels, as androgens increase aggressive tendencies (Wobber *et al.* 2013; Mazur & Booth 1998), muscle mass and metabolism (Josephs *et al.* 2006), facilitate the production of sperm (Bouchard *et al*. 1986) and enhance anatomical characteristics associated with sexual selection such as weaponry and display traits (Weinberg *et al*. 2015; Higham *et al.* 2013; Fink *et al.* 2007b; Setchell & Dixson 2001a & b; Thornton & Gangestad 1999). Such attributes are all conducive to improving a male's competitive abilities and, subsequently, his reproductive success.

1.1.4: Prenatal sex hormones and personality

In addition to differences in behaviour across species, there is also variation within species that may be attributable to differences in PAE (Knickmeyer *et al*. 2005). Personality traits can have important effects on factors such as reproductive fitness and survival (Iwanicki & Lehmann 2015; Morton *et al*. 2015; Neumann *et al*. 2013; Shuett *et al*. 2010; Smith & Blumstein 2008), are of adaptive value to the individuals displaying them and are therefore likely to be under considerable selective pressure (Iwanicki & Lehmann 2015; Dammhahn 2012; Seyfarth *et al*. 2012; Weiss *et al*. 2012; Koski 2011; Sih & Bell 2008; Dall *et al*. 2004; Sih *et al.* 2004). In association with ecological factors (Burton *et al*. 2013), proximate mechanisms (e.g. PAE) may exert an influence over the expression of personality traits in ways that are favourable to individual fitness (Sih 2011; Sih & Bell 2008). Although there is a large body of literature investigating personality in humans and non-human primates (Larson *et al.* 2017; Freeman & Gosling 2010), the neuroendocrinological mechanisms underpinning differences in the expression of personality traits are still not fully understood (Trumble *et al*. 2015; Sih & Bell 2008).

Higher PAE are implicated in the increased expression of a number of personality traits in humans and non-human primates including assertiveness and aggressiveness (Ribeiro *et al*. 2016; Wacker *et al*. 2013; Berenbaum & Resnick 1997

Dixson 1980). In humans, men tend to score higher than women on measures of assertiveness, aggression and social dominance (Wacker *et al.* 2013; Campbell 2006; McCrae & Terracciano 2005), suggesting a link between greater expression of these traits and higher PAE. Human females exposed to synthetic progestin (similar in action to androgen) in utero were more individualistic, independent and self-assured than their unexposed siblings and females treated with synthetic oestrogen. Oestrogen treated females, in contrast, displayed more group-orientated and group-dependent personality types (Reinisch 1977). Juvenile female rhesus macaques (*Macaca mulatta*) which were artificially exposed to abnormally high prenatal androgens showed masculinised play behaviour and reduced interest in infants compared with controls (Thornton *et al.* 2009; Wallen 2005). The evidence suggests that prenatal sex hormone exposure can influence the expression of personality traits within and between the sexes. The behavioural predispositions brought about by PAE may be essential for enabling individuals to successfully navigate their natural and social environments (Ross and Young 2009; Coleman *et al*. 2011) and it may be possible to identify relationships between personality traits and the proximate mechanisms underlying their expression.

1.1.5: The 2D:4D ratio

The periods in development when sex hormones have their organising effects on the neural systems that result in behaviour are also the periods when digit growth is influenced by androgen and oestrogen receptor activity (Zheng & Kohn 2011). The ratio of the lengths of the second (2D) and fourth digits (4D) of the hands (2D:4D ratio) is a proposed biomarker which can be used as a postnatal measure of PAE (Zheng & Cohn 2011; Manning 2011). Sex hormones affect the 2D:4D ratio during the early stages of foetal development in humans and the trait is unchanged by the rise in sex hormone levels at puberty (Manning *et al*. 2004a; 2003), remaining relatively stable throughout postnatal growth (Knickmeyer *et al*. 2011; McIntyre *et al*. 2005). In humans, men typically have lower (more masculine) 2D:4D ratios of <1 and women tend to have higher (more feminine) 2D:4D ratios of ≥1 (Manning *et al*. 2000; 1998) and this sexual dimorphism is apparent from nine weeks of gestation (Malas *et al*. 2006).

1.1.6: Development of the 2D:4D ratio

Sex hormone levels differ between the sexes, both pre- and postnatally and the sex difference in 2D:4D ratio arises as a result of the developing digits differing in their sensitivity to prenatal androgens and oestrogens (Zheng & Cohn 2011). Sex hormone receptor activity is higher in the 4D where androgens increase chondrocyte proliferation and oestrogens inhibit it. Consequently, as females are typically exposed to higher oestrogen levels during development, this has the effect of reducing the growth of the 4D resulting in higher (more feminine) 2D:4D ratios. Males, however, are exposed to higher androgen levels which stimulates the growth of the 4D resulting in lower (more masculine) 2D:4D ratios (Zheng & Cohn 2011). Therefore, lower 2D:4D ratios in males are the result of exposure to higher PAE and higher 2D:4D ratios in females are due to exposure to lower PAE and higher prenatal oestrogen effects (POE) (Tapp *et al*. 2011; Zheng & Cohn 2011). Individuals of the same sex can also show disparity in 2D:4D ratio which likely reflects individual differences in PAE (Wacker *et al.* 2013; Manning 2002); individuals experiencing higher PAE during development display lower (more masculine) 2D:4D ratios than those exposed to lower PAE (Zheng & Cohn 2011).

1.1.7: The 2D:4D ratio in humans

In human men, lower 2D:4D ratios (high inferred PAE) are correlated with higher sperm counts (Manning *et al.* 1998), larger family size (Klimek *et al.* 2014), greater hand-grip strength (Fink *et al*. 2006) and greater sporting ability (Manning & Taylor 2001). In women, lower 2D:4D ratios are associated with reduced fertility (Cattrall *et al*. 2005), higher social boldness (assertiveness) (Lindová *et al.* 2008) and higher reactive aggression (Benderlioglu & Nelson 2004). Low 2D:4D ratios are linked to improved endurance running ability (Manning *et al*. 2007) and masculine personality types in both sexes (Kim *et al.* 2014). Men and women with lower 2D:4D ratios display higher drives for social status, greater dominance-related behaviours (Millet & Dewitte 2009; 2007; Manning & Fink 2008) and are perceived by others as more dominant (Neave *et al*. 2003), further implicating PAE as influencing individual social behaviour and competitive ability in humans. Using marriage systems as an index of sexual selection, Manning *et al.* (2004b) observed that 2D:4D ratios tended to be lower in polygynous societies than in monogamous societies. This observation implies a link between PAE and competition between men for wives (Manning *et al*. 2004b). Although the possible effects of specific environmental variables and latitude have been controlled for in cross-cultural analyses (Minocher *et al.* 2018), to my knowledge previous studies investigating the relationship between PAE and human marriage systems have failed to control for the effects of populations' shared ancestry (Manning *et al.* 2004a; Manning 2008). As a great deal of the variation in human behaviour (cultural and biological) can be attributed to phylogeny (Minocher *et al.* 2018), doubts can be raised about the results of previous studies and the nature of the relationship between PAE and human marriage systems remains unresolved.

1.1.8: The 2D:4D ratio in non-human primates

There is variation in the 2D:4D ratio across anthropoid primate species (Nelson & Shultz 2010), and this is apparent even between closely related species. For example, chimpanzees (*Pan troglodytes*) display lower 2D:4D ratios than bonobos (*P. paniscus*) and this difference has been attributed to the female-dominated social system and increased tolerance in bonobos compared to the male-dominated social system of chimpanzees (McIntyre *et al.* 2009; Hare *et al.* 2007). This implies that variation in PAE may be involved in facilitating the increase or reduction in specific traits and behaviours according to the requirements of a species' social system. There is also evidence of variation in 2D:4D ratios within primate species correlating with variation in their behaviour. For example, female cercopithecine primates with lower 2D:4D ratios had higher positions in the dominance hierarchy (*Papio ursinus*: Howlett *et al.* 2015; *P. ursinus* and *P. hamadryas*: Howlett *et al.* 2012; *M. mulatta*: Nelson *et al.* 2010) and displayed higher rates of aggression (*P. ursinus:* Howlett *et al*. 2015) which implies a link between PAE and the individual expression of these behaviours in cercopithecines and perhaps other primate species.

Nelson & Shultz (2010) in their cross-species analysis of anthropoid primates found that 2D:4D ratios decreased with increasing intrasexual competition levels in both sexes, pointing to an association between PAE and intrasexual competition in male and female anthropoid primates. However, as Nelson & Shultz (2010) limited their sample to 37 species of anthropoid primate, it is unclear whether the observed trends will be sustained in a larger sample with a greater range of primate taxa, including strepsirrhines. This makes inclusion of a wider range of primate species an interesting avenue of research.

1.1.9: 2D:4D ratio measurement methods

A number of different methods and apparatus have been used to measure the 2D:4D ratio in humans and other animals (e.g. scaled tubes - Nicholls *et al.* 2008; radiographs - Paul *et al*. 2006; scanned images - Bailey & Hurd 2005; photocopies - Manning *et al*. 2005; direct caliper measurements - Scutt & Manning 1996), and the accuracy and reliability of these measurement methods are known to vary considerably (Allaway *et al.* 2009; Kemper & Schwerdtfeger 2009; Voracek *et al*. 2007a; Voracek & Dressler 2006). For example, the methods used to measure primate 2D:4D ratios in the Nelson & Shultz (2010) study are known to be vulnerable to high degrees of error, both with regards to the number of different measurers (inter-observer reliability) and differences in the apparatus used to take the measurements (measurement precision). The authors acknowledge this but state that repeatability estimates were within acceptable ranges (Nelson & Shultz 2010). However, in a study comparing 2D:4D ratio measurement techniques, Allaway *et al*. (2009) found that inter-observer reliability was much lower than intra-observer reliability even among expert 2D:4D ratio measurers. The 2D:4D ratio measurements in the Nelson & Shultz (2010) study were taken by a large number of institution staff who were untrained and inexperienced in taking these measurements (other than reading an instruction sheet). Therefore, it is likely that inter-measurer reliability was even lower than that reported among expert measurers. Additionally, measurement precision is known to vary according to the tools used to measure the 2D:4D ratio (Kemper & Schwerdtfeger 2009). Kemper & Schwerdtfeger (2009) found that precision was lowest for ruler measurements and they also suggest that inter-measurer reliability is insufficient for this apparatus. The use of different measuring tools (rulers or callipers) in Nelson & Shultz (2010) study, therefore, further reduces the reliability of their 2D:4D ratio data.

Allaway *et al*. (2009) reported most consistency among measurers when computer-assisted image analysis software was employed and found computer-assisted indirect measurement of 2D:4D ratios to be more accurate than direct measurements with callipers and indirect measurements from photocopies and scans. This result was mirrored in Kemper & Schwerdtfeger (2009) who found measurement precision to be greatest when computer-assisted image analysis software was used to measure 2D:4D ratios, in comparison to indirect measurements of scanned images using callipers or rulers. Another study reported high inter- and intra-observer reliability when using digital photographs of children's palms on a Perspex® table top and computer-assisted measurement software to indirectly measure 2D:4D ratios (Ranson *et al*. 2013). The 2D and 4D of the hands are measured from the basal crease (where the finger joins the palm) to the tip of the extended digit (Figure 1.1.1). Computer-assisted image analysis software provides the measurer with advantages which are not available using other methods (e.g. zooming) and which assist in the accurate identification of these landmarks (Kemper & Schwerdtfeger 2009). Computer-assisted measurement methods thus appear to be superior to other known methods in terms of measurement precision and inter- and intra-measurer reliability. In light of this, insofar as possible, I employ computer-assisted image analysis software methods to measure human and non-human primate 2D:4D ratios in this thesis.

1.1.10: Thesis aims

The evidence points to the 2D:4D ratio being a valid biomarker for noninvasively measuring PAE in humans and non-human primates. Using improved methodology, the broad aim of this thesis is to assess the degree to which PAE may act as a proximate mechanism affecting the expression of primate behaviour in ways that are ultimately adaptive. More specifically:

1) To investigate the relationship between PAE and mating behaviour and intrasexual competition in male non-human primates.
2) To explore the potential relationship between PAE and marriage systems in humans.
3) To investigate the relationship between PAE and aspects of social behaviour and intrasexual competition in female non-human primates.

4) To examine the role of PAE as a neuroendocrinological mechanism underlying variation in the expression of individual personality traits in primates.

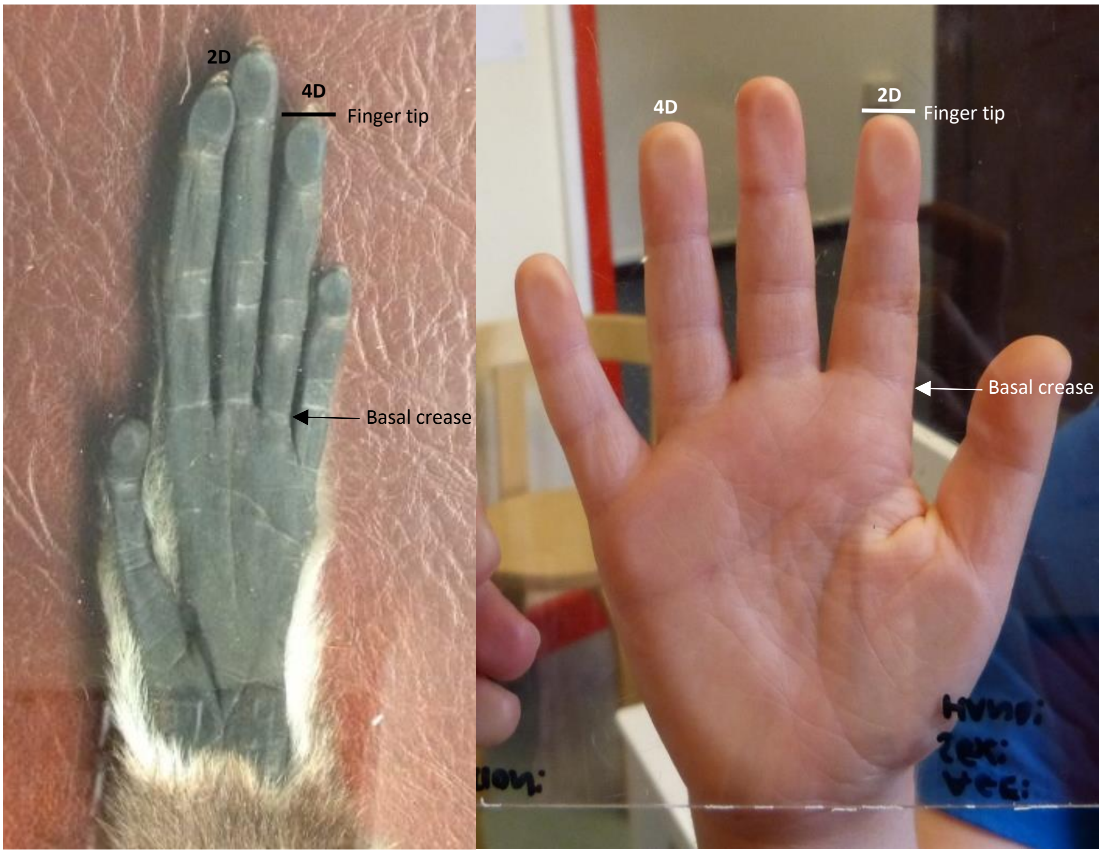

Figure 1.1.1: Examples of digital photographs used to indirectly measure the digits in human and non-human primate study subjects using computer-assisted image analysis software. The measurement landmarks (basal crease and fingertip) are highlighted and the images show (a) the left hand of an adult female lar gibbon (*Hylobates lar*) and (b) the right hand of a human boy.

1.1.11: Thesis outline

Each chapter examines a distinct aspect of PAE on behaviour in primates using the 2D:4D ratio as a proxy. Chapter 2 focusses on the role of PAE as a proximate mechanism affecting male intrasexual competition in non-human primates using phylogenetically controlled analyses. Similarly, Chapter 3 examines the relationship between PAE and human marriage systems, whilst controlling for the non-independence of populations as a result of shared ancestry. In Chapter 4 I investigate the relationship between PAE and female intrasexual competition and social relationships in non-human primates, again controlling for relatedness between species. In Chapter 5 I explore the role of PAE in the expression of behaviour at the individual level by examining the relationship between 2D:4D ratios and personality traits in ring-tailed lemurs (*Lemur catta*), robust capuchin monkeys (*Sapajus* spp.) and human children (*Homo sapiens*) using quantifiable behavioural variables measured under experimental conditions. Chapter 6 provides a general discussion of the preceding chapters. Here, I return to the aims of the thesis and discuss whether these have been achieved, the strengths of each study are considered, alongside directions for future research.

- Chapter 2 -

Prenatal androgen effects as a proximate mechanism underlying intrasexual competition in male non-human primates

Abstract

The nature and intensity of intrasexual competition selects for variation in behaviour and the developmental and neurobiological processes that regulate and reinforce these behavioural phenotypes. The ratio between the lengths of the second and fourth digits of the hands (2D:4D ratio) can be used as a biomarker to assess an individual’s exposure to prenatal androgen effects (PAE). Using the 2D:4D ratio and phylogenetically controlled methods, this study aimed to investigate the relationship between PAE and intrasexual competition in male non-human primates, with a particular focus on mating systems. In general, males characterised by monogamous mating systems had the highest 2D:4D ratios, followed closely by polyandrous males (low inferred PAE). Polygynandrous and polygynous males had the lowest 2D:4D ratios (high inferred PAE). Male 2D:4D ratios also varied significantly with the form of polygyny and polygynandry relative to the requirements for males to display aggressive and competitive behaviours over cooperative and other prosocial behaviours in each mating system. There were no relationships between 2D:4D ratio and anatomical traits associated with male intrasexual competition levels (male canine tooth size and canine tooth dimorphism), or between 2D:4D ratio and male mating skew or reproductive skew. The results indicate that PAE may act as a proximate mechanism underpinning the expression of behaviour in male primates in ways that are adaptive to their mating system. Cooperation, competition and the proximate mechanisms which underlie their expression are closely linked, and in order to fully understand the relationship between PAE and mating systems in non-human primates, it is imperative to consider selection for cooperative and affiliative behaviour in tandem with selection for behaviours associated with male intrasexual competition.

2.1: Introduction

2.1.1: Non-human primate mating systems

Sexual selection is an evolutionary force which can influence the morphology, physiology and behaviour of a species and selects for traits which lead to greater mating and reproductive success in both sexes (Kappeler & van Schaik 2004; Andersson 1994). According to sexual selection theory, males should compete for access to receptive females as they are the major limiting resource in male reproductive success (Trivers 1972) and this male intrasexual competition manifests in the form of species' mating sytems (Kappeler & van Schaik 2004). A variety of mating systems are observed in primate species (Kappeler & van Schaik 2002). Monogamous mating systems are those in which both males and females typically mate with only one member of the opposite sex. There are different 'levels' of monogamy, including genetic monogamy where a state of sexual exclusivity exists between a mated pair (French *et al.* 2018; Díaz-Muñoz & Bales 2016) and social monogamy which in basic terms can be described as a male and female living as a pair (with or without offspring) over an extended period of time (Díaz-Muñoz & Bales 2016). Sexual exclusivity between a pair is implied in social monogamy but mating outside of the monogamous relationship can occur in both sexes (French *et al.* 2018). However, without molecular studies to determine paternity, it is often not possible to determine if pair-living primates are engaging in sexual exclusivity (genetic monogamy) or not. Polyandrous mating systems occur where one female mates with multiple males, and each male mates only with her. Spatial dispersion of females, infanticide avoidance and the need for infant care by the male seem to be related to monogamous and polyandrous mating systems (Koenig *et al*. 2013).

Polygyny is a common mating system in primates and describes one male mating with several females, each female mating only with him. Cases in which both males and females mate with multiple members of the opposite sex are termed polygynandry (Kappeler & van Schaik 2002). Polygyny and polygynandry take several forms. In spatial polygyny, agonistically dominant males defend access to a number of females. This system is often seen in solitary species and involves males defending large ranges which overlap with the ranges of several females. In female-defence polygyny, one or more males directly defends a group of females against rivals (Kappeler & van Schaik 2002). In harem polygyny, a single male defends exclusive mating access to a group of females. In cooperative female-defence polygyny, a group of males work together to defend access to a group of females with which most males will mate. Cooperative resource-defence polygyny describes coalitions of males defending a territory and subsequently the females within it from other groups (Kappler & van schaik 2002; Koenig *et al*. 2013). This form of polygyny, alongside lekking, was not thought to exist among primates (Kappeler & van Schaik 2002) but Koenig *et al*. (2013) argue that it is present in all major primate radiations. Although in the literature these are widely described as forms of polygyny, as males and females typically mate with multiple partners, these are better described as forms of polygynandry. Another mating system seen in primates is currently termed scramble competition polygyny, in which roving males seek out receptive females which they leave shortly after mating in order to acquire more mates. In this case, both sexes usually mate with a number of partners (Kappeler & van Schaik 2002) and again, it could more accurately be described as a polygynandrous than a polygynous mating system.

Another form of polygynandry occurs in primates which I will refer to here as ‘contest competition polygynandry’. This differs from scramble competition polygynandry in that it applies to species in which males and females live in permanent association and there is active competition between males in a group for access to receptive females. As a distinction from forms of cooperative defence polygynandry, males do not cooperate to defend females from sexual rivals. Unlike in spatial and harem polygyny, monopolisation of females is generally not possible and both sexes typically mate with multiple partners. Male competitive strategies can include physical fighting and mate guarding (Girard-Buttoz *et al*. 2014; Bercovitch 1997), along with more subtle techniques such as sneak copulations (Soltis *et al*. 2001). However, polygynous, monogamous and polyandrous mating can occur within this mating system due to various factors such as the operational sex ratio (Kruger 2010; Mitani *et al*. 1996), female reproductive synchrony (Ruiz-Lambides *et al*. 2017; Ostner *et al*. 2008), reproductive seasonality (Chism & Rogers 1997), male dominance rank (Di Fiore 2003; Cowlishaw & Dunbar 1991), incomplete control (Kutsukake & Nunn 2006), and female choice (Periera & Weiss 1991). It is crucial to consider the form that competition between males takes when investigating the possible effects of sexual competition on a trait (Weckerly 1998). Therefore, it is important to distinguish between this and other mating systems already classified due to the different stages at which males face sexual competition and the variation in male relationships which play key roles in shaping their behaviour and physiology (see Table 2.1.1 for information on forms of polygyny and polygynandry along with descriptions of typical mating patterns seen in the sexes for each).

Table 2.1.1: Forms (subcategories) of polygyny and polygynandry with details on original and updated terminology (used in the current study), brief descriptions of each and the mating patterns of males and females.

Original terminology	**Updated terminology**	**Description**	**Mating pattern**
Spatial polygyny	Spatial polygyny	A single agonistically powerful male defends access to a number of females within his range.	Males mate with several females. Females mate with one male.
Harem polygyny	Harem polygyny	A single male defends exclusive mating access to a group of females.	Males mate with several females. Females mate with one male.
Cooperative defence polygyny	Cooperative defence polygynandry	A group of males cooperatively defend a territory and the females within it/mating access to a group of females.	Males and females mate with multiple partners.
Scramble competition polygyny	Scramble competition polygynandry	Roving males seek out and mate with females before moving on in search of more mates.	Males and females mate with multiple partners.
Polygynandry	Contest competition polygynandry	Species live in permanent mixed-sex groups, males actively compete for access to receptive females, male monopolisation of females is usually not possible.	Males and females mate with multiple partners.

2.1.2: Reproductive skew and mating skew in male non-human primates

The reproductive success and mating success of individual males can vary widely across taxa, depending largely on the mating system (Dubuc *et al*. 2014; Kappeler & van Schaik 2002). Male mating success describes the number of matings a male achieves whereas reproductive success refers to the number of offspring a male sires. It should be noted that mating success does not necessarily predict reproductive success (Strier *et al*. 2011; Engelhardt *et al.* 2006), likely as a result of other factors such as the timing of mating relative to the period of fertility, sperm competition and cryptic female choice (Dubuc *et al*. 2014; Engelhardt *et al*. 2006; Widdig *et al*. 2004; Periera & Weiss 1991). In monogamous mating systems, male variance in reproductive success is roughly equivalent to that of females (Kappeler & van Schaik 2002). However, for polygynous and polygynandrous species, male reproductive success can be heavily skewed in favour of agonistically powerful (in solitary species or those with uni-male groups) or higher-ranking males (in multi-male groups with hierarchical male relationships) (Gogarten & Koenig 2013; Strier *et al*. 2011; Saltzman *et al*. 2009; Widdig *et al*. 2004; Kappeler & van Schaik 2002; Wimmer & Kappeler 2002).

Dominant males can defend exclusive access to fertile females and in doing so often gain the highest number of copulations with the most females. Reproductive skew is described as high if one or a few males monopolise reproduction and low reproductive skew indicates there is a more even spread of paternity across males (Gogarten & Koenig 2013). In a study on Northern muriquis (*Brachyteles hypoxanthus*), which live in egalitarian patrilocal societies with tolerant relationships between group members, male reproductive skew was very low, with the most successful male siring only 18% of infants (Strier *et al*. 2011). Additionally, in seasonally breeding Barbary macaques (*Macaca sylvanus*) the correlation between male dominance rank and reproductive success is weak due to the fact that multiple females are receptive simultaneously and dominant males are unable to monopolise exclusive access to them (Thierry & Aureli 2006). In comparison, dominant males achieved 69% of paternity in mandrills (*Mandrillus sphinx*: Setchell *et al.* 2005), 91% in verreaux's sifakas (*Propithecus verreauxi*: Kappeler & Schäffler 2008) and 85% in mountain gorillas (*Gorilla beringei beringei*: Bradley *et al*. 2005). The level of reproductive skew can even reach 100% in some species. For example, in a group of western lowland gorilla (*G. gorilla gorilla*), the dominant silverback male was found to be the sire of all of the offspring in his group (Inoue *et al*. 2013). This emphasises the important impact that dominance can have on reproductive success in male primates (Engelhardt *et al*. 2006).

Launhardt *et al*. (2001) found great disparity in reproductive success among individual males in the seasonally breeding grey langur (*Semnopithecus entellus*). The difference they observed was determined by the type of group the males inhabited, whether single- or multi-male and, in the case of the latter, their dominance position within the group. In single-male groups, paternity was monopolised entirely by the harem holder. In multi-male groups however, the dominant male fathered 57% of infants, 22% of infants were fathered by other males within the group and 21% of infants were attributed to extra-group males (Launhardt *et al*. 2001). Unlike males of single-male groups, the dominant males in multi-male groups were unable to control sole reproductive access to fertile females. This is likely due to factors related to female reproductive synchrony and/or other female mating strategies (Clutton-Brock & Huchard 2013). This suggests that any behavioural and/or anatomical traits which could increase a male’s chance of being a harem holder in a single-male group or attaining the dominant position in a multi-male group would be under strong selective pressure due to the substantial reproductive benefits these positions confer (Di Fiore 2003; Launhardt *et al*. 2001).

2.1.3: Androgens and direct male intrasexual competition

Androgens are known to increase competitive abilities, and, in many species, behaviours used to gain, maintain and improve social status are often observed in high testosterone individuals (Josephs *et al*. 2006; Josephs *et al*. 2003; Kraus *et al*. 1999). In the face of a challenge, testosterone levels rise and trigger behaviours which are conducive to dominating rivals (Mazur & Booth 1998) and testosterone levels are related to reproductive effort in males (Wobber *et al.* 2013). Wobber *et al.* (2013) found considerable species differences in testosterone production from infancy through to puberty when comparing the closely related chimpanzee (*Pan* *troglodytes*) and bonobo (*P. paniscus*). Chimpanzee testosterone levels decline slightly from infancy into juvenility where they remain low until a marked increase at puberty, and this increase is more prominent among males than females. On the other hand, bonobos of both sexes show stable testosterone levels across the same developmental period. This difference corroborates with variation in mating competition between males of the two species, with both intrasexual competition and aggression being higher in chimpanzees. This observation demonstrates that the ontogenetic pattern of testosterone production can undergo relatively swift evolutionary change in accordance with differences in male relationships and reproductive strategies.

Modifications in developmental trajectories frequently give rise to phenotypic changes between species (Wobber *et al.* 2013; Wobber *et al.* 2010; Carroll 2008) and variation in prenatal androgen effects (PAE) could be responsible for the regulation of intrasexual competition and mating systems in males. The ratio between the lengths of the second and fourth digits of the hands (2D:4D ratio) is a proposed biomarker for the organisational effects of prenatal androgens and oestrogens in individuals, with lower (more masculine) 2D:4D ratios being associated with higher PAE (Manning 2011; Zheng & Cohn 2011). A study by Cain *et al.* (2012) on male dark-eyed juncos (*Junco hyemalis*) found a negative relationship between 2D:4D ratio and adult testosterone production. Variation in exposure to prenatal sex hormones (inferred from 2D:4D ratios) correlated with the ability to elevate testosterone, such that low 2D:4D ratio birds displayed higher testosterone production in the face of a physiological challenge than high 2D:4D ratio birds (Cain *et al*. 2012). This suggests that PAE can have long-term impacts on adult testosterone production and consequently on any physiological processes and behaviours facilitated by these hormones in adult animals (Cain *et al*. 2012).

In humans, low 2D:4D ratio (inferred high PAE) individuals have been known to compete harder for mates and have more sexual partners (Manning & Fink 2008) and Nelson & Shultz (2010) report that non-pair-bonded anthropoid primate species tend to have lower 2D:4D ratios and pair-bonded species tend to have higher 2D:4D ratios. This is in keeping with the theory that higher PAE may be adaptive for males which experience high intrasexual competition levels through improving their competitive abilities (Nelson & Shultz 2010). This study provides a promising starting point in this avenue of research, but some methodological issues make confirmation of this result with improved methods desirable. In addition to concerns regarding the accuracy and reliability of their 2D:4D ratio measurements, their allocation of primate species to either pair-bonded or non-pair-bonded categories cannot fully encompass the fine-grained variation in male intrasexual competition and subsequent variation in the strength of selection for PAE; an oversight requiring rectification.

High levels of direct competition between males over access to receptive females brings about selection for traits which increase male competitive ability, such as large body size and weaponry (Leigh *et al*. 2008; Dubuc *et al*. 2014). One morphological feature often observed in primates that experience high levels of competition is enlarged canine teeth. In mandrills, adult male canine size correlates closely with male life-time reproductive success and males who successfully sired offspring had larger canines than males which had not sired offspring (Leigh *et al*. 2008). Canine size is typically a sexually dimorphic trait with males having larger canines than females, and the dimorphism is viewed as an outcome of male sexual selection (Plavcan 1998). The intensity of mating competition that males face has been found to covary with the degree of sexual dimorphism in canine size (Kay *et al*. 1988). In other words, the greater the intrasexual competition between males for access to females, the larger their canine teeth compared with females (Kay *et al*. 1988; Kappeler & van Schaik 2002). Androgens have been implicated in the development of teeth in spotted hyenas (*Crocuta crocuta*) but how sex hormones may affect tooth development in primates is less clear (Dempsey *et al*. 1999). Research in humans by Dempsey *et al*. (1999) found that in opposite-sex twin pairs, girls had larger (masculinised) teeth than girls from same-sex twin pairs or those who were gestated alone. These girls would have been exposed to higher PAE due to androgen transfer in utero from their brothers. The observed masculinisation was true for all teeth, but the effect appeared to be smallest in the diameter of maxillary canines. This suggests that, compared to in other teeth, PAE may have less impact on sexual dimorphism in the maxillary canines and the authors speculate that canine size and sexual dimorphism may be controlled by a mechanism not shared with other teeth (Dempsey *et al.* 1999). The degree of sexual dimorphism in canine size varies across primates and is more apparent in haplorhine primates characterised by polygynous and polygynandrous mating systems (Plavcan 2001). Male and female strepsirrhines, in contrast, tend to show little to no dimorphism in either body size or canine tooth size (Plavcan 2001; Kappeler 1996a).

2.1.4: Androgens and indirect male intrasexual competition

In many primate species, competition between males does not only take place prior to copulation. Post-copulatory mechanisms, such as sperm competition, can have great influence over male reproductive success in some species (Engelhardt *et al*. 2006). Sperm competition occurs when males cannot fully monopolise females and females mate with multiple males during their fertile phase (polygynandrous and polyandrous species). Paternity is therefore determined in the female reproductive tract after mating. Under these circumstances, the quality and quantity of sperm in a male's ejaculate can have a marked effect on the likelihood that he will father any offspring (Engelhardt *et al.* 2006). A male's reproductive success is therefore dependent on his ability to outcompete his rivals at the pre- and/or post-copulatory level.

Large testes size, mate guarding behaviours and repeated copulation by males are noted among primates and can be construed as adaptations to sperm competition. Male Wied's marmosets (*Callithrix kuhlii*) living in polyandrous groups mate at higher rates than males living in monogamous groups (Schaffner & French 2004). In long-tailed macaques (*M. fascicularis*), males have high testes-to-body-weight ratio (Harcourt *et al*. 1981) and produce high numbers of viable sperm (Schrod 2002) which suggests high levels of sperm competition in this species. A study by Engelhardt *et al.* (2006), found that reproduction is highly skewed in favour of high ranking long-tailed macaque males. However, males are not able to completely monopolise females which led to the suggestion that dominant males had an advantage at the sperm competition level. In addition to direct competition through female monopolisation, indirect sperm competition may have a significant effect on the reproductive success of dominant males (Engelhardt *et al*. 2006), a result paralleled in rhesus macaques (*M. mulatta*) (Dubuc *et al*. 2014). Spermatogenic efficiency is very high in the grey mouse lemur (*Microcebus murinus*), a species characterised by scramble competition polygynandry with intense competition between males over receptive females (Witsuba *et al*. 2003; Fietz 1999; Perret 1992). Grey mouse lemurs also display highly motile and unusually long sperm, characteristics which may reflect high levels of sperm competition within their mating system (Witsuba *et al.* 2003; Anderson & Dixson 2002; Gomendio & Roldan 1991). In cases when males are not always able to physically exclude their rivals, sperm competition may be a more important factor in male reproductive success than the physical ability to defend access to females.

Both testis volume and spermatogenesis are proposed to be androgen dependent (Pasqualini *et al*. 1986), and this may in part explain observed differences in testosterone levels across primate species (Muehlenbein *et al*. 2002; Coe *et al*. 1992). Testosterone facilitates the production of sperm in the male testes and higher testosterone levels result in higher sperm numbers (Bouchard *et al*. 1986). Sperm count and testosterone levels have been found to be higher in men with low 2D:4D ratios (Hong *et al*. 2012; Manning *et al.* 1998) and so high PAE could have implications for sperm competition in species in which females mate with multiple males (polygynandry and polyandry). Selection for high PAE is likely to be favoured under conditions where males experience both direct and indirect intrasexual competition and low in species in which males experience neither form of competition. Developing in a prenatal environment high in androgens could have advantageous effects for male primates in terms of gaining high status and outcompeting sexual rivals, particularly for polygynandrous species in which males must compete on both pre- and post-copulatory levels (Table 2.1.2).

Table 2.1.2: Occurrence of direct competition between males for access to females and/or indirect sperm competition between males in each mating system and the expected strength of selection for PAE based on male intrasexual competition.

Mating system	**Direct competition**	**Sperm competition**	**Strength of selection for PAE**
Monogamy	NO	NO	Low
Polyandry	NO	YES	Moderate
Harem polygyny	YES	NO	Moderate
Spatial polygyny	YES	NO	Moderate
Scramble competition polygynandry	NO	YES	Moderate
Cooperative defence polygynandry	YES	YES	High
Contest competition polygynandry	YES	YES	High

2.1.5: Monogamy: the roles of androgens, oestrogens, oxytocin & vasopressin

Unlike other mating systems, the males of species characterised by monogamy are not expected to face either direct or indirect competition for access to their mate during her fertile period. Behavioural characteristics associated with monogamy include coordinated behaviour and joint territorial defence, spatial and temporal proximity of a pair, bi-parental care of offspring, high levels of mate-directed sociality and a partner preference (the existence of a pair-bond) (French *et al*. 2018; Díaz-Muñoz & Bales 2016). Species classified within the scope of social monogamy may display some or all of these elements to a greater or lesser extent (French *et al*. 2018).

There is a link between PAE and the postnatal expression of behaviours associated with oestrogen and the hypothalamic neuropeptides oxytocin (OT) and vasopressin (VA). In a study on humans, participants with lower 2D:4D ratios (high inferred PAE) scored high on testosterone-related behaviours whereas those with higher 2D:4D ratios scored high on behaviours associated with oestrogen/OT (Fisher *et al.* 2010), while high 2D:4D ratios in children are connected with the development of prosocial behaviours (Fink *et al.* 2007a; Williams *et al.* 2003). Oestrogen, OT and VA play essential roles in regulating complex social and reproductive behaviours; the most notable among these for monogamous species are aspects of pair bonding and parental behaviour (Vargas-Pinilla *et al.* 2015; Lee *et al.* 2009; Neumann 2008). Oestrogen activity underpins many of the behavioural effects of OT (Razzoli *et al.*

2003; Young *et al*. 1998) and both OT & VA are necessary for social bonding in primates (Vargas-Pinilla *et al*. 2015). The OT system also stimulates paternal care and male tolerance of infants and, alongside VA, plays key roles in mate-directed sociality and partner preference (French *et al*. 2018).

Among eutherian mammals, the OT sequence is highly conserved (Ren *et al*. 2015) but variations in the sequence have been identified in several species of New World monkey, an observation hypothesised to be related to social monogamy (Ren *et al.* 2015; Vargas-Pinilla *et al.* 2015). Even a small alteration in the amino acid sequence can radically modify the structure and properties of OT and the eighth amino acid appears to be the most important for biological functions regulated by OT. Larger litter size in callitrichids is related to having a Pro-8 variation in the OT sequence (Vargas-Pinilla *et al*. 2015). Pair-bonded common marmosets (*C. jacchus*) treated with the Pro-8 OT variant interacted less (in terms of their social and sexual behaviour) with opposite sex strangers (Cavanaugh *et al.* 2014) further demonstrating that the OT/OT receptor system has a fundamental role in regulating key features of social monogamy (French *et al*. 2018; Ren *et al*. 2015; Cavanaugh *et al*. 2014).

Variation in male sex hormones also have notable influences over the behaviour of monogamous male primates. Although present in both monogamous and non-monogamous species, mate guarding behaviour in monogamous primates is crucial for preserving the monogamous relationship. It involves selective aggression towards same-sex intruders (facilitated by androgens) and/or protecting the pair-bond via heightened mate-directed sociality and proximity (facilitated by oestrogen/OT/VA) (French *et al*. 2018). Testosterone secretion in males may be an adaptive response to guard against potential reproductive conflict or immediate challenges (French *et al.* 2018). Elevated testosterone levels in males are linked with an increased motivation to mate whereas reduced testosterone levels are associated with increased parental effort and the presence of dependent offspring (Clark & Galef 1999). Species with high levels of male-infant contact and in which males contribute greatly to offspring care have lower circulating androgen levels than males which engage in low levels of offspring care (Nunes *et al*. 2001). In many small bodied New

World monkey species, male infant care is paramount to offspring survival and males are primed for the arrival of infants through a reduction in testosterone levels during the female's pregnancy (Zeigler *et al*. 2004). PAE play an important part in mediating many of the competitive behaviours which it is necessary for monogamous males to express in order to acquire mates, guard mates and defend their territories from intruders (French *et al.* 2018). However, aspects of a monogamous mating system, as discussed above, are likely to favour selection for increased prenatal oestrogen effects (POE) and/or reduced PAE in monogamous male primates.

2.1.6: Oestrogen, OT and VA: implications for other mating systems

Although they have profound effects on the behaviour of socially monogamous animals, oestrogen, OT and VA are vital for regulating social behaviour generally. The expression of affiliative behaviour is associated with oestrogen (Witt *et al*. 1992) and differences in OT levels consistent with the social environment can be observed in closely related species; for example, cerebrospinal fluid free OT levels are lower in the less affiliative pigtail macaque (*M. nemestrina*) than in the more affiliative bonnet macaque (*M. radiata*) (Rosenblum *et al*. 2002). OT and VA are necessary for the identification of familiar individuals (Bielsky & Young 2004) and OT facilitates social motivation and approach behaviour (Lim & Young 2006). In a study on meerkats (*Suricata suricatta*), Madden & Clutton-Brock (2011) found that experimental treatment with OT resulted in individuals of both sexes displaying higher levels of prosocial behaviours and reduced aggression. For primates living in multi-male groups, in which males are in the constant presence of sexual rivals, the ability to display some affiliative and tolerant behaviours towards conspecifics may reduce rates of potentially costly agonistic encounters. OT is linked to bonding among team-mates in humans (Pepping & Timmermans 2012), which is important in the context of 'cooperating-to-compete'. OT could have a similar role in regulating cooperative and tolerant behaviours between males characterised by polyandry and cooperative defence polygynandry. Selection for an increase in POE and/or a reduction in PAE could be advantageous (though not to the same extent as for monogamous species) for these males in terms of their motivation to cooperate to defend females/territory from extra-group males and to tolerate the presence of within-group competitors.

Where OT promotes prosocial and cooperative behaviour, testosterone has both organisational and activational roles in promoting aggressive and competitive behaviour. In human studies, these diametric effects on behaviour in comparable situations have been generally observed (Crespi 2016). For example, OT increases the expression of trust and paternal care behaviours (Van Ijzendoorn & Bakermans-Kranenburg 2012; Weisman *et al.* 2012) whereas testosterone decreases their expression (Bos *et al.* 2012; Gettler *et al.* 2011). OT decreases the expression of non-defensive aggression (Choleris *et al.* 2008) and testosterone increases it (Crespi 2016; Montoya *et al*. 2012; Carré *et al*. 2011). Testosterone is related to selective attention to threatening faces, which can be interpreted as individuals who may pose a status threat. Low testosterone individuals were found to look away from threatening faces whereas high testosterone individuals spent more time looking at angry or threatening faces (van Honk *et al.* 1999). OT, however, has the opposite effect and causes a reduction in attention to angry faces (Domes *et al*. 2013), reaffirming the opposing effects of testosterone and OT and demonstrating that higher testosterone individuals are lower in OT and vice-versa (Crespi 2016; Gabor *et al.* 2012; McCall & Singer 2012; van Anders *et al.* 2011). In the context of intrasexual competition, it is likely that the interplay between androgens and oestrogens (both pre- and postnatally) moderates the expression of affiliative and cooperative as well as agonistic and competitive behaviours in a manner which is adaptive to the social and mating system.

2.1.7: Summary of aims

This is the first study to explore variation in 2D:4D ratio in both strepsirrhine and haplorhine male primates. The primary aim of this study is to investigate the relationship between variation in PAE (inferred from 2D:4D ratios) and male intrasexual competition across the Order Primates using improved methodology. Specifically, I aim to:

1) Examine the relationship between PAE and mating systems (including forms of polygyny and polygynandry as subcategories) as a qualitative measure of male sexual competition.

2) Investigate the relationship between PAE and two quantifiable measures of male sexual competition - mating skew and reproductive skew.
3) Test if a relationship exists between PAE and male canine tooth size and sexual dimorphism in canine size - anatomical characteristics associated with male intrasexual competition.

2.1.8: Hypotheses and predictions

2a) Higher PAE are favoured in males of species that experience high levels of indirect sperm competition and direct competition for mates.

(i) When considering broad categories of mating system; monogamous males will have the highest 2D:4D ratios, followed by polyandrous males, then polygynous males, with polygynandrous males (facing both direct and indirect competition) having the lowest 2D:4D ratios.

(ii) When considering specific subcategories of mating system; males in species characterised by harem polygyny and spatial polygyny (facing only direct competition) will have higher 2D:4D ratios than males characterised by forms of polygynandry (facing both direct and indirect competition). Species characterised by scramble competition polygynandry (facing only indirect competition) will have higher 2D:4D ratios than males characterised by other forms of polygynandry (facing both direct and indirect competition).

(iii) Species with higher male reproductive skew will have lower 2D:4D ratios.

(iiii) Species with higher male mating skew will have lower 2D:4D ratios.

2b) Higher PAE contribute to the increased expression of many sexually dimorphic anatomical traits which improve male intrasexual competitive ability.

(i) Males of species with larger canine teeth will have lower 2D:4D ratios.

(ii) Males of species with greater canine dimorphism will have lower 2D:4D ratios.

2.2: Methods

2.2.1: Study subjects

I collected 2D:4D ratio data between March 2016 and November 2017 on captive primates housed in 29 zoos, wildlife/safari parks and primate research centres in the UK and Europe and one sanctuary in South Africa (see Appendix 2.1). Study subjects comprised animals from juvenile to adult ages. The 2D:4D ratio is fixed early prenatally (Galis *et al*. 2010), is relatively stable during postnatal development (Knickmeyer *et al*. 2011; Lombardo & Thorpe 2008) and does not change appreciably during puberty (Králík *et al.* 2014; Manning *et al.* 2003, 2004a; Manning 2002), providing justification for the use of non-adult animals in this study.

2.2.2 Soliciting institutions

I contacted the research and/or education departments of these institutions via email, describing my research and requesting to carry out my study with the primates in their collection. Once I had gained their consent, I either posted or delivered the necessary equipment and methodological details and, where applicable, made arrangements to visit the institution to collect data myself (see 2.2.3.1).

2.2.3: Data collection

2.2.3.1: 2D:4D ratio measurements

To obtain 2D:4D ratio measurements of captive primates I employed the digital photographic and computer-assisted image analysis software method as described in Howlett *et al*. (2015). Hand images were collected in two ways. First, I took advantage of instances when animals were being handled (e.g. for veterinary treatment) and requested that zoo staff take digital photographs of the hands of the animals with palms held flat against a clear Perspex® sheet with fingers straight and fully extended (Figure 2.2.1). Institutions were provided with three Perspex® sheets of different sizes for use on larger or smaller primate species. I provided staff with an instruction sheet detailing the protocol, the position that the primate hands and fingers must be presented in and example photographs with information on the landmarks used to measure the digits (see Appendix 2.2). In these cases, each hand was photographed three times for each animal. Any images which did not adhere to the criteria outlined in the protocol were discarded.

I also obtained hand images using the 'free photo' method as described in Howlett *et al*. (2015). From public viewing areas at the institutions, I observed captive primates moving freely around their enclosures and opportunistically took photographs whilst hands were in optimum positions for digit measurements using a Panasonic FZ250 digital camera in 'burst shooting' mode (camera set to take 12 frames per shot). Photographs were taken from both the dorsal and ventral sides of the hands (Figures 2.2.2 & 2.2.3). For each individual, I identified three photos for each hand in which digits were in the optimal positions: digits in a flat and straight position with the entire length of the digits and measurement landmarks visible (Figures 2.2.1, 2.2.2 & 2.2.3). For purposes of data reliability (Allaway *et al*. 2009), I carried out all measurements of 2D:4D ratios from these photographs using the computer-assisted image analysis software program Image Processing and Analysis in Java (ImageJ).

Figure 2.2.1: Examples of Perspex® hand photos received from zoos (a) black-capped squirrel monkey (*Saimiri boliviensis*), (b) tufted capuchin (*Sapajus apella*) and (c) chimpanzee (*Pan troglodytes*). Digit lengths were then measured from these photos using ImageJ.

I measured the second and fourth digits five times for each photograph, giving a total of 15 measurements for each digit per individual. I used the mean of these 15 measurements as the measurement for that digit. I calculated the 2D:4D ratio of each hand by dividing the length of the second digit by the length of the fourth digit for each individual. I calculated the mean 2D:4D ratio (M2D:4D) by averaging the right 2D:4D ratio (R2D:4D) and left 2D:4D ratio (L2D:4D). I then averaged individual 2D:4D ratio measurements within each species to obtain species values for R2D:4D, L2D:4D and M2D:4D. These species averages are the 2D:4D ratio measures used in analyses.

Figure 2.2.2: Example of hand photos taken using the 'free photo' method from the dorsal surface of the hand as animals moved around their enclosures (a) Guinea baboon (*Papio papio*), (b) white-naped mangabey (*Cercocebus lunulatus*), (c) close-up of white-naped mangabey hand.

Figure 2.2.3: Examples of photos taken using the 'free photo' method from the ventral surface when primates held their hands against the viewing windows of their enclosures; (a) Lion-tailed macaque (*Macaca silenus*), (b) Sulawesi black-crested macaque (*Macaca nigra*), (c) Alaotran gentle lemur (*Hapalemur alaotrensis*) (d) Golden lion tamarin (*Leontopithecus rosalia*), (e) Common squirrel monkey (*Saimiri sciureus*) (f) Buffy-headed capuchin (*Sapajus xanthosternos*).

For some individuals, 2D:4D ratios were only available for one hand due to factors such as missing limbs, digit injuries or poor image quality. Data for these individuals were excluded from the sample and only those individuals with 2D:4D ratio data for both hands were used in subsequent analyses. The final dataset comprised the R2D:4D, L2D:4D and M2D:4D of 406 male primates across 73 species (Table 2.2.1; Figure 2.2.4).

2.2.3.2: Anatomical considerations

Variation in hand morphology in primates is associated with substrate use (the degree of arboreality versus terrestriality) (Kivell *et al*. 2016; Richmond 2007; Lemelin & Schmitt 1998; Jouffroy *et al*. 1993) and so I collected substrate use data for each species from the published literature and incorporated this variable as a factor in all analyses. Primates were classified as either arboreal (68-100% arboreal), arboreal/terrestrial (34-67% arboreal) or terrestrial (0-33% arboreal). If substrate use data were not available as percentages, I used categorical classifications given by the authors of the publications (see Appendix 2.3).

In humans, allometry has been suggested to play a role in the sex difference observed in 2D:4D ratios, such that men have lower 2D:4D ratios because they have longer fingers than women (Lolli *et al*. 2017; Kratochvíl & Flegr 2009; but see Manning 2010), alluding to a link between 2D:4D ratio and body size. Since the 2D:4D ratio is fixed early in prenatal development and is generally stable throughout postnatal growth (Manning & Fink 2018; Galis *et al*. 2010), it is unlikely that allometry has considerable influence over the development of this trait. However, in order to account for the potential effects of body size on 2D:4D ratio, I collected average male body mass (in grams) data for each species from the published literature and included this variable as a factor in all analyses (see Appendix 2.4).

2.2.3.3: Male mating variables

I collated data from various existing sources on mating system, mating system subcategory, reproductive skew, and mating skew (see Appendices 2.5, 2.6 & 2.7 for the comprehensive list of sources). Species characterised by both social and/or genetic monogamy are placed under the umbrella of monogamy in this study. As it is difficult to determine whether males are defending the resources or the females in a territory from outgroup males and, as levels of intrasexual competition for females are likely to be similar in both cases, I grouped cooperative resource-defence polygynandry and cooperative female-defence polygynandry under the label ‘cooperative defence polygynandry’. Reproductive skew is defined as the percentage of alpha or resident male paternity. If more than one value was available for a species (representing different groups/populations), I took the average of these as the reproductive skew value of the species as a whole. Mating skew is defined as the percentage of alpha or resident male mating success. When more than one value was available for a species, I followed the method as described above for reproductive skew to create one value for each species.

Data were not available for all variables for every species and the number of species for each variable is as follows: mating system – 73 species, mating system subcategory – 72 species, reproductive skew – 22 species, mating skew – 18 species (Table 2.2.1, see Appendices 2.5, 2.6 & 2.7).

2.2.3.4: Male canine variables

I obtained maxillary canine tooth crown height (CCH) data (millimetres) from Plavcan & Ruff (2008). CCH is measured from the base at the cementum-enamel junction to the apex of the tooth. I calculated CCH dimorphism by dividing male CCH (MCCH) by female CCH (FCCH). CCH data were available for 45 species (see Appendix 2.8 for species values).

2.2.4: Statistical methods

2.2.4.1: Normality & multicollinearity

I conducted all non-phylogenetically controlled analyses using IBM SPSS Statistical software version 24 and used Shapiro-Wilk tests throughout when assessing normality of the data. Data for male R2D:4D, L2D:4D and M2D:4D were normally distributed, as was reproductive skew. Male body mass, MCCH, CCH dimorphism and mating skew were not normally distributed and so these variables were log-transformed. All other variables were categorical. Due to the inclusion of substrate use and body mass as factors in all analyses, I tested for multicollinearity of the predictor variables in each analysis using the variance inflation factor (VIF). I found no evidence of multicollinearity among the independent variables. I obtained variance inflation factors (VIF) of between 1 and 1.434 indicating no issues with multicollinearity.

2.2.4.2: 2D:4D ratio measurement reliability

I used the intraclass correlation coefficient (ICC) set to the 'absolute agreement' definition to test intra-observer reliability. The ICC showed that 2D:4D ratio measurements were highly repeatable for both hands across all species collectively and within primate families (Appendix 2.9).

I investigated differences in male R2D:4D and L2D:4D using a paired *t*-test (two-tailed). R2D:4D and L2D:4D in males were not significantly different ($t_{72} = 0.417$, P = 0.678) and were tightly correlated ($r = 0.949$, df = 72, P = <0.001), justifying the use of M2D:4D in subsequent analyses.

2.2.4.3: Phylogenetic signal

Phylogenetic signal describes non-independence among species or "the tendency for closely related species to resemble each other more than they resemble species drawn at random from a phylogenetic tree" (Blomberg & Garland 2002 pg. 905). The phylogenetic signal of a trait can be measured using a quantitative measure of phylogenetic independence known as Pagel's lambda (λ) (Pagel 1997, 1999). $\lambda = 0$ indicates the trait has no phylogenetic signal, meaning it evolved independently of phylogeny and closely related species are no more alike than more distantly related species. $\lambda = 1$ means that there is strong phylogenetic signal in the trait, close relatives are more similar to each other than distant relatives and the trait evolved according to the Brownian motion model of evolution (Felsenstein 1985; Grafen 1989). Although there is phylogenetic signal in traits with λ values between 0 and 1, these evolved under processes other than pure Brownian motion (Freckleton *et al.* 2002; Pagel 1997, 1999).

I tested for phylogenetic signal in my variables using Pagel's λ and the packages Devtools and Models of Trait Macroevolution on Trees (motmot) in the statistical software program R version 3.4.1 "Single candle" using *10kTrees* (version 3) phylogeny with associated taxonomy from GenBank for the phylogenetic trees (Arnold *et al*. 2010). I found statistically significant λ values for all variables other than mating skew and reproductive skew (Appendix 2.10). As all measures of 2D:4D ratio exhibited significant phylogenetic signal, the use of phylogenetically controlled methods is justified, and the results reported throughout are those of phylogenetically controlled analyses.

2.2.4.4: Controlling for species' relatedness

The 2D:4D ratio is brought about in part by PAE, which are in turn modulated by the social and ecological environment. Therefore, in all analyses, I assigned 2D:4D ratio measures as the dependent variables and anatomical, ecological and social variables as the independents. When carrying out cross-species comparative analysis it is necessary to control for phylogenetic history and the evolutionary non-independence of traits across taxa (Garamszegi 2014; Nunn 2011; Purvis & Webster 1999; Harvey & Pagel 1991). Whereas standard statistical tests of association assume independence of data points (Felsenstein 1985), phylogenetically controlled tests allow the potential non-independence of the residuals resulting from phylogenetic relatedness between species to be controlled for (Garamszegi 2014).

To test for relationships between male 2D:4D ratios and the variables of interest (substrate use, male body mass, mating system, mating system subcategory, mating skew, reproductive skew, MCCH and CCH dimorphism), I carried out phylogenetically controlled analyses in R version 3.4.1 "Single candle" using *10kTrees* (version 3) phylogeny (Arnold *et al*. 2010). I used Phylogenetic Generalized Least Squares (PGLS) analysis using the package Comparative Analysis of Phylogenetics and Evolution in R (caper). I used Pagel's λ to estimate the degree of phylogenetic autocorrelation between models using a maximum likelihood (ML) approach. I ran the analysis across a block of 200 phylogenetic trees for each variable and used the software FigTree (version 1.4.3) to illustrate phylogenetic trees.

Molecular data were not available for six species in *10kTrees* phylogeny (*Saguinus labiatus, Callicebus cupreus, Mico melanurus, Cercocebus chrysogaster, Cercocebus lunulatus* and *Propithecus coronatus*) and so, using the R package Analysis of Phylogenetics and Evolution (ape), I added these species into the trees based on their relationships to sister taxa which were present in *10ktrees* phylogeny. *S. labiatus* is in the *S. mystax* group (Groves 2001) and I followed phylogeny from Perelman *et al*. (2011) in which *S. labiatus* diverged from *S. mystax* approximately 1.75 million years ago (mya) (Perelman *et al*. 2011; Groves 2001). *Callicebus moloch* and *C. cupreus* are sister species which diverged approximately 3.65 mya (Byrne *et al.* 2016; Perelman *et al.* 2011). *M. melanurus* is in the *Mico* subgenus and I treated it as monophyletic with other *Mico* species and included it using information on phylogeny from Garbino (2015). I incorporated *C. chrysogaster* using *C. torquatus* which it diverged from ~ 3.33 mya. I integrated *C. lunulatus* using its sister species, the Sooty mangabey (*C. torquatus atys*). *C. lunulatus* was widely considered a subspecies of *C. t. atys* (Groves 2001) until recent taxonomic reassessment elevated it to species level (Oates *et al*. 2016; Mittermeir *et al.* 2013). Genetic data suggests that *P. coronatus* and *P. deckenii* are in fact the same subspecies and so I substituted *P. deckenii* for *P. coronatus* in the phylogeny (Pastorini *et al*. 2001; Tattersall 1988 but see Thalmann *et al.* 2002). I then pruned species which were used to incorporate missing taxa but were not relevant to subsequent analyses (no 2D:4D ratio data) from the final trees prior to analysis.

Table 2.2.1: Dataset with male right (R2D:4D), left (L2D:4D) and mean (M2D:4D) 2D:4D ratio with standard deviation (SD) for each species. Substrate use (sub use) categories, male body mass (grams), species' mating system and subcategory (subcat) with male reproductive skew (rep. skew), mating skew (mat. skew), male canine crown height (MCCH) and canine crown height dimorphism (CCHdi). All data are based on wild animals unless otherwise stated. See Appendices 2.3-2.8 for the sources of these data.

Species[a]	**n**[b]	**R2D:4D**	**SD**	**L2D:4D**	**SD**	**M2D:4D**	**SD**	**Sub use**[c]	**Body mass (g)**	**Mating system**[d]	**Sub cat**[e]	**Rep. skew (%)**	**Mat. skew (%)**	MCCH (mm)	CCH di
Eulemur collaris	4	0.730	0.044	0.745	0.013	0.738	0.023	A	2375	PGA	CC	xxx	xxx	xxx	xxx
Eulemur coronatus	4	0.748	0.029	0.749	0.046	0.748	0.032	A	1280	PGA	CC	xxx	xxx	9.43	1.11
Eulemur flavifrons	1	0.690	0.000	0.720	0.000	0.705	0.000	A	1880	PGA	CC	xxx	xxx	xxx	xxx
Eulemur fulvus	3	0.756	0.008	0.770	0.029	0.763	0.014	A	2250	PGA	CC	80**	xxx	11.87	1.18
Eulemur macaco	1	0.692	0.000	0.717	0.000	0.705	0.000	A	2350	PGA	CC	xxx	xxx	10.58	1.02
Eulemur mongoz	2	0.787	0.037	0.751	0.024	0.769	0.030	A	1410	MO	MO	xxx	xxx	9.63	1.19
Eulemur rubriventer	2	0.739	0.003	0.719	0.001	0.729	0.002	A	1980	MO	MO	100	xxx	10.49	1.05
Hapalemur alaotrensis	7	0.651	0.041	0.655	0.034	0.653	0.018	A	1400	MO	MO	91.53	xxx	xxx	xxx
Lemur catta	19	0.777	0.039	0.785	0.026	0.779	0.025	A/T	2213	PGA	CC	xxx	28.1	10.86	1.19
Prolemur simus	2	0.605	0.002	0.649	0.043	0.627	0.023	A	2150	PG	HP	xxx	xxx	xxx	xxx
Varecia rubra	2	0.758	0.021	0.768	0.000	0.763	0.010	A	3630	PGA	CC	xxx	xxx	xxx	xxx
Varecia variegata variegata	5	0.829	0.033	0.805	0.044	0.817	0.022	A	3630	PGA	CC	xxx	xxx	13.08	1.04
Propithecus coronatus	1	0.786	0.000	0.724	0.000	0.755	0.000	A	3206	PA	PA	xxx	xxx	xxx	xxx
Microcebus murinus	4	0.668	0.028	0.685	0.036	0.676	0.028	A	59	PGA	SC	54.5	xxx	2.07	1.00
Galago senegalensis	1	0.683	0.000	0.704	0.000	0.693	0.000	A	227	PG	SP	xxx	xxx	4.01	1.11
Alouatta caraya	6	0.876	0.047	0.898	0.048	0.887	0.047	A	6420	PGA	CD	100	68.5	14.74	1.54
Ateles fusciceps rufiventris	8	0.845	0.021	0.873	0.048	0.859	0.027	A	8890	PGA	CC	xxx	xxx	xxx	xxx
Ateles paniscus	3	0.878	0.039	0.869	0.063	0.873	0.045	A	9110	PGA	CC	xxx	xxx	12.11	1.57
Callicebus cupreus	5	0.824	0.016	0.814	0.011	0.819	0.005	A	1020	MO	MO	xxx	xxx	xxx	xxx
Pithecia pithecia	8	0.749	0.033	0.731	0.041	0.740	0.027	A	1940	PGA	CC	xxx	xxx	8.90	1.17
Cebus capucinus	1	0.860	0.000	0.919	0.000	0.889	0.000	A	3680	PG	HP	74.5	xxx	14.25	1.58

Table 2.2.1 *continued.*

Species[a]	n[b]	**R2D:4D**	**SD**	**L2D:4D**	**SD**	**M2D:4D**	**SD**	**Sub use**[c]	**Body mass (g)**	**Mating system**[d]	**Sub cat**[e]	**Rep. skew (%)**	**Mat. skew (%)**	MCCH (mm)	CCHdi
Sapajus apella	6	0.924	0.051	0.946	0.061	0.935	0.052	A	3650	PGA	CC	77.03	38.18	14.10	1.46
Sapajus xanthosternos	12	0.903	0.033	0.910	0.050	0.907	0.027	A	2714	PGA	CC	xxx	xxx	xxx	xxx
Saimiri boliviensis	13	0.840	0.058	0.887	0.037	0.864	0.035	A	1015	PGA	CC	xxx	xxx	6.65	1.61
Saimiri sciureus	26	0.887	0.035	0.901	0.035	0.894	0.030	A	852	PGA	CC	xxx	xxx	xxx	xxx
Callimico goeldii	2	0.834	0.061	0.860	0.021	0.847	0.020	A	278	MO	MO	xxx	xxx	xxx	xxx
Callithrix geoffroyi	1	0.934	0.000	0.898	0.000	0.916	0.000	A	290	MO	MO	xxx	xxx	xxx	xxx
Callithrix jacchus	1	0.906	0.000	0.917	0.000	0.912	0.000	A	362	PA	PA	77.78	76.2	5.08	1.06
Cebuella pygmaea	1	0.903	0.000	0.935	0.000	0.919	0.000	A	110	MO	MO	xxx	xxx	3.08	1.03
Leontopithecus chrysomelas	5	0.962	0.025	0.962	0.005	0.962	0.014	A	620	MO	MO	xxx	xxx	xxx	xxx
Leontopithecus rosalia	3	0.954	0.009	0.946	0.012	0.950	0.004	A	620	MO	MO	xxx	xxx	xxx	xxx
Mico argentatus	3	0.878	0.026	0.835	0.013	0.856	0.014	A	333	MO	MO	xxx	xxx	xxx	xxx
Mico melanurus	2	0.893	0.007	0.885	0.014	0.889	0.003	A	370	MO	MO	xxx	xxx	xxx	xxx
Saguinus imperator	6	0.998	0.037	1.003	0.043	1.001	0.026	A	474	PA	PA	xxx	xxx	xxx	xxx
Saguinus labiatus	1	0.968	0.000	0.964	0.000	0.966	0.000	A	490	MO	MO	100	xxx	xxx	xxx
Saguinus midas	2	0.930	0.047	0.934	0.036	0.932	0.006	A	515	PA	PA	xxx	xxx	5.37	0.99
Saguinus oedipus	5	1.006	0.062	0.997	0.022	1.001	0.028	A	418	MO	MO	xxx	xxx	xxx	xxx
Cercocebus chrysogaster	1	0.853	0.000	0.824	0.000	0.839	0.000	A/T	12000	PGA	CC	xxx	xxx	xxx	xxx
Cercocebus lunulatus	2	0.832	0.045	0.853	0.045	0.842	0.045	A/T	9900	PGA	CC	xxx	xxx	xxx	xxx
Cercocebus torquatus	4	0.847	0.046	0.843	0.049	0.845	0.008	A/T	9740	PGA	xxx	xxx	xxx	xxx	xxx
Cercopithecus diana	5	0.873	0.023	0.827	0.025	0.850	0.023	A	5200	PG	HP	xxx	xxx	19.94	1.62
Cercopithecus lhoesti	7	0.862	0.039	0.840	0.027	0.851	0.019	A/T	5970	PG	HP	xxx	xxx	19.93	1.84
Cercopithecus lowei	1	0.827	0.000	0.865	0.000	0.846	0.000	A/T	5800	PG	HP	xxx	xxx	xxx	xxx
Cercopithecus neglectus	5	0.831	0.015	0.860	0.039	0.845	0.024	A/T	7350	PG	HP	xxx	xxx	20.68	1.78

Table 2.2.1 *continued.*

Species[a]	**n[b]**	**R2D:4D**	**SD**	**L2D:4D**	**SD**	**M2D:4D**	**SD**	**Sub use[c]**	**Body mass (g)**	**Mating system[d]**	**Sub cat[e]**	**Rep. skew (%)**	**Mat. skew (%)**	MCCH (mm)	CCHdi
Chlorocebus pygerythrus	1	0.862	0.000	0.809	0.000	0.835	0.000	A/T	4260	PGA	CC	xxx	xxx	xxx	xxx
Colobus guereza	2	0.751	0.077	0.771	0.008	0.761	0.035	A	13500	PG	HP	90	100	20.31	1.51
Colobus polykomos	1	0.846	0.000	0.733	0.000	0.789	0.000	A	9900	PG	HP	xxx	xxx	19.13	1.77
Erythrocebus patas	2	0.784	0.004	0.757	0.008	0.771	0.002	T	12400	PG	HP	50	100	26.50	2.13
Macaca fascicularis	11	0.804	0.020	0.808	0.032	0.806	0.015	A/T	5360	PGA	CC	71	26	24.09	2.26
Macaca fuscata	8	0.846	0.019	0.835	0.029	0.841	0.013	A/T	11000	PGA	CC	50	43.9	19.56	2.04
Macaca hecki	1	0.874	0.000	0.832	0.000	0.853	0.000	A/T	11200**	PGA	CC	xxx	xxx	24.36	2.06
Macaca mulatta	13	0.805	0.049	0.818	0.027	0.811	0.026	A/T	7710	PGA	CC	24*	27.6*	16.97	2.07
Macaca nemestrina	3	0.860	0.033	0.851	0.057	0.856	0.043	A/T	11200	PGA	CC	xxx	56.35	28.89	2.36
Macaca nigra	22	0.850	0.044	0.837	0.041	0.844	0.031	A/T	9890	PGA	CC	64.63	23.1	29.73	2.61
Macaca silenus	14	0.830	0.040	0.832	0.034	0.832	0.022	A	8900	PGA	CC	xxx	xxx	24.66	2.44
Macaca sylvanus	17	0.803	0.041	0.797	0.041	0.800	0.032	T	11100	PGA	CC	24	28	22.81	2.02
Mandrillus leucophaeus	4	0.850	0.019	0.834	0.035	0.842	0.020	A/T	20000	PGA	CC	xxx	61	47.97	4.10
Mandrillus sphinx	15	0.831	0.051	0.862	0.063	0.847	0.043	A/T	24500	PGA	CC	72.35	80*	49.58	5.26
Papio hamadryas	18	0.847	0.050	0.831	0.039	0.839	0.059	T	16900	PG	HP	xxx	xxx	30.64	2.74
Papio papio	25	0.835	0.036	0.852	0.036	0.843	0.029	T	19000	PG	HP	xxx	xxx	xxx	xxx
Papio ursinus	16	0.899	0.045	0.871	0.051	0.885	0.038	T	29800	PGA	CC	68.65	43	46.53	3.84
Presbytis melalophos	1	0.777	0.000	0.794	0.000	0.785	0.000	A	6590	PG	HP	xxx	xxx	13.95	1.71
Theropithecus gelada	5	0.779	0.039	0.796	0.025	0.787	0.027	T	19000	PG	HP	100	xxx	39.62	3.23
Trachypithecus auratus	3	0.799	0.016	0.768	0.023	0.783	0.004	A	6656	PG	HP	xxx	xxx	xxx	xxx
Trachypithecus francoisi	1	0.774	0.000	0.829	0.000	0.802	0.000	A	7700	PG	HP	xxx	xxx	17.91	1.72
Tracypithecus obscurus	2	0.767	0.028	0.773	0.006	0.770	0.011	A	7900	PG	HP	xxx	xxx	15.44	1.81
Hylobates agilis	1	1.030	0.000	0.990	0.000	1.010	0.000	A	5880	MO	MO	xxx	xxx	xxx	xxx

Table 2.2.1 *continued.*

Species[a]	n[b]	**R2D:4D**	**SD**	**L2D:4D**	**SD**	**M2D:4D**	**SD**	**Sub use**[c]	**Body mass (g)**	**Mating system**[d]	**Sub cat**[e]	**Rep. skew (%)**	**Mat. skew (%)**	MCCH (mm)	CCHdi
Hylobates lar	1	1.049	0.000	1.059	0.000	1.054	0.000	A	5900	MO	MO	90.5	91.7	18.32	1.16
Hylobates pileatus	3	1.040	0.014	0.992	0.032	1.016	0.016	A	5500	MO	MO	xxx	xxx	16.75	0.99
Nomascus leucogenys	3	0.971	0.020	0.976	0.030	0.974	0.007	A	7410	MO	MO	xxx	xxx	xxx	xxx
Symphalangus syndactylus	4	1.039	0.037	1.041	0.055	1.040	0.041	A	11900	MO	MO	xxx	100	21.45	1.19
Gorilla gorilla gorilla	4	0.903	0.014	0.913	0.015	0.908	0.010	A/T	170400	PG	HP	100	xxx	30.26	1.74
Pan troglodytes	2	0.900	0.007	0.874	0.063	0.887	0.028	A/T	59700	PGA	CD	48.5	21.5	21.72	1.42

[a] Taxonomy from Groves 2001 with some exceptions (see Appendix 2.3).

[b] Number of individuals.

[c] Substrate use: A = arboreal, A/T = arboreal/terrestrial, T = terrestrial.

[d] Mating system: MO = monogamy, PA = polyandry, PG = polygyny, PGA = polygynandry.

[e] Mating system subcategory: CC = contest competition polygynandry, SC =scramble competition polygynandry, CD = cooperative defence polygynandry, SP = spatial polygyny, HP = harem polygyny.

*Data from free-ranging populations.

**Data from captive animals.

xxx Data not available.

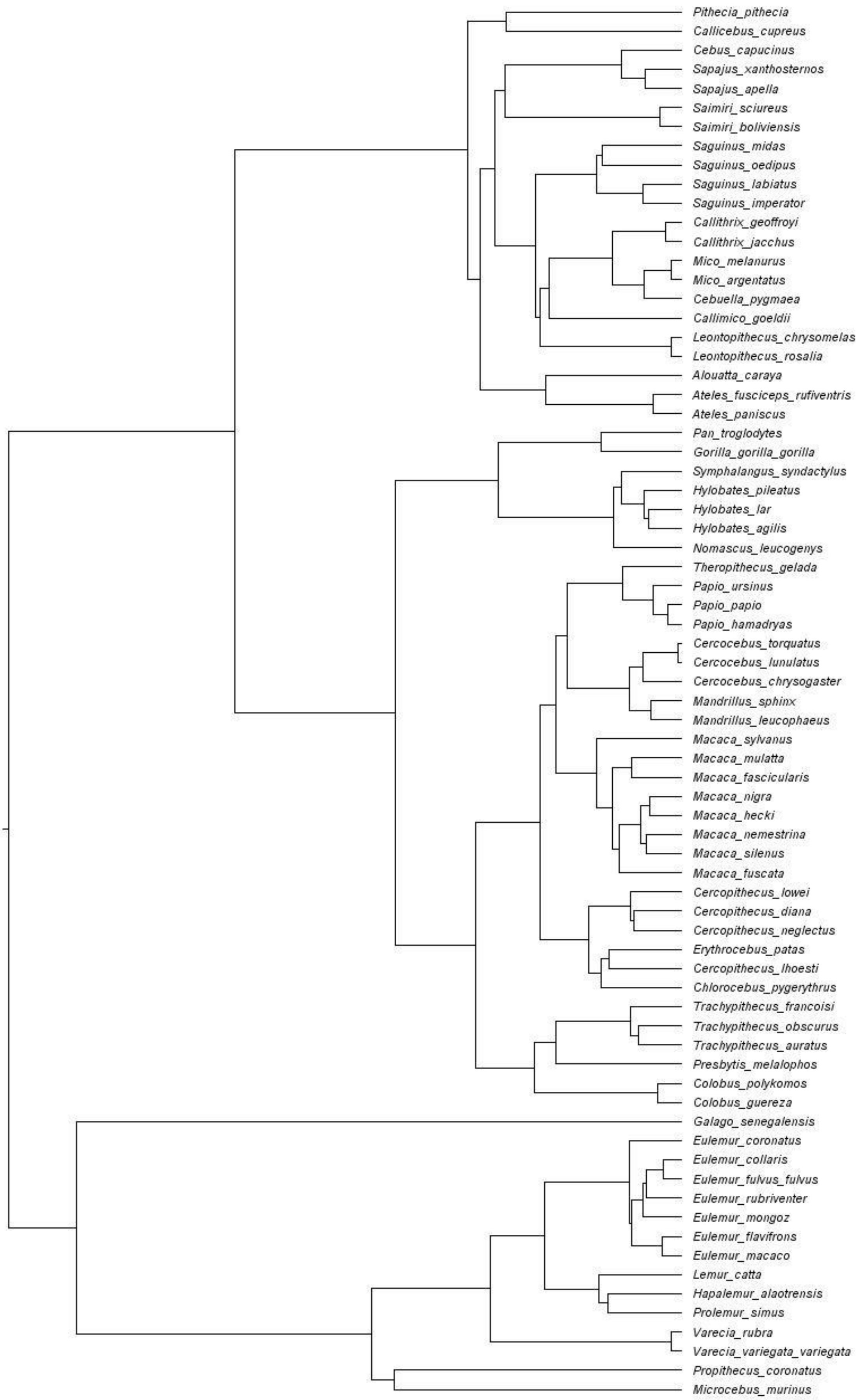

Figure 2.2.4: Phylogenetic tree with all 73 primate species represented.

2.3: Results

2.3.1: Anatomical considerations

There were no significant relationships between substrate use and any of the 2D:4D ratio measures. There were no significant relationships between male body mass and any of the 2D:4D ratio measures (Table 2.3.1). However, considering there is variation in primate hand morphology related to substrate use adaptations and in light of recent criticism of 2D:4D ratio studies which do not take allometry into account, male body mass and substrate use were included as factors in all analyses.

Table 2.3.1: Results of the PGLS regression testing for an effect of substrate use and male body mass on male 2D:4D ratio.

Variables	***t***	**p**	**df**	**λ**	**Adj.r^2**	**Estimate**	**± s.e**
Male R2D:4D & substrate use	-0.523	0.603	71	0.999	-0.010	-0.482	0.918
Male L2D:4D & substrate use	0.108	0.911	71	0.998	-0.014	0.111	1.037
Male M2D:4D & substrate use	-0.264	0.793	71	0.999	-0.013	-0.282	1.085
Male R2D:4D & Male body mass	0.815	0.421	69	1.000	0.058	1.275	1.558
Male L2D:4D & Male body mass	0.831	0.411	69	1.000	0.058	1.492	1.742
Male M2D:4D & Male body mass	0.921	0.363	69	1.000	0.060	1.689	1.829

2.3.2: Mating system

There were significant associations between mating system and all male 2D:4D ratio measures (Table 2.3.2). Monogamous species had the highest 2D:4D ratios, closely followed by polyandrous species. Polygynandrous species and polygynous species had the lowest 2D:4D ratios (Figure 2.3.1).

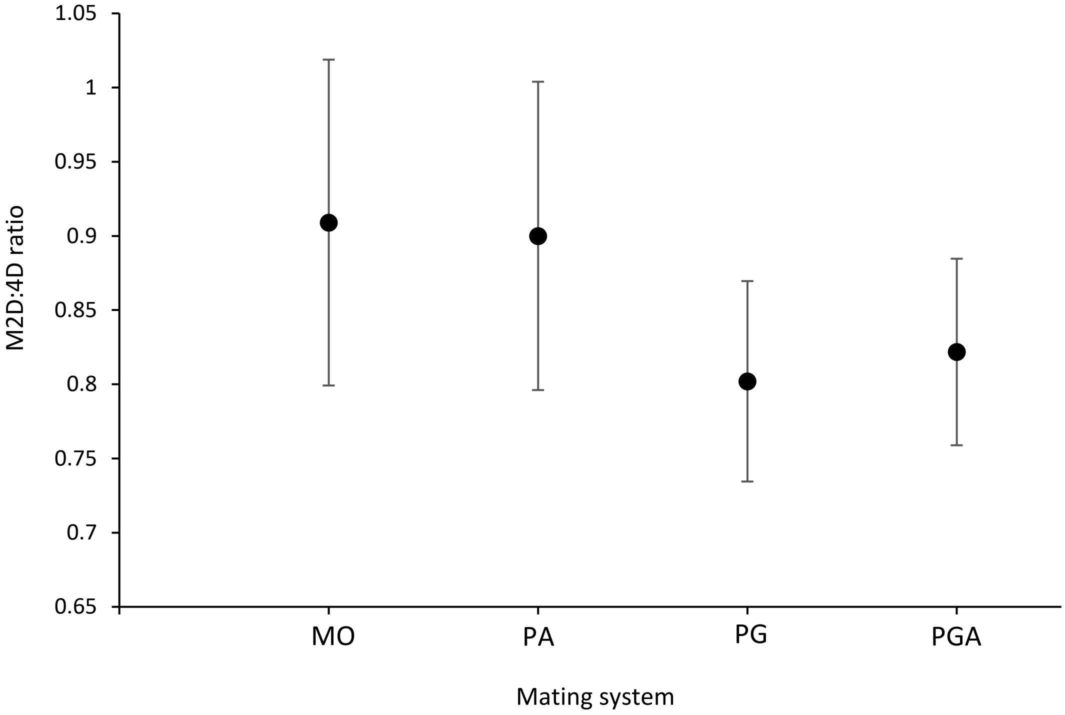

Figure 2.3.1: Relationship between male M2D:4D (group mean ± standard deviation) and species mating system. MO = Monogamy, PA = Polyandry, PG = Polygyny, PGA = Polygynandry.

2.3.3: Mating system subcategory

There were significant associations between mating system subcategory and all male 2D:4D ratio measures (Table 2.3.2). In general, monogamous species had the highest 2D:4D ratios, followed by species characterised by polyandry, cooperative defence polygynandry, contest competition polygynandry and harem polygyny. The only two species characterised by spatial polygyny and scramble competition polygynandry had the lowest 2D:4D ratios (Figure 2.3.2) and when these species were excluded from the analyses the significant relationship remained (Table 2.3.2).

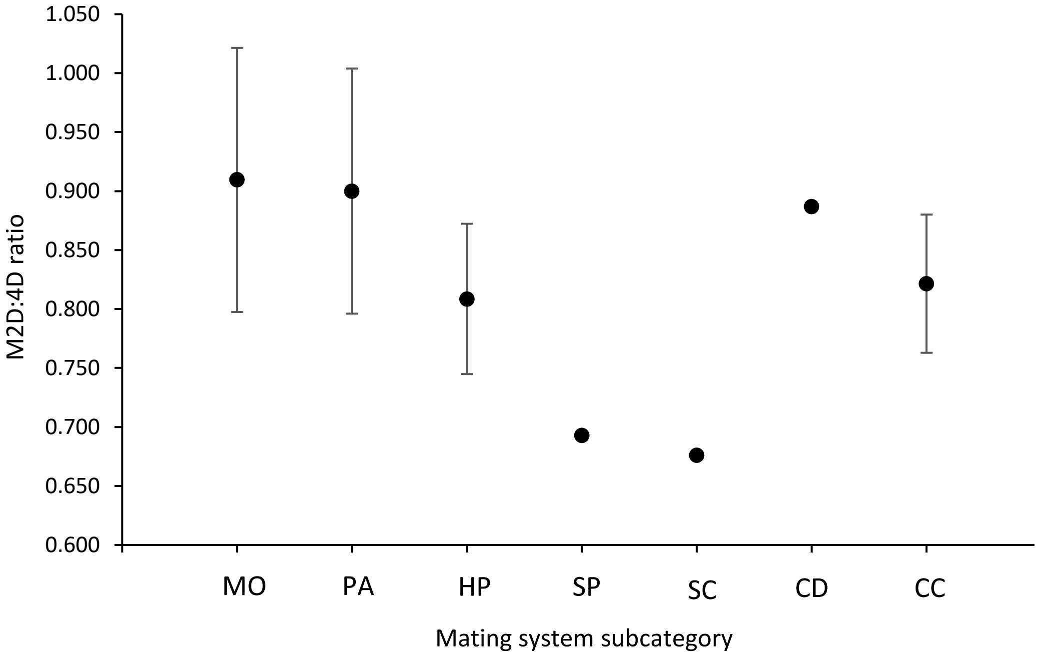

Figure 2.3.2: Relationship between male M2D:4D ratio (group mean ± standard deviation) and mating system subcategory (MO = monogamy, PA = polyandry, HP = harem polygyny, SP = spatial polygyny, SC = scramble competition polygynandry, CD = cooperative defence polygynandry, CC = contest competition polygynandry.

Table 2.3.2: Results of the PGLS regression testing for an effect of mating systems on male 2D:4D ratio while controlling for substrate use and male body mass. Model variables are indicated in bold with the control variables taken into account, parameters for individual control variables are displayed below these. Significant results are indicated in bold.

Variables	*t*	p	Estimate	**± s.e**	df	**λ**	Adj.r^2
Male R2D:4D & Mating system	**-4.851**	**<0.001**	**-5.980**	**1.230**	**69**	**0.003**	**0.364**
Substrate use	1.078	0.285	0.241	0.223			
Body mass	3.288	**0.002**	0.302	0.092			
Male L2D:4D & Mating system	**-4.004**	**<0.001**	**-5.299**	**1.320**	**69**	**0.003**	**0.308**
Substrate use	1.077	0.285	0.251	0.233			
Body mass	2.952	**0.004**	0.281	0.095			
Male M2D:4D & Mating system	**-4.503**	**<0.001**	**-5.786**	**1.287**	**69**	**0.002**	**0.342**
Substrate use	1.068	0.289	0.243	0.227			
Body mass	3.138	**0.003**	0.293	0.093			
Male R2D:4D & Mating system subcategory	**-5.273**	**<0.001**	**-12.101**	**2.295**	**68**	**0.000**	**0.479**
Substrate use	1.009	0.316	0.425	0.421			
Bodymass	4.949	**<0.001**	0.849	0.171			
Male L2D:4D & Mating system subcategory	**-4.252**	**<0.001**	**-10.581**	**2.487**	**68**	**0.000**	**0.421**
Substrate use	1.011	0.315	0.450	0.446			
Body mass	4.467	**<0.001**	0.805	0.180			
Male M2D:4D & mating system subcategory	**-4.828**	**<0.001**	**-11.642**	**2.412**	**68**	**0.000**	**0.454**
Substrate use	0.995	0.323	0.430	0.431			
Body mass	4.732	**<0.001**	0.830	0.175			
Male R2D:4D & mating system subcategory (excluding *M. murinus, G. senegalensis*)	**-4.569**	**<0.001**	**-7.736**	**1.693**	**66**	**0.000**	**0.406**
Substrate use	1.104	0.273	0.331	0.299			
Body mass	3.464	**0.001**	0.470	0.135			

Table 2.3.2 *continued.*

Variables	*t*	p	Estimate	**± s.e**	df	**λ**	Adj.r^2
Male L2D:4D & mating system subcategory (excluding *M. murinus, G. senegalensis*)	**-3.617**	**<0.001**	**-6.535**	**1.808**	**66**	**0.000**	**0.348**
Substrate use	1.056	0.295	0.332	0.315			
Body mass	3.252	**0.002**	0.463	0.142			
Male M2D:4D & mating system subcategory (excluding *M. murinus, G. senegalensis*)	**-4.152**	**<0.001**	**-7.344**	**1.769**	**66**	**0.000**	**0.381**
Substrate use	1.074	0.286	0.330	0.306			
Body mass	3.357	**0.001**	0.466	0.138			

2.3.4: Reproductive skew

No significant associations were found between male reproductive skew and any of the 2D:4D ratio measures and no significant relationships between the variables were found when monogamous species were excluded from the analysis (Table 2.3.3, Figure 2.3.3).

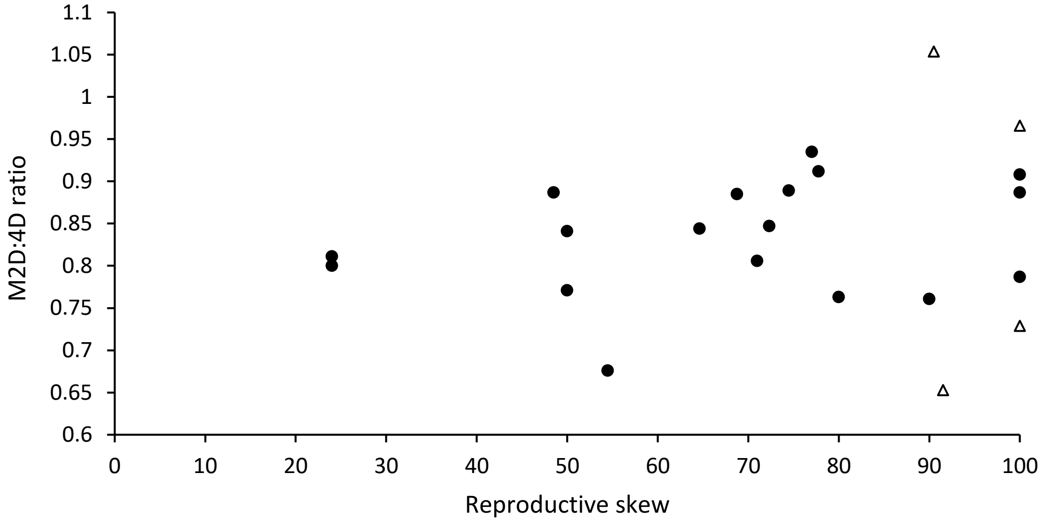

Figure 2.3.3: The relationship between reproductive skew and M2D:4D ratio. Monogamous species (white triangles), non-monogamous species (black circles).

2.3.5: Mating skew

There were no significant relationships between male mating skew and any of the 2D:4D ratio measures (Figure 2.3.4) and the lack of significant associations held after monogamous species were excluded from the analysis (Table 2.3.3).

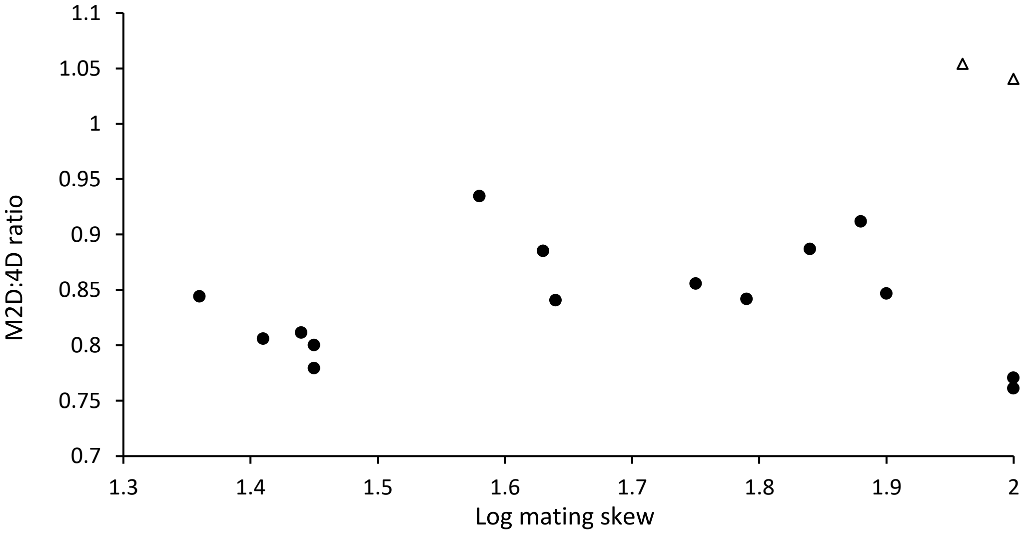

Figure 2.3.4: The relationship between log mating skew and male M2D:4D ratio. Monogamous species (white triangles), non-monogamous species (black circles).

Table 2.3.3: Results of the PGLS regression testing for an effect of male reproductive and mating skew on male 2D:4D ratio while controlling for substrate use and male body mass. Model variables are indicated in bold with the control variables taken into account, parameters for individual control variables are displayed below these. Significant results are indicated in bold.

Variables	*t*	*p*	Estimate	**± s.e**	df	**λ**	Adj.r^2
Male R2D:4D & Reproductive skew (all species)	0.208	0.837	9.902	47.684	18	0.000	0.223
Substrate use	-2.863	**0.010**	-21.075	7.365			
Body mass	1.460	0.162	4.635	3.178			
Male L2D:4D & Reproductive skew (all species)	0.172	0.865	8.134	47.284	18	0.000	0.222
Substrate use	-2.781	**0.012**	-21.017	7.560			
Body mass	1.460	0.162	4.670	3.203			
Male M2D:4D & Reproductive skew (all species)	0.191	0.850	9.110	47.684	18	0.000	0.223
Substrate use	-2.822	**0.011**	-21.035	7.455			
Body mass	1.457	0.162	4.650	3.188			
Males R2D:4D & Reproductive skew (excluding monogamous species)	0.045	0.964	3.670	81.403	14	0.000	0.160
Substrate use	-2.303	**0.037**	-18.490	8.031			
Body mass	1.544	0.145	5.676	3.387			
Males L2D:4D & Reproductive skew (excluding monogamous species)	0.333	0.744	27.052	81.367	14	0.000	0.166
Substrate use	-2.022	0.062	-17.324	8.572			
Body mass	1.367	0.193	5.061	3.699			
Males M2D:4D & Reproductive skew (excluding monogamous species)	0.190	0.852	15.571	82.070	14	0.000	0.162
Substrate use	-2.175	**0.047**	-18.011	8.282			
Body mass	1.449	0.169	5.367	3.704			
Male R2D:4D & Mating skew (all species)	0.643	0.531	1.301	1.952	14	0.495	0.101
Substrate use	-0.714	0.487	-0.183	0.255			
Body mass	-0.150	0.882	-0.023	0.152			

Table 2.3.3 *continued*.

Variables	*t*	*p*	Estimate	± s.e	df	λ	Adj.r^2
Male L2D:4D & Mating skew (all species)	0.744	0.470	1.569	2.009	14	0.531	-0.089
Substrate use	-0.560	0.585	-0.149	0.265			
Body mass	-0.176	0.862	-0.027	0.151			
Male M2D:4D & Mating skew (all species)	0.739	0.472	1.502	1.997	14	0.479	-0.094
Substrate use	-0.613	0.549	-0.160	0.260			
Body mass	-0.159	0.876	-0.024	0.150			
Males R2D:4D & Mating skew (excluding monogamous species)	-0.327	0.749	-0.917	2.809	12	0.133	-0.225
Substrate use	-0.118	0.907	-0.032	0.266			
Body mass	-0.217	0.832	-0.033	0.150			
Males L2D:4D & Mating skew (excluding monogamous species)	-0.274	0.788	-0.815	2.997	12	0.217	-0.223
Substrate use	-0.269	0.792	-0.073	0.272			
Body mass	-0.221	0.829	-0.033	0.151			
Males M2D:4D & Mating skew (excluding monogamous species)	-0.352	0.731	-1.028	2.942	12	0.197	-0.218
Substrate use	-0.246	0.809	-0.066	0.266			
Body mass	-0.207	0.839	-0.031	0.151			

2.3.6: Canine measurements

There were no significant associations between any of the male 2D:4D ratio measures and either MCCH or CCH dimorphism (Figure 2.3.5a & b). Additionally, there were no significant associations between any of the 2D:4D ratio measures and either MCCH or CCH dimorphism when strepsirrhine and haplorhine primates were analysed separately (Table 2.3.4).

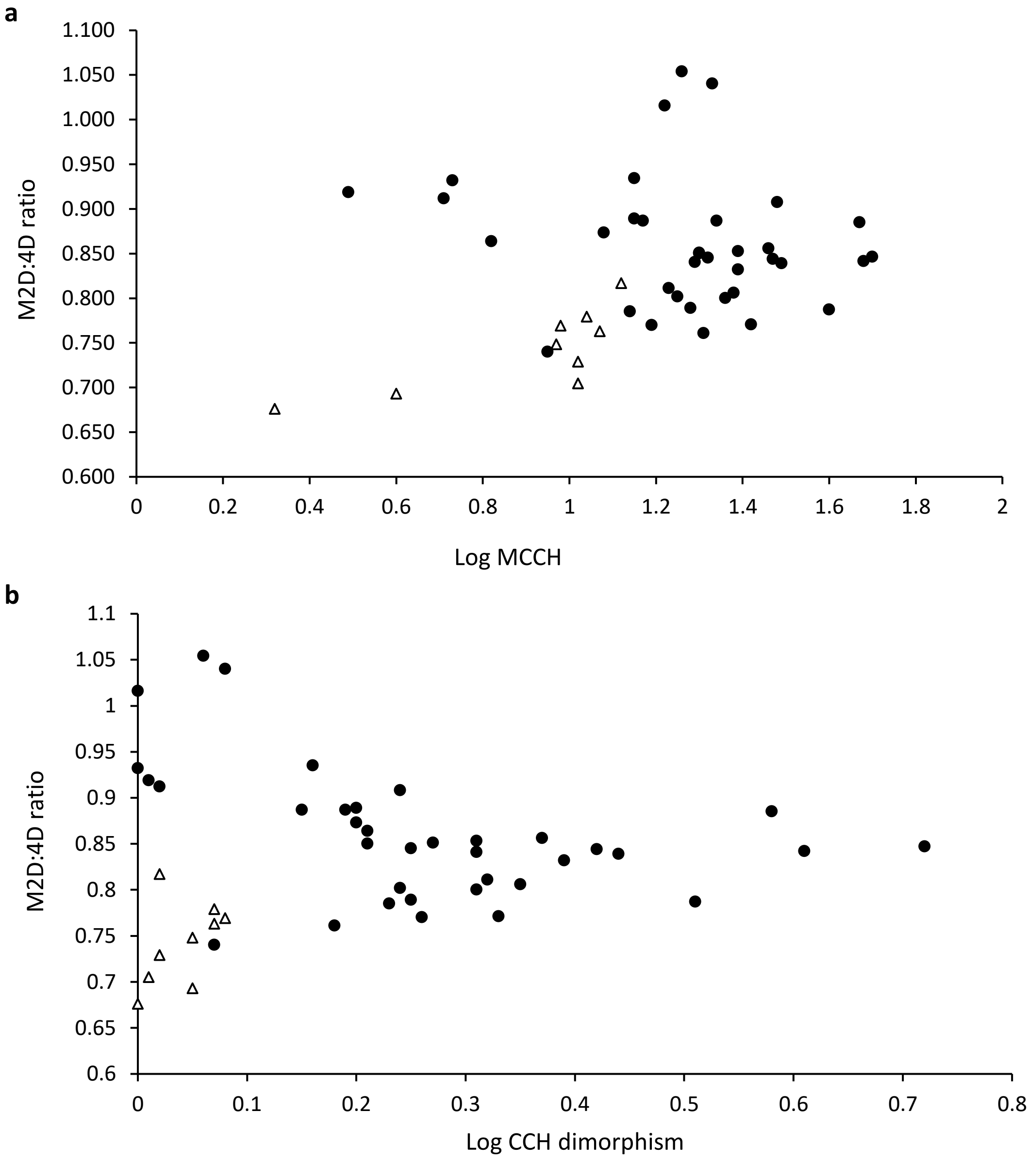

Figure 2.3.5: Association between (a) log MCCH and male M2D:4D ratio measures and (b) log CCH dimorphism and male M2D:4D ratio measures for all species. Haplorhines (black circles), strepsirrhines (white triangles).

Table 2.3.4: Results of the PGLS regression testing for an effect of canine tooth size variables on male 2D:4D ratio while controlling for substrate use and male body mass. Model variables are indicated in bold with the control variables taken into account, parameters for individual control variables are displayed below these. Significant results are indicated in bold.

Variables	*t*	*p*	Estimate	± s.e	df	λ	Adj.r^2
Male R2D:4D & CCH (all species)	1.896	0.065	1.744	0.940	41	1.000	0.135
Substrate use	1.455	0.154	0.158	0.108			
Body mass	1.898	0.065	<0.000	<0.000			
Male L2D:4D & CCH (all species)	1.912	0.063	1.938	1.013	41	1.000	0.136
Substrate use	1.442	0.157	0.157	0.109			
Body mass	1.731	0.091	<0.000	<0.000			
Male M2D:4D & CCH (all species)	2.001	0.052	2.004	1.050	41	1.000	0.150
Substrate use	1.513	0.138	0.163	0.108			
Body mass	1.816	0.077	<0.000	<0.000			
Male R2D:4D & MCCH (Strepsirrhines only)	1.236	0.274	2.407	1.922	5	1.000	0.631
Substrate use	0.363	0.731	0.103	0.279			
Body mass	3.046	**0.031**	<0.000	<0.000			
Male L2D:4D & MCCH (Strepsirrhines only)	1.236	0.274	2.407	1.922	5	1.000	0.631
Substrate use	0.363	0.731	0.103	0.279			
Body mass	3.046	**0.031**	<0.000	<0.000			
Male M2D:4D & MCCH (Strepsirrhines only)	1.273	0.261	3.123	2.367	5	1.000	0.635
Substrate use	0.272	0.796	0.077	0.274			
Bodymass	2.760	**0.042**	<0.000	<0.000			

Table 2.3.4 *continued.*

Variables	*t*	*p*	Estimate	**± s.e**	df	**λ**	Adj.r^2
Male R2D:4D & MCCH (Haplorhines only)	0.613	0.544	0.611	0.999	32	1.000	0.084
Substrate use	1.191	0.243	0.127	0.106			
Body mass	1.888	0.068	<0.000	<0.000			
Male L2D:4D & MCCH (Haplorhines only)	0.695	0.492	0.722	1.034	32	1.000	0.087
Substrate use	1.207	0.236	0.128	0.107			
Body mass	1.818	0.078	<0.000	<0.000			
Male M2D:4D & MCCH (Haplorhines only)	0.732	0.469	0.822	1.120	32	1.000	0.088
Substrate use	1.227	0.229	0.131	0.107			
Body mass	1.855	0.073	<0.000	<0.000			
Male R2D:4D & CHH dimorphism (all species)	0.012	0.974	0.018	1.553	41	0.962	0.041
Substrate use	0.199	0.843	0.036	0.178			
Body mass	2.017	0.050	0.201	0.100			
Male L2D:4D & CHH dimorphism (all species)	0.613	0.543	1.015	1.657	41	0.966	0.050
Substrate use	0.029	0.773	0.052	0.179			
Body mass	1.926	0.061	0.193	0.100			
Male M2D:4D & CHH dimorphism (all species)	0.163	0.866	0.266	1.617	41	0.970	0.031
Substrate use	0.168	0.867	0.029	0.174			
Body mass	1.850	0.072	0.171	0.092			
Male R2D:4D & CCH dimorphism (Strepsirrhines only)	0.416	0.703	0.339	0.829	5	0.014	-0.125
Substrate use	0.980	0.372	0.088	0.089			
Body mass	0.073	0.925	0.002	0.031			

Table 2.3.4 *continued*.

Variables	*t*	*p*	Estimate	**± s.e**	df	**λ**	Adj.r^2
Male L2D:4D & CCH dimorphism (Strepsirrhines only)	0.447	0.686	0.536	1.240	5	0.015	-0.123
Substrate use	0.804	0.458	0.077	0.096			
Body mass	0.026	0.951	0.001	0.032			
Male M2D:4D & CCH dimorphism (Strepsirrhines only)	0.612	0.583	0.602	1.013	5	0.015	-0.103
Substrate use	0.877	0.421	0.079	0.090			
Body mass	-0.066	0.954	-0.002	0.032			
Male R2D:4D & CCH dimorphism (Haplorhines only)	-0.028	0.977	-0.050	1.795	32	0.981	0.038
Substrate use	-0.179	0.858	-0.037	0.204			
Body mass	2.029	0.051	0.254	0.125			
Male L2D:4D & CCH dimorphism (Haplorhines only)	0.620	0.540	1.148	1.850	32	0.981	0.052
Substrate use	-0.036	0.970	-0.007	0.204			
Body mass	2.036	0.051	0.260	0.127			
Male M2D:4D & CCH dimorphism (Haplorhines only)	0.304	0.763	0.595	1.958	32	0.984	0.041
Substrate use	-0.111	0.912	-0.023	0.206			
Body mass	2.019	0.052	0.253	0.125			

2.4: Discussion

Hypotheses for mating systems are generally supported but results are not all in the predicted direction. Consistent with the results of Nelson & Shultz (2010), monogamous (pair-bonded) males had the highest 2D:4D ratios, an indication of selection for reduced PAE/increased POE associated with many of the behaviours responsible for facilitating and reinforcing this mating system in primates (French *et al*. 2018; Díaz-Muñoz & Bales 2016). Elevated levels of testosterone have a suppressive effect on the immune system and it makes sense therefore, for selection to favour a reduction in its production in males for whom developing in and maintaining high androgen levels is not advantageous, particularly those characterised by monogamy (Wobber *et al.* 2013). Monogamous male Lemuridae have lower 2D:4D ratios than monogamous Callitrichidae, Pitheciidae and Hylobatidae, a difference which most likely represents phylogenetic differences in the prevalence of ectaxonic, paraxonic and mesaxonic hand morphology among the families. Another contributing factor could be the form that paternal care takes in strepsirrhines. The fact that these species often use the strategies of 'infant parking' and/or infant carrying by subadult female group members, means paternal care in terms of infant carrying by the male is not as essential as it is for the small bodied New World species in which males do most of the infant carrying and transportation (Tecot *et al*. 2012; Wright 1990). Close association with offspring and infant carrying would require a reduction in androgens which may not be necessary in strepsirrhine males which do not perform these tasks. Future research into PAE and monogamous mating systems in primates should also take into account the intensity and form of paternal care as this has profound effects on male physiology (Zeigler *et al*. 2004).

There was little difference in 2D:4D ratios between monogamous and polyandrous males but, on average, polyandrous males had lower 2D:4D ratios than monogamous males and higher 2D:4D ratios than males characterised by polygyny and polygynandry. It has been observed that tolerant relationships often exist between males in many polyandrous species (Díaz-Muñoz *et al*. 2014; Garber 1994). Polyandrous moustached tamarin males (*Saguinas mystax)* for example, mate and show no evidence of intrasexual aggression or mate guarding behaviour during the females' fertile period (Garber *et al*. 1993). It is interesting to note that male 2D:4D ratios of species characterised by polyandry and cooperative defence polygynandry are similar. This may reflect selection for an increase in cooperation and bonding and a reduction in aggression between males in these two mating systems (Pepping & Timmerman 2012; Madden & Clutton-Brock 2011). Among polygynandrous species, males characterised by cooperative defence polygynandry have the highest 2D:4D ratios. Cooperative and affiliative behaviours are moderated by oestrogens and their neuropeptides and selection for these may counter selection for competitive behaviours associated with increased PAE, resulting in higher 2D:4D ratios than would be expected of polygynandrous males.

Males experiencing contest competition polygynandry are faced with high levels of both pre- and post-copulatory competition. However, contrary to predictions, these species do not display the lowest 2D:4D ratios. Similar, though less pronounced, selection for reduced PAE/increased POE may be holding sway in other polygynandrous species in which males have to live alongside their competitors. In these circumstances it may be beneficial to express a degree of cooperative, affiliative and tolerant behaviours (Hill & van Hoof 1994) which are mediated by oestrogen, OT and VA (French *et al*. 2018). The observation that polygynandrous males, although arguably experiencing highest levels of sexual competition (pre- and post-copulatory), have higher 2D:4D ratios than polygynous species may be an indication of the interplay between the PAE necessary for competition and the POE necessary for cooperation.

Species characterised by forms of female-defence polygyny, on the other hand, are often solitary (Müller & Thalmann 2000; Bearder 1987), occur in single-male-groups or one-male-units within multi-male groups (Terborgh & Janson 1986) and these social organisations afford little opportunity or necessity for cooperative and affiliative interactions between males. Therefore, selection is likely to favour traits associated with competitive abilities which enable males to monopolise reproduction within their group or range. Returning to the example of the grey langurs studied by Launhardt *et al.* (2001), due to the disparity in reproductive success between harem-holding polygynous males and those that live in multi-male-multi-female groups (regardless of their dominance position), there is likely to be strong selection for traits which enable a male to become a harem-holding male and to monopolise reproductive access to a group of females. In line with this, the lowest 2D:4D ratios are found in males characterised by harem polygyny, spatial polygyny and scramble competition polygynandry. Polygynous males may be under the strongest selection for high PAE and this may explain why 2D:4D ratios are lowest overall among males characterised by polygynous mating systems, not polygynandrous mating systems. However, it should be noted that the 2D:4D ratio data for scramble competition polygynandry and spatial polygyny are each based on only one solitary strepsirrhine species (*Microcebus murinus* and *Galago senegalensis* respectively) and as strepsirrhine species generally have lower 2D:4D ratios than haplorhine primates, it is important to consider this when interpreting these results. The overall pattern of the results was not altered by the removal of these two species (and consequently the two mating system subcategories) from the analysis, but more 2D:4D ratio data would be informative for exploring selection for PAE in species characterised by spatial polygyny and scramble competition polygynandry. It could be reasoned that some differences in inter-specific 2D:4D ratio is a result of allometry, phylogenetic constraint or functional adaptations to substrate use (Lolli *et al*. 2017; Lemelin & Schmitt 1998; Jouffroy *et al.* 1993). However, there were no significant relationships between substrate use or male body mass and any of the 2D:4D ratio measures. Additionally, I controlled for the potential effects of these two variables and phylogeny in all analyses and the relationships between male 2D:4D ratios and mating system and mating system subcategory were significant suggesting that these factors are not driving the results.

The relationship between 2D:4D ratio and reproductive skew was nonsignificant. Alpha/resident male paternity was not higher in species with lower 2D:4D ratios (inferred higher PAE). Additionally, no association was found between male mating skew and measures of 2D:4D ratio among male primates. Mating success was not higher in species with lower 2D:4D ratios than species with higher 2D:4D ratios. This outcome could be attributable to the monogamous hylobatids and callitrichids, which display comparatively high 2D:4D ratios, mating and reproductive success.

However, the results were still not significant when monogamous species were excluded from the analysis and the relationship between 2D:4D ratios and these variables is far from clear. High reproductive and mating skew rely on males being able to monopolise females and this ability is constrained by a variety of socioecological factors (dominance rank, group composition, female dispersion), not least the mating system itself (Dubuc *et al*. 2014; Kappeler & van Schaik 2002). The relationship between PAE and these variables is likely to be more apparent between individual males at the species level via the positive impact that PAE have on an individual's competitive abilities, drive for sexual encounters and dominance rank (Schwarz *et al*. 2011; Manning & Fink 2008; Hönekopp *et al*. 2006). For example, male primates with lower 2D:4D ratios (high PAE) characterised by polygynandry are likely better able to outcompete their less androgenised sexual rivals due to the behavioural predispositions brought about by high PAE. This is supported by the link between dominance rank and male reproductive success in many species (Di Fiore 2003) including polygynandrous macaques (Engelhardt *et al*. 2006) and mandrills (Setchell *et al.* 2005; Dixson *et al*. 1993).

The results may also be, in part, a manifestation of small sample sizes. Although becoming more common due to ever improving molecular methods, paternity studies were not frequently carried out on wild primate populations (Di Fiore 2003). Additionally, it is extremely difficult to observe mating behaviour in wild primates, particularly small arboreal species inhabiting dense forests (Di Fiore 2003) and this may explain why so little data on mating skew are available. It is difficult to ascertain whether these insignificant results are due to the absence of a biological effect or simply due to low statistical power resulting from small sample sizes. The relationship between PAE and mating success is worthy of further study, alongside molecular data (reproductive skew), to unravel the association between the effects of prenatal sex steroids on the pre- and post-copulatory mechanisms influencing reproductive fitness in male primates.

Relationships between 2D:4D ratio measures, MCCH and CCH dimorphism were non-significant, although the relationships were near significance for M2D:4D and MCCH in the analysis which included all species and data trended in the predicted direction for both variables, with lower 2D:4D ratios being associated with larger MCCH and greater CCH dimorphism. The failure to find a significant association between 2D:4D ratio measures and canine variables cannot be attributed to a lack of sexual dimorphism in this trait in many strepsirrhine species since associations between MCCH and CCH dimorphism were still not significant when the two suborders were analysed separately. The lack of a significant relationship between the canine variables and 2D:4D ratio (inferred PAE) measures could be attributed to similar processes described by Demsey *et al*. (1999) in humans. Their results indicated that levels of prenatal androgens can affect the size of teeth but the effect on canine teeth may be weaker than on other teeth. My results lend support to their suggestion that canine size and dimorphism may be controlled by mechanisms that are not shared with other teeth and which are not wholly dependent on PAE (Dempsey *et al*. 1999). These results confirm those of previous studies in that the 2D:4D ratio is not a good predictor of PAE on this sexually selected anatomical trait (Nelson 2011).

2.4.1: Summary

Overall, monogamous males generally displayed the highest 2D:4D ratios (low inferred PAE), followed by polyandrous, polygynandrous and finally polygynous species (high inferred PAE). 2D:4D ratios vary with the form of polygyny and polygynandry in relation to the requirement for aggressive and competitive behaviours over cooperative and other prosocial behaviours. I deduce that the 2D:4D ratio is not a good predictor of the involvement of PAE in the development of canine size and canine dimorphism or behavioural measures of male pre-copulatory (mating skew) and post-copulatory (reproductive skew) intrasexual competition. However, 2D:4D ratios may provide information about PAE on brain patterning and its subsequent behavioural predispositions which are specific and conducive to the level of intrasexual competition faced by male non-human primates.

This study has improved on previous work in terms of having more reliable 2D:4D ratio measurements, using appropriate mating system terminology and examining relationships between PAE and the different forms of polygyny and polygynandry observed in non-human primates. The results suggest that PAE (inferred from 2D:4D ratios) may act as a proximate mechanism underpinning the expression of behaviour in male primates in ways that are adaptive to their mating system. Cooperation, competition and the proximate mechanisms which underlie their expression are closely linked. The results emphasise that, in order to fully understand the relationship between PAE and mating systems in non-human primates, it is necessary to consider the strength of selection for cooperative and affiliative behaviour alongside selection for behaviours associated with the level of sexual competition between males.

- Chapter 3 -

Prenatal androgen effects as a proximate mechanism underlying variation in human marriage systems

Abstract

Prenatal androgen effects (PAE) are associated with both social bonding and mating systems in non-human primates such that where intrasexual competition is higher, selection for high PAE is stronger. Whether or not this pattern holds among humans, however, is not fully understood. Using the 2D:4D ratio as a proxy for PAE, this study aimed to investigate the relationship between PAE and intrasexual competition (in the form of marriage systems) in humans using both non-phylogenetic and phylogenetically-controlled methods. Non-phylogenetic analysis revealed that there were no associations between 2D:4D ratios and marriage systems in males, but that monogamous females had higher mean 2D:4D ratios than polygynous females, possibly as a result of the higher intrasexual competition among women in polygynous populations. However, once phylogeny had been taken into account, no associations were found between male or female 2D:4D ratios and marriage system. Males and females in polygynous populations did not have lower 2D:4D ratios than those in monogamous populations. It may be that, as males are the competing sex, there is still strong selective pressure for high PAE regardless of the marriage system. Likewise, due to its positive impact on female fertility, sexual selection may favour higher prenatal oestrogen effects (POE) and lower PAE in females, again, regardless of the marriage system. This suggests that the marriage system practised by a population does not incur considerable selection for higher or lower PAE in either sex in humans, although additional studies that include more non-monogamous populations may provide further insights. The results support the stipulation that, in order to avoid false positives, controlling for phylogenetic non-independence is necessary when carrying out cross-cultural comparative analysis in human populations.

3.1: Introduction

3.1.1: Human marriage systems

Marriage is a universal institution and societies of modern humans practise a wide variety of mating systems, a diversity which is not seen in other species (Przybyta 2013; Apostolou 2007; Murdock 1949). This variation includes monogamous marriage which describes marriage between a single man and woman, polyandrous marriages involve two or more men sharing a wife and polygynous marriages occur when two or more women share a husband. Humans are not as polygynous as other primate species (Kruger 2010), although 82% of human societies reportedly permit polygyny (Marlowe 2000). The use of one human mating system can be favoured over another under particular circumstances. Key ecological factors such as the form of subsistence (Przybyta 2013; Marlowe 2000), level of male contribution to subsistence (Ellsworth 2016; Marlowe 2000), pathogen load (Dow & Eff 2013; Marlowe 2003; Low 2000; Low 1990) and ecologically determined cultural factors which influence variation in male wealth/resource control (Przybyta 2013; Kruger 2010) can all influence the adaptive value of any given strategy.

In addition to ecological factors, cultural trait transmission is also predicted to influence variation in human marriage systems (Dow & Eff 2013). Dow & Eff (2013) found that the observed pattern of monogamy in human populations is influenced by the combined effects of linguistic and spatial transmission processes. They posit that societies may adopt monogamous practises from neighbouring populations or else inherit the trait from ancestral cultures (Dow & Eff 2013). However, there is little support for cultural factors such as the level of democracy (Kanazawa & Still 1999), religion (Dow & Eff 2013; Barber 2008) or gender discrimination (Barber 2008) being significant factors shaping marriage systems in human populations, suggesting that ecology may play a greater role.

Polyandry is rare (Archetti 2013; Przybyta 2013; Murdock 1967) and typically occurs in societies which believe in partible paternity (Beckerman & Valentine 2002) or where co-husbands are related (e.g. brothers sharing a wife) (Archetti 2013; Beall & Goldstein 1981). Polyandrous societies are generally found in small-scale, egalitarian populations which rely on hunting, gathering and horticulture for the production of food (Starkweather & Hames 2012). This marriage system has been documented in 53 human societies in various parts of the world, notably 28 societies in the Tibetan plateau, many Inuit cultures and the populations of the Marquesas Islands (Archetti 2013; Starkweather & Hames 2012; Cassidy & Lee 1989). Polyandrous marriage as a strategy may be a response to a shortage of women and/or high rates of male mortality (Starkweather & Hames 2012). Societies in which males contribute heavily to subsistence tend to be monogamous (Marlowe 2003). Monogamy is more common among agricultural and fishing societies in which men are tied to the territory they possess and cannot support numerous wives and their offspring (Przybyta 2013). Additionally, monogamy is thought to be favoured in such societies because male resources (in the form of land/fishing territories) depreciate in value when shared amongst numerous offspring, reducing their overall fitness (Archetti 2013; Pryzbyta 2013). Male parental investment has also been linked with the evolution of predominantly monogamous marriage in humans (Marlowe 2000). When paternal investment within a society is high, females benefit by 'resource shopping' and mating monogamously. Conversely, where paternal investment is low, females do better to 'gene shop', choosing partners based on genetic quality and mating polygynously (Marlowe 2000).

Polygynous populations can be more easily sustained in environmentally rich areas with no geographical barriers which favour the movement of individuals between groups and in societies in which male resources are easily divisible amongst offspring and are not depleted as a result of division (Archetti 2013; Przybyta 2013). These factors may explain why polygyny is often the marriage system practised by pastoralist societies. Polygyny is also more prevalent where women contribute more to subsistence and in areas of higher pathogen stress, suggesting that, in these situations, women's choice of marriage partner is greatly influenced by male physical fitness (Ellsworth *et al.* 2013; Przybyta 2013; Low 1990). Completed fertility (the average number of children born to women of the same cohort by the end of their reproductive lives, Barber 2008) is lower in polygynous women than monogamous women and therefore, polygynous marriage is of benefit to most women in a society only when there is extreme variance in male quality, both in terms of genetics (Minocher *et al*. 2018; Barber 2008) and resources which limit female reproduction (Barber 2008; Kanazawa & Still 1999). Disparity in male socio-economic status and resource control account for polygyny in many human societies (Kruger 2010; Barber 2008) and a recent study found that, after phylogeny, the strongest predictors of polygyny were pathogen stress and assault frequency (Minocher *et al.* 2018). These can be interpreted as females choosing males with better genes on the assumption that their offspring will inherit their father's pathogen resistance and male intrasexual competition/coercion, respectively. Both of these variables are consistent with marriage systems in humans being shaped by the influence of sexual selection on the reproductive strategies of the sexes.

Researchers often draw on aspects of sexual selection theory to explain variation in human marriage systems (Betzig 2012; Marlowe 2003; Marlowe 2000; Cowlishaw & Mace 1996; Low 1990). Sexual selection is a strong and fast acting evolutionary process (Moorad *et al*. 2011) which favours traits which enhance mating and reproductive success (Carter & Kushnick 2018). Male intrasexual competition, mate guarding, and coercion have all been posited as important factors influencing marriage systems in humans (Minocher *et al*. 2018; Kruger 2010; Marlowe 2000). Variation in reproductive success is higher for males than for females (Brown *et al*. 2009) and the amount of variation in male reproductive success within a population may influence the strength of male mating competition, resulting in the development of more hazardous behavioural and physiological strategies (Kruger 2010). Polygynous mating systems confer strong advantages to male fitness by lengthening reproductive tenure and reproductive rates (Moorad *et al.* 2011). Polygyny is indicative of high male-male competition for females (Kruger 2010) and competition for mates is a strong selective force in humans (Moorad *et al*. 2011; Kruger 2010; Betzig 1986). Therefore, traits which increase male reproductive success should be favoured under such circumstances.

3.1.2: The influence of marriage systems on selection for prenatal androgen effects in men

Androgens (both pre- and postnatal) are particularly important hormones for increasing competitive ability in animals (Burley & Foster 2004; Kaiser & Sachser 2005; Meise *et al*. 2016) and for the expression of behaviours associated with gaining and maintaining high status (Lindman *et al*. 1987; Booth *et al*. 1989; Josephs *et al*. 2003; Josephs *et al*. 2006) and defeating rivals (Higley 1996; Benderlioglu & Nelson 2007; McIntyre *et al*. 2007), including aggression (Christiansen & Knussmann 1987; Mazur & Booth 1998). Positive relationships have been found between salivary testosterone levels and intrasexual competition scores among men (Borráz-Leon *et al.* 2018). The ratio between the second (2D) and fourth (4D) digits of the hands (2D:4D ratio) is a biomarker for variation in prenatal androgen effects (PAE) to prenatal oestrogen effects (POE) experienced by individuals (Manning 2011; Zheng & Cohn 2011; Manning *et al.* 1998). The 2D:4D ratio is a negative correlate of PAE and a positive correlate of POE (Manning 2011; Zheng & Cohn 2011; Manning *et al*. 1998, 2000) and is sexually dimorphic in humans, with men generally displaying lower (more masculine) 2D:4D ratios than women (Manning *et al.* 1998). Men with lower 2D:4D ratios (inferred high PAE) tend to be partnered with more attractive, and presumably more fertile, women (Kuna & Galbarczyk 2018). Men with lower 2D:4D ratios display greater facial masculinity (Weinberg *et al.* 2015; Fink *et al.* 2005; Neave *et al*. 2003), greater facial symmetry (Fink *et al.* 2004a) and tend to be taller than higher 2D:4D ratio men (Fink *et al*. 2003). Therefore, the 2D:4D ratio can be a valuable predictor of PAE on male reproductive characteristics which can have lasting influences on their mating value.

An association has been observed between PAE and social bonding and mating systems in non-human primates, such that selection for high PAE/low POE is stronger in species with higher male intrasexual competition (Nelson & Shultz 2010; Chapter 2). Due to the organisational effects of prenatal androgens on behaviour and physiology in men, high PAE should also be favoured under conditions of high male intrasexual competition in humans (Butovskaya *et al.* 2015; Przybyta 2013; Manning *et al*. 2004b). Therefore, it is likely that there is a greater selective advantage for men belonging to societies in which male contest competition is high (polygynous societies) to be exposed to higher PAE than men in societies with lower male contest competition (monogamous societies). However, even in predominantly monogamous societies, high PAE have the potential to positively affect a male's reproductive fitness through positive influences on male attractiveness and reproductive effort (Alvergne *et al.* 2009; Manning & Fink 2008). The 2D:4D ratio was negatively associated with reproductive success in a sample of European men such that those with lower 2D:4D ratios (higher PAE) had greater reproductive success (Manning *et al*. 2000). This result was mirrored more recently in a Polish sample which also reported that low 2D:4D ratio men had more children than high 2D:4D ratio men (Klimek *et al.* 2014).

Marlowe (2000) found that the value placed on male aggressiveness within a society was positively related to the degree of polygyny in a cross-cultural sample of 186 societies. This variable was the strongest predictor of polygyny, more so even than father-infant proximity and male contribution to subsistence (Marlowe 2000). Additionally, a recent cross-cultural study found that male aggressiveness is most intense when intrasexual selection was strong (societies with a high degree of polygynous marriages) (Carter & Kushnick 2018). When comparing the Hadza and Datooga societies of Tanzania, Butovskaya *et al.* (2015) found that Datooga men scored higher for traits such as physical and verbal aggression, dominance, anger and hostility than Hadza men. Datooga man also had lower 2D:4D ratios than Hadza men in both hands (Butovskaya *et al.* 2015). These results, which indicate higher PAE among Datooga men in comparison to Hadza men, were attributed to differences in the degree of polygyny between the two societies. The Datooga are polygynous pastoralists whereas the Hadza are hunter-gatherers characterised by limited polygyny. Additionally, Hadza women often choose their marriage partners and Hadza society is egalitarian in which the display of dominant and aggressive behaviour is not favoured (Butovskaya *et al.* 2015; Butovskaya *et al*. 2012). This suggests that aggressive tendencies among males in a population may reflect male intrasexual competition levels which are shaped by the marriage system they practise (Marlowe 2000).

Men and women may also choose partners with traits enabling them to better cope with the harsh life-style imposed by certain environments and subsistence activities. These would likely be testosterone dependent traits which are correlates of low 2D:4D ratio and as such high PAE. A preference for masculinised mates in both sexes has been noted among hunter-gatherer populations which suffer more heavily from environmental stresses (Sorokowski *et al*. 2012). Among the Himba of Namibia, a semi-nomadic population, low 2D:4D ratio individuals of both sexes married at earlier ages and were more likely to be married than high 2D:4D ratio individuals (Sorokowski *et al.* 2012). The Himba practise arranged marriage with male relatives deciding on a woman's husband. However, polygamy is the norm in this population with both men and women having extramarital partners (Sorokowski *et al*. 2012). The fact that Himba men with lower 2D:4D ratios married at younger ages may be unsurprising (Sorokowski *et al.* 2012) as low 2D:4D ratio males likely display other physical and behavioural traits associated with developing in an environment high in PAE such as masculine facial features (Burriss *et al.* 2007), superior endurance running ability (Manning *et al.* 2007), greater strength (Fink *et al*. 2006) and higher drives for social status (Millet & Dewitte 2008). These traits enhance male competitive ability and may increase their attractiveness as mates in societies where a man's ability to provide for his family (e.g. through hunting) is crucial. Additionally, these masculine men are likely able to collect the assets needed to marry their first wife earlier (Sorokowski *et al*. 2012).

In polyandrous marriages co-husbands have equal sexual access to their wife, contribute to provisioning the family unit and to raising offspring (Starkweather & Hames 2012). Polyandry therefore requires a significant level of tolerant and cooperative behaviour among men, particularly in terms of a reduction in dominance behaviours, aggression towards rivals and sexual jealousy. Testosterone levels in adults and PAE are known to increase tendency towards competitive and aggressive behaviours among men (Bailey & Hurd 2005; Mazur & Booth 1998). Conversely, oxytocin (OT) and vasopressin (VA) are hypothalamic neuropeptides regulated by oestrogen activity and all three hormones are key to the formation of pair-bonds in humans and other animals (Vargas-Pinilla *et al.* 2015; Lee *et al.* 2009; Neumann

2008). In humans, OT is also linked to cooperative behaviour (Crespi 2016) and bonding among team-mates (Pepping & Timmermans 2012). Various studies have pointed towards a negative relationship between PAE and the postnatal expression of behaviours associated with oestrogen, OT & VA (Fisher *et al.* 2010; Fink *et al.* 2007a; Williams *et al.* 2003). The attributes necessary for co-husbands to express towards one another would suggest that reduced selection for behaviours associated with PAE (dominance, aggression), and increased selection for behaviours associated with POE (cooperation, affiliation), would be favourable among men in polyandrous marriage systems.

3.1.3: The influence of marriage systems on selection for PAE in women

Physical traits which act as indicators of reproductive value in women (e.g. skin pigmentation and breast size) correlate with oestrogen and/or progesterone levels and these hormones are vital for facilitating conception and maintaining pregnancy (Kuna & Galbarczyk 2018; Puts 2010). 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). The 2D:4D ratio is higher in women with lighter skin and light skin is oestrogen dependent, with men preferring women with lighter than average skin as this is a signal of fertility (Ihara & Aoki 1999; Manning *et al*. 2004b). The 2D:4D ratio was found to positively relate to female reproductive success in women from several European countries (Manning *et al*. 2000). Women with low (masculine) 2D:4D ratios tend to have lower reproductive success and a higher susceptibility to parasitic infection (Saino *et al.* 2006; Flegr *et al.* 2008) which comes from developing in a prenatal environment high in androgens. Masculine 2D:4D ratios are associated with conditions causing infertility in women (Cattrall *et al*. 2005) and previous studies have shown that men prefer women's hands with feminised 2D:4D ratios (Saino *et al*. 2006).

In contrast to men's preferential choice of women displaying traits indicative of developing in an environment high in POE, Sorokowski *et al*. (2012) report that Himba men prefer women with more masculine 2D:4D ratios who are likely to have been exposed to high PAE (Sorokowski *et al.* 2012). This is unusual as human males are typically attracted to women displaying traits associated with high POE as signals of fertility (Manning *et al.* 1998). This observation could be due to the fact that, in hunter-gatherer and subsistence societies, women are expected to do a large proportion of the heavy work and food provisioning for their families (Holden & Mace 1999; Özener *et al.* 2014). This is the case among the Himba, with women being responsible for the more labour-intensive work (Sorokowsi *et al.* 2012). Higher levels of prenatal testosterone allow individuals of both sexes to be competitive and masculinised female offspring are likely to be more robust and competitive under stressful environmental conditions (Kaiser & Sachser 2005; Meise *et al*. 2016).

Although the amicability of relationships between co-wives undoubtedly varies across and within societies (Seeley 2012; Madhavan 2002), polygynously married women engage in intrasexual competition over shared resources and co-wives are often reported as being hostile towards one another (Mulder 1992) and sometimes even towards their co-wives' offspring (Han & Foltz 2015; Strassman 1997). Reproductive conflicts between co-wives arise as a result of competition over the resources necessary for reproduction such as food and money, alongside their husband's attention and investment in their offspring (Betzig 1989). In a study of polygynous Malian women, a mother's rank amongst her co-wives determined her child's nutritional status, such that children of junior wives were more likely to suffer from wasting and stunted growth (Han & Foltz 2015). Reproductive conflict is also evident in matrilineal duolocal societies where women do not share husbands but are co-resident and share the resources they need to reproduce with their female kin (Ji *et al.* 2013). In one such communally breeding population, reproductive success declined as the number of female kin within a household increased, and older sisters had greater reproductive success as a result of dominance over their younger sisters (Ji *et al.* 2013). The greater reproductive competition experienced by polygynously married women (in terms of both resources and their husband's attention) relative to monogamously or polyandrously married women, may favour increased PAE among women in polygynous populations. The ability to outcompete and/or attain dominance over co-wives would be an advantage for a woman under such circumstances, as it is likely to result in a larger proportion of resources, increased paternal investment and improved offspring survival.

3.1.4: The association between latitude, PAE and marriage systems

There is considerable geographic variation in the distribution of polygyny among human populations with regards to latitude (Murdock 1967; Manning *et al*. 2004b). Societies at lower latitudes tend to have higher levels of polygynous marriage whereas at higher latitudes more monogamous marriage appears to occur, as evidenced by higher full sibling fractions in populations inhabiting higher latitudes (Ellsworth *et al*. 2016). Pathogens tend to be more prevalent at lower latitudes and this may account for the observed pattern: polygyny is more prevalent where pathogen stress is higher (the tropics) and women are 'gene shopping' (Barber 2008; Ember *et al*. 2007; Low 1990). The 2D:4D ratio also varies across and within human populations in relation to latitude (Manning *et al*. 2004a; Butovskaya *et al*. 2013). In a survey by Manning *et al.* (2004a), Chinese children had the highest mean 2D:4D ratios and lived at the highest latitude whereas the lowest 2D:4D ratios were present in Jamaican children which lived at the lowest latitude. A study by Butovskaya *et al*. (2013) also found that latitude was significantly related to right hand 2D:4D ratio in humans of both sexes (restricted to those of Russian ethnicity) from five regions of Russia, with the highest 2D:4D ratios present in those belonging to the most northern population.

This pattern may reflect differences in subsistence activities of the people inhabiting different latitudes which could be influenced by the richness of the area, bringing about a reduction in male contest competition at higher latitudes (increased monogamy). Higher 2D:4D ratios (lower PAE) in populations at higher latitudes may be a bi-product of both monogamous marriage and male preference for lighter skinned females. Light skin evolved in northern latitudes through sexual selection by males for lighter skinned females which experienced a prenatal environment high in oestrogen. However, in southern latitudes, light skin is maladaptive and so is not maintained by natural selection (Ihara & Aoki 1999).

3.1.5: Summary of aims

Marriage systems manifest as population-level traits which arise as a result of decisions made by individuals in response to various environmental and inherited cultural factors (Henrich *et al*. 2012; Walker *et al.* 2011). The cultural practises and beliefs of populations which speak the same language or which neighbour one another tend to be more similar (Dow & Eff 2013). The genetic makeup of such populations also tends to be more alike (Dow & Eff 2013; Barbujani *et al*. 1997) and so genomic resemblances should be accounted for in any cross-cultural study. Much of the variation in human behaviour, whether cultural or biological in nature, can be attributed to phylogeny (Minocher *et al.* 2018), underscoring the importance of controlling for non-independence of data points owing to phylogenetic relatedness. Thus, I will explore the potential relationship between PAE (inferred from 2D:4D ratios) and marriage systems in humans, controlling for the non-independence of populations as a result of shared ancestry in addition to the effects of latitude.

3.1.6: Hypotheses and predictions

3a) Males belonging to societies characterised by high levels of polygynous marriage may be subject to increased androgenisation (higher PAE) due to higher levels of competition between men for wives, whereas males in predominantly monogamous societies may experience reduced selection for high PAE due to lower levels of male intrasexual competition.

> *(i)* Male 2D:4D ratios will be lower in populations which practise polygyny relative to those which are predominantly monogamous.

3b) Higher levels of intrasexual competition may select for increased PAE among females of polygynous populations relative to females of monogamous populations.

> *(i)* Female 2D:4D ratios will be lower in polygynous populations relative to monogamous populations.

3.2: Methods

3.2.1: Study subjects

Study subjects included 13,532 individuals (6,648 male and 6,884 female) from 52 human populations native to 25 countries. Data were restricted to non-clinical samples from predominantly adult individuals (18+ years of age) but some data from children (6-17 years of age) were used in this study (see Appendix 3.1 for details). The 2D:4D ratio is fixed early in prenatal development (Galis *et al*. 2010) and does not change appreciably during puberty (Králík *et al.* 2014; Manning *et al.* 2003, 2004a; Manning 2002), providing justification for the use of children in this study.

3.2.2: Data collection

3.2.2.1: 2D:4D ratio measurements

Population averages of the 2D:4D ratio of the right (R2D:4D) and left (L2D:4D) hands and the mean (M2D:4D) of both hands in males and females were collected from the published literature. Data for all three 2D:4D ratio measures were not available for both sexes in every population. Human male data comprise R2D:4D from 43 populations, L2D:4D from 40 populations and M2D:4D from 49 populations. Female data comprise R2D:4D from 40 populations, L2D:4D from 37 populations and M2D:4D from 48 populations (see Appendix 3.1 for information on the populations included in each analysis). Additionally, due to sampling bias of the published literature, few data were available for North and South American populations and a large proportion of Africa and South-East Asia. Much of Europe, India and China, on the other hand, were fairly well represented (Figure 3.2.1).

When investigating direct and indirect 2D:4D ratio measurement methods, Allaway *et al*. (2009) reported an average intraclass correlation coefficient (ICC) of 0.93 for 2D:4D ratios measured directly using calipers and an average ICC of 0.92 for indirect methods (caliper measurements of photocopies, printed scans and computer-assisted image analysis). Computer-assisted 2D:4D ratio measurement was the most accurate and had the highest inter-measurer consistency among methods with a mean ICC = 0.96 (Allaway *et al.* 2009) and Kemper & Schwerdtfeger (2009) mirrored this result in their comparison of indirect methods. They reported that indirect measurements of scanned images using rulers had the lowest overall reliability being on average ICC = 0.78. All measurement methods compared have ICC = >0.75 suggesting the potential for sufficient inter-measurer agreement (Allaway *et al*. 2009; Kemper & Schwerdtfeger 2009; Voracek *et al*. 2007a). However, in this study, only 2D:4D ratio data collected via methods considered to be acceptably precise and reliable (ICC = >0.8) were used (Appendix 3.1). These include direct caliper measurements of digits (38 samples), indirect caliper measurements from photocopies/digital scans of digits (10 samples) and indirect measurements of digits using computer-assisted image analysis software (CIAS) (5 samples). Data from self-measured 2D:4D ratios were not used in this study as the reliability of self-measured data are reported to be considerably lower than those of experienced measurers (Hönekopp & Watson 2010). Although it is by no means ideal to use 2D:4D ratio data gathered using different measurement methods, it was necessary in order to gain a sufficiently large and diverse sample of human 2D:4D ratios.

3.2.2.2: Marriage system

I collected data on marriage systems reported for populations in this study from the published literature (Appendix 3.2). The marriage systems of the populations in this study were: monogamy (no polygyny or polygyny is extremely rare), limited polygyny (<20% of women in polygynous marriages) and general polygyny (>20% of women in polygynous marriages). There were no polyandrous populations in this sample.

3.2.2.3: Latitude

Both 2D:4D ratio and marriage system are known to vary with latitude (Butovskaya *et al*. 2013; Manning *et al*. 2004a; Low 1990; Murdock 1967) with many polygynous societies occurring close to the equator (White 1988). Therefore, data on latitude (°North or °South of the equator) were collected for the locations of each of the 52 2D:4D ratio populations using Google Maps (maps.google.com) (Appendix 3.1).

3.2.3: Statistical analysis

I used Shapiro-Wilk tests throughout when assessing skew of data and conducted both phylogenetically controlled and non-phylogenetically controlled analyses.

Phylogenetic analysis allows for the relatedness between human populations to be accounted for in exploring relationships between traits. The 2D:4D ratio is a product of variation in PAE, which are in turn moderated by the social and ecological environment. As such, in all analyses, 2D:4D ratio measures were assigned as the dependent variables and marriage system as the independent variable. Latitude was included as a factor in all analyses. I carried out all phylogenetically controlled analyses in R version 3.4.1 “Single candle” and conducted all non-phylogenetically controlled analyses using IBM SPSS Statistical software version 24.

3.2.3.1: Phylogenetic signal

I tested for phylogenetic signal in my variables using Pagel’s λ (a quantitative measure of phylogenetic independence) and the packages Devtools and Models of Trait Macroevolution on Trees (motmot.2.0) using the human phylogenetic tree described in Section 3.2.3.2. λ = 0 indicates the trait has no phylogenetic signal, meaning it evolved independently of phylogeny and closely related populations are no more alike than more distantly related populations. λ = 1 means that there is strong phylogenetic signal in the trait, closely related populations are more similar to each other than distantly related ones and the trait evolved according to the Brownian motion model of evolution (Felsenstein 1985; Grafen 1989). Phylogenetic signal is present in traits with λ values between 0 and 1, but these traits evolved under processes other than pure Brownian motion (Freckleton *et al*. 2002; Pagel 1997, 1999).

Statistically significant Pagel’s λ values were present for marriage system only and, as this is the independent variable in all analysis, the use of phylogenetically controlled methods is justified. None of the 2D:4D ratio measures showed significant phylogenetic signal and this suggests that the compliment of non-phylogenetically controlled analysis is warranted (Appendix 4.3).

3.2.3.2: Human phylogenetic tree

Data from the Duda & Zrzavý (2016) supertree of modern human populations were used. This supertree is based on a mixture of linguistic and genetic data from 388 individual phylogenies. A phylogenetic tree representing the 52 populations in my sample was provided by Dr Pavel Duda and comprised 37 supertree populations (Table 3.2.1). Where several 2D:4D ratio populations were subsumed under the same supertree population (e.g. 5 populations of ethnic Russians), the 2D:4D ratios of these populations were averaged to give a single right, left and mean 2D:4D ratio measure for that supertree population. For three populations which were not present in the supertree, closely related populations (i.e. neighbouring or linguistically related) were used as proxies and these are presented on the phylogenetic tree with the population they represent in parentheses (Figure 3.2.2). I used the software FigTree (version 1.4.3) to illustrate the phylogenetic tree.

3.2.3.3: Non-phylogenetically controlled analysis

I investigated relationships between 2D:4D ratio measures and marriage system in human populations using multiple linear regression models, controlling for latitude throughout. Non-phylogenetically controlled analyses use data from all 52 2D:4D ratio populations as presented in Appendices 3.1 & 3.2.

3.2.3.4: Phylogenetically controlled analysis

Phylogenetically controlled analysis allows for the relatedness between human populations to be accounted for in exploring relationships between traits. In order to control for relatedness between human populations when testing for relationships between 2D:4D ratio and marriage systems, I used Phylogenetic Generalized Least Squares (PGLS) regression analysis using the package Comparative Analysis of Phylogenetics and Evolution in R (caper).

Figure 3.2.1: Map showing the geographical location of the 52 human populations used in this study, each population is indicated by an orange circle.

Table 3.2.1: The 37 supertree populations used in phylogenetically controlled analyses with corresponding marriage system, 2D:4D ratio and latitude data. Proxy populations are followed by the population they represent in parentheses.

Supertree Population	**Marriage System**	**Male R2D:4D**	**Male L2D:4D**	**Male M2D:4D**	**Female R2D:4D**	**Female L2D:4D**	**Female M2D:4D**	**Latitude °N/°S**
Igbo	GP	0.960	0.940	0.950	0.970	0.950	0.960	4.85
Yoruba	GP	0.960	0.940	0.950	0.970	0.950	0.960	7.59
Efik [Ijaw]	GP	xxx	xxx	0.950	xxx	xxx	0.960	4.50
Herero [Himba]	GP	0.939	xxx	xxx	0.996	xxx	xxx	22.96
Zulu	GP	xxx	xxx	0.940	xxx	xxx	0.950	29.86
Hadza	LP	0.972	0.979	0.976	0.980	0.990	0.985	3.90
Datooga	GP	0.960	0.960	0.960	0.970	0.980	0.975	3.63
Dani [Yali]	GP	0.950	0.970	0.960	0.940	0.950	0.945	4.27
Uyghur	MO	0.940	xxx	xxx	0.950	xxx	xxx	42.52
Korean	MO	0.952	0.950	0.951	0.971	0.973	0.972	36.81
Japanese	MO	0.950	0.940	0.945	0.960	0.960	0.960	36.20
Malay	MO	0.982	0.987	0.985	0.977	0.984	0.981	3.07
Maonan	MO	0.938	0.940	0.939	0.944	0.943	0.944	24.83
Bouyei	MO	0.966	0.954	0.960	0.984	0.985	0.985	26.84
Hani	MO	0.932	0.942	0.937	0.952	0.955	0.954	24.48
Southern Han Chinese	MO	0.948	0.937	0.943	0.958	0.952	0.955	27.32
Hui	MO	0.934	0.932	0.933	0.952	0.952	0.952	37.19
Northern Han Chinese	MO	0.959	0.954	0.956	0.971	0.965	0.968	34.50**
Telugu	MO	0.971	0.967	0.969	0.980	1.004	0.992	16.45
Tulu	MO	1.010	0.970	0.990	0.980	0.970	0.975	12.91
Hungarian	MO	xxx	xxx	0.965	xxx	xxx	0.970	46.07

Table 3.2.1 *continued.*

Supertree Population	**Marriage System**	**Male R2D:4D**	**Male L2D:4D**	**Male M2D:4D**	**Female R2D:4D**	**Female L2D:4D**	**Female M2D:4D**	**Latitude °N**
Mordvin	MO	xxx	xxx	0.969	xxx	xxx	0.993	54.24
Finnish	MO	xxx	xxx	0.940	xxx	xxx	0.960	60.16
Berber	LP	0.945	xxx	xxx	0.957	xxx	xxx	34.00
Rajbanshi	MO	0.970	0.960	0.965	0.970	0.960	0.965	22.99
Marathi	MO	0.960	0.957	0.959	0.982	0.980	0.981	17.93
Hindi	MO	0.964	0.962	0.963	0.976	0.972	0.974	27.50**
Punjabi	MO	0.945	0.955	0.950	xxx	xxx	xxx	29.06
Greek	MO	0.974	0.973	0.974	1.002	1.001	1.002	39.07
Brazilian Portuguese	MO	0.955	0.962	0.959	0.953	0.963	0.958	18.51
Spanish	MO	0.970	0.964	0.967	0.976	0.972	0.974	37.18*
Lithuanian	MO	0.950	0.953	0.952	0.971	0.973	0.972	55.17
Polish	MO	0.981	0.981	0.981	0.997	0.998	0.998	51.04**
Russian	MO	0.969	0.971	0.970	0.985	0.986	0.985	53.03**
Swedish	MO	xxx	xxx	0.950	xxx	xxx	1.010	60.13
German	MO	0.965	0.963	0.964	xxx	xxx	0.970	50.29***
English	MO	0.968	0.970	0.969	0.982	0.980	0.981	52.45*

xxx Data not available

*Where the supertree population includes 2D:4D ratio data from populations living outside of their ancestral country then the latitude for the ancestral population was used.

**Where the supertree population represents several 2D:4D ratio populations within a country then the average latitude of these populations was used.

***This is the average latitude between Austrian and German 2D:4D ratio populations which were subsumed under the same supertree population.

Marriage system categories: monogamy (MO), limited polygyny (LP) and general polygyny (GP).

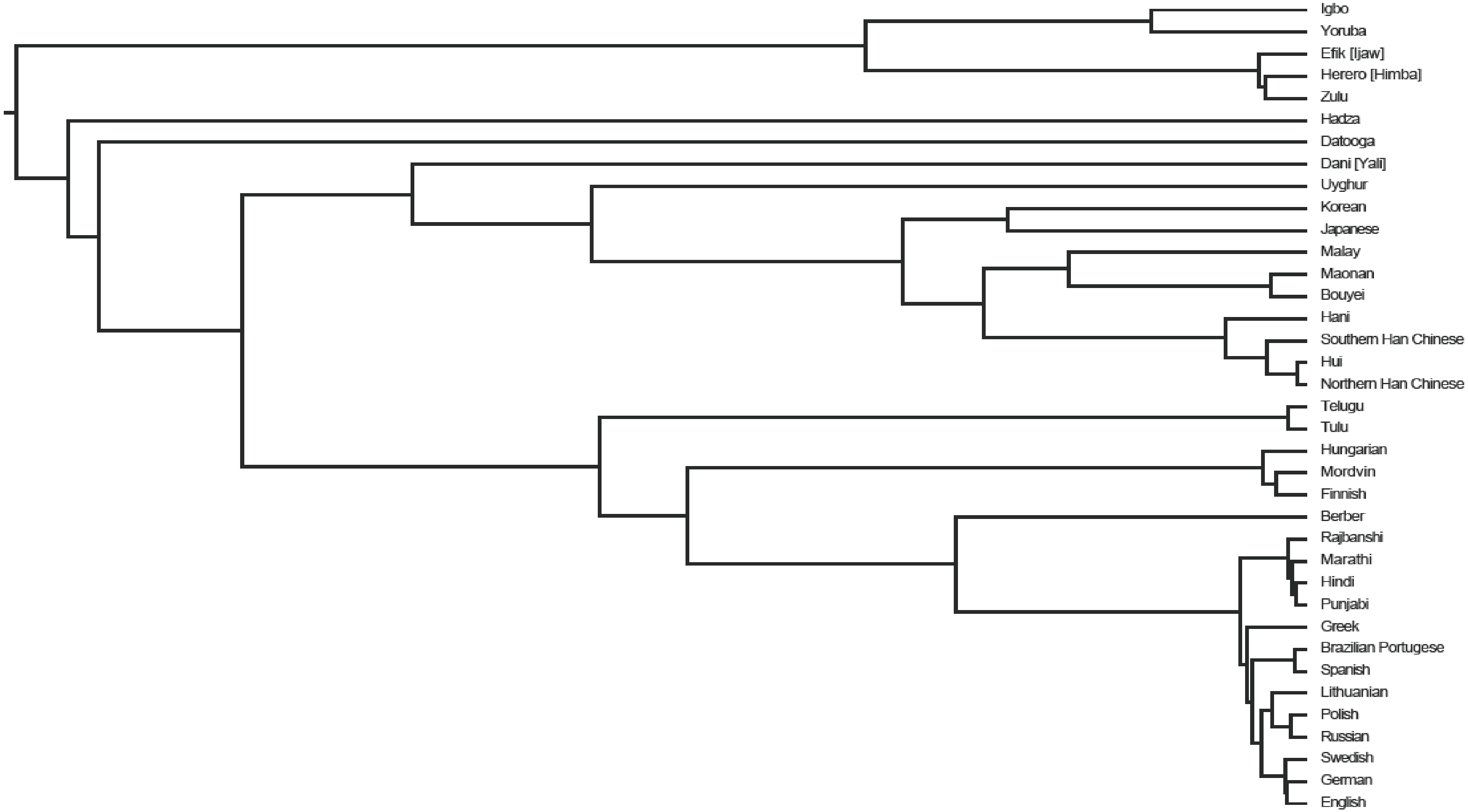

Figure 3.2.2: Phylogenetic tree displaying the 37 supertree populations which reflect the 52 2D:4D ratio populations used in this study. The three proxy populations are followed by the population they represent in parentheses.

3.3: Results

3.3.1: Latitude

There were no significant relationships between latitude and male 2D:4D ratios in either non-phylogenetically controlled (R2D:4D – $F_{1,42}$ = 0.211, r^2 = 0.072, P = 0.649; L2D:4D – $F_{1,39}$ = 1.707, r^2 = 0.207, P = 0.199; M2D:4D - $F_{1,48}$ = 0.494, r^2 = 0.102, P = 0.486) or PGLS analysis (Table 3.3.1). Non-phylogenetic analysis revealed no significant relationships between latitude and female R2D:4D ($F_{1,39}$ = 3.486, r^2 = 0.290, P = 0.070) or L2D:4D ($F_{1,36}$ = 2.614, r^2 = 0.264, P = 0.115) nor did PGLS analysis (Table 3.3.2). However, there was a significant relationship between female M2D:4D and latitude in non-phylogenetically controlled analysis ($F_{1,45}$ = 6.242, r^2 = 0.352, P = 0.016) with females of populations inhabiting lower latitudes having lower M2D:4D ratios (Figure 3.3.1), but the significant relationship was not maintained in PGLS analysis (Table 3.3.1). There was a significant relationship between latitude and marriage system in non-phylogenetically controlled analysis ($F_{1,51}$ = 23.806, r^2 = 0.568, P = <0.001) such that higher levels of polygyny are associated with populations inhabiting lower latitudes (Figure 3.3.2), but this significant result was not mirrored in PGLS analysis (Table 3.3.1).

Table 3.3.1: Results of the PGLS regression testing for an effect of latitude on 2D:4D ratios and marriage system.

Variables	*t*	*p*	Estimate	± s.e	df	λ	Adj.r^2
Latitude & Marriage System	-1.606	0.117	-10.860	6.761	35	0.988	0.042
Latitude & Male R2D:4D	-0.930	0.360	-104.066	111.880	29	0.978	-0.004
Latitude & Male L2D:4D	-1.063	0.297	-176.473	165.970	26	0.984	-0.005
Latitude & Male M2D:4D	-1.862	0.072	-247.584	133.000	32	0.987	-0.070
Latitude & Female R2D:4D	1.288	0.208	167.064	129.690	27	0.978	0.023
Latitude & Female L2D:4D	0.757	0.456	95.048	125.503	24	0.974	0.017
Latitude & Female M2D:4D	0.882	0.385	99.049	112.312	31	0.995	-0.007

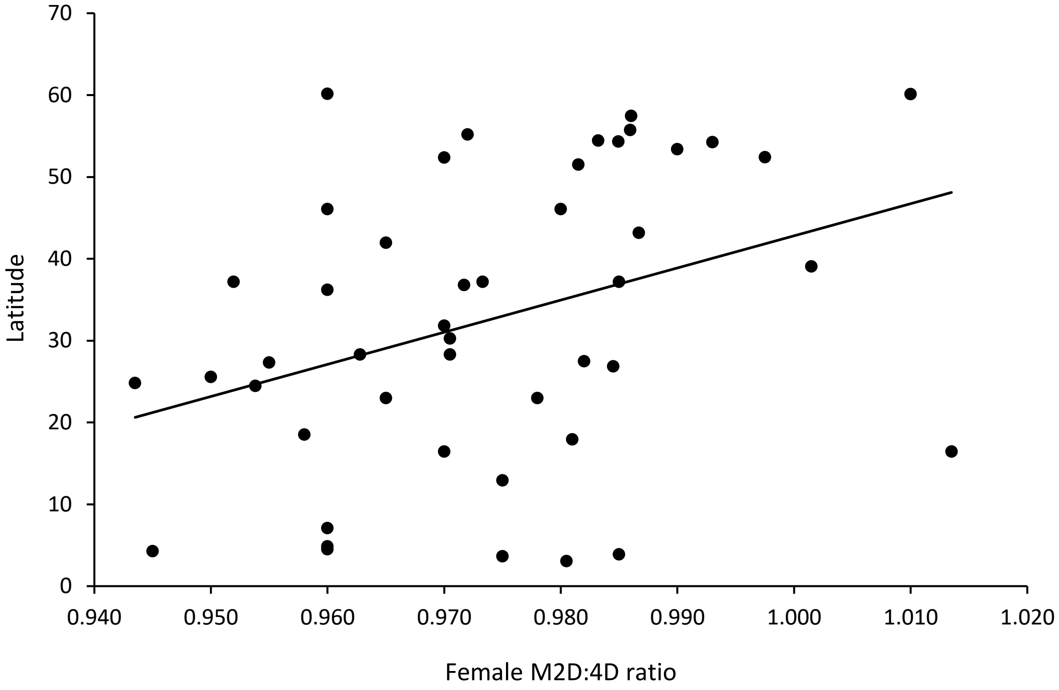

Figure 3.3.1: Relationship between latitude and female M2D:4D ratio based on data from the 52 2D:4D ratio populations.

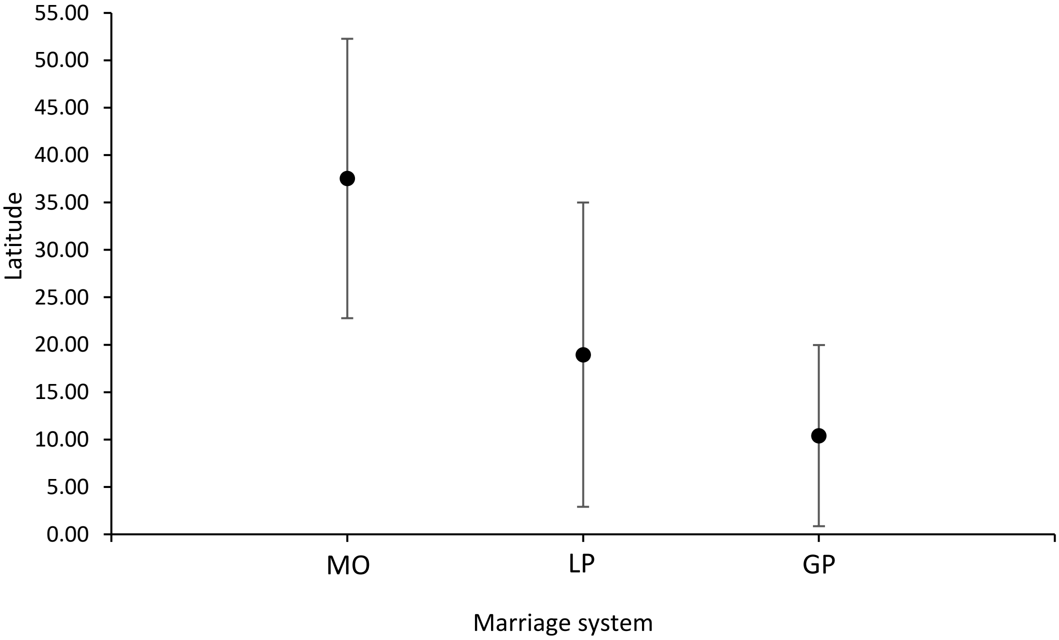

Figure 3.3.2: The average latitude (mean ± standard deviation) of populations practising each marriage system based on data from the 52 2D:4D ratio populations. MO = monogamy, LP = limited polygyny, GP = general polygyny.

3.3.2: Marriage system

Non-phylogenetically controlled analysis revealed no significant relationships between any of the 2D:4D ratio measures and marriage system in males (R2D:4D - $F_{2,42} = 0.903$, $r^2 = 0.208$, P = 0.413; L2D:4D - $F_{2,39} = 0.833$, $r^2 = 0.208$, P = 0.443; M2D:4D- $F_{2,48} = 1.145$, $r^2 = 0.218$, P = 0.327) or between marriage system and female R2D:4D ($F_{2,39} = 1.709$, $r^2 = 0.291$, P = 0.195) or female L2D:4D ($F_{2,36} = 1.593$, $r^2 = 0.293$, P = 0.218). There was a significant relationship between marriage system and female M2D:4D ($F_{2,45} = 3.882$, $r^2 = 0.391$, P = 0.028) such that female M2D:4D decreased with increasing levels of polygyny (Figure 3.3.3). However, this relationship did not hold true in PGLS analysis where there were no significant associations between marriage system and any of the 2D:4D ratio measures in either sex (Table 3.3.2).

Table 3.3.2: Results of the PGLS regression testing for an effect of marriage system on 2D:4D ratio while controlling for latitude. Model variables are indicated in bold with the control variable taken into account, parameters for latitude are displayed below these.

Variables	*t*	*p*	Estimate	± s.e	df	λ	Adj.r^2
Male R2D:4D & Marriage system	-0.882	0.385	2.786	2.809	28	1	-0.009
Latitude	-1.338	0.192	-0.006	0.005			
Male L2D:4D & Marriage system	-0.275	0.785	-1.163	4.221	25	1	-0.003
Latitude	-1.380	0.179	-0.007	0.005			
Male M2D:4D & Marriage system	-0.691	0.495	-2.026	2.933	31	1	-0.008
Latitude	-1.483	0.148	-0.006	0.004			
Female R2D:4D & Marriage system	-0.506	0.617	-1.738	3.433	26	1	-0.013
Latitude	-1.008	0.322	-0.005	0.005			
Female L2D:4D & Marriage system	-0.512	0.613	-1.581	3.088	23	1	-0.001
Latitude	-1.217	0.236	-0.006	0.005			
Female M2D:4D & Marriage system	-0.497	0.623	-1.180	2.375	30	1	-0.001
Latitude	-1.219	0.232	-0.005	0.004			

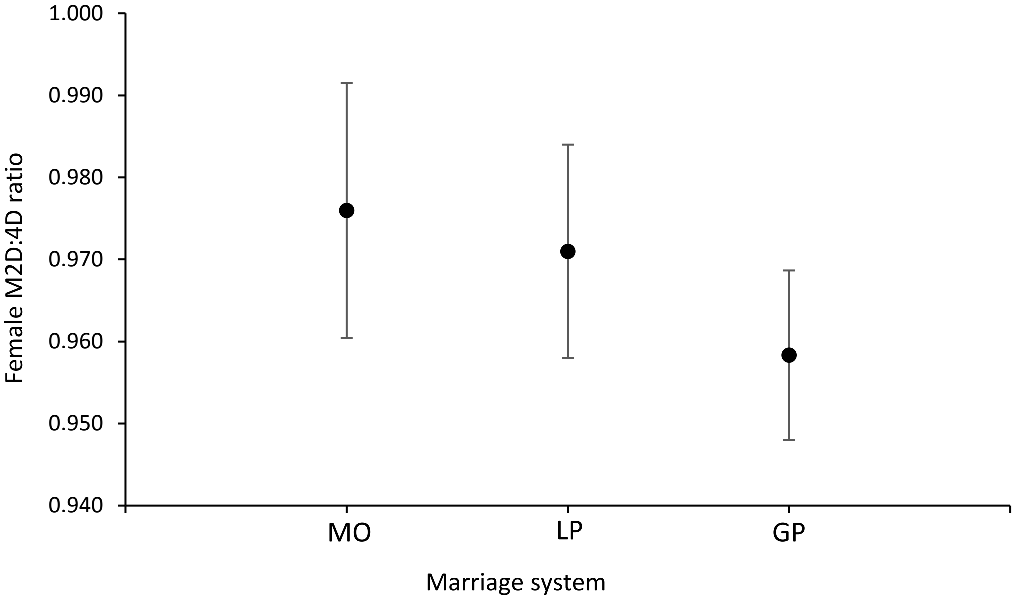

Figure 3.3.3: Relationship between female M2D:4D (mean ± standard deviation) and marriage systems based on data from the 52 2D:4D ratio populations. MO = monogamy, LP = limited polygyny, GP = general polygyny.

3.4: Discussion

None of the 2D:4D ratio measures displayed significant phylogenetic signal which is perhaps not surprising since it is a physical trait in members of the same species. However, there was strong phylogenetic signal in marriage systems, supporting the use of phylogenetic methods (Dow & Eff 2013). Results support those of previous studies which found 2D:4D ratio to vary with latitude in human populations, populations at higher latitudes have higher 2D:4D ratios (lower PAE) than populations at lower latitudes (Manning *et al*. 2004a; Butovskaya *et al*. 2013). Additionally, as observed elsewhere, marriage systems showed a strong association with latitude, with polygyny being more prevalent at lower latitudes (Murdock 1967; Ellsworth *et al*. 2016). These patterns likely reflect differential selection for PAE/POE among populations living at different latitudes through the combined effects of sexual selection and natural selection. Both polygyny and PAE appear to be higher at lower latitudes, likely as a result of adaptations to various ecological pressures, such as the richness of the environment and high pathogen prevalence, which favour polygyny (and increased male-male competition) and the factor of higher sunlight levels at lower latitudes which favour darker skin pigmentation (reduced sexual selection for high POE in females) (Manning *et al.* 2004b).

Contrary to the main prediction, no significant associations were found between any of the male 2D:4D ratio measures and the marriage system practised by a population in either non-phylogenetic or phylogenetically controlled analyses. Men in polygynous societies with the greatest competition for mates did not have lower 2D:4D ratios than males of monogamous societies which experience relaxed male intrasexual competition. It may be that, as males are the competing sex, there is still strong selective pressure for high PAE regardless of the marriage system practised, as many of the behaviours and physical attributes resulting from the organisational effects of androgens are effective in improving male reproductive success (Manning & Fink 2008; Millet & Dewitte 2008; Burriss *et al.* 2007; Fink *et al*. 2006; Fink *et al.* 2004a). Another possibility for the lack of significant results between male 2D:4D ratios and marriage systems is the under-representation of societies practising forms of polygyny and polyandry. Six populations were described as practising general polygyny, only two as practising limited polygyny and there were no polyandrous populations in the sample at all. Monogamous marriage likely arose due to an increase in agriculture amongst the historical societies of Europe and Asia (Archetti 2013). The fact that a significant portion of the individuals in my sample originate from Europe and Asia makes it likely that the over-representation of these geographical areas caused the dataset to be strongly biased in favour of monogamous populations (~85%) and this imbalance was due to a bias in the populations for which 2D:4D ratio data were available. Before any definitive conclusions can be drawn regarding the relationship between PAE and human male intrasexual competition, it would be beneficial to carry out the analysis with 2D:4D ratio data measured by a single measurer using the digital photographic and computer-assisted image analysis software method and with a more balanced marriage system dataset (encompassing societies practising all marriage systems).

There were no significant associations between female R2D:4D or L2D:4D in either the phylogenetically controlled or non-phylogenetically controlled analyses. However, the non-phylogenetic analysis between female M2D:4D and marriage system was significant and monogamous females had higher 2D:4D ratios than polygynous females, possibly as a result of the greater intrasexual competition among women in polygynous populations favouring higher PAE. Obtaining this result in females and not males is unusual as we would expect sexual selection to have a greater effect on the males, as the competing sex, than on the females in a population. The association between female M2D:4D and marriage system (non-phylogenetic analysis) and female M2D:4D and latitude (non-phylogenetic analysis) could be to do with selective mating. More monogamous populations tend to be found at higher latitudes, and male selection for feminised women (low PAE/high POE) may result in higher 2D:4D ratios in females at higher latitudes in populations which are also monogamous. Selection for high POE females can be maintained at higher latitudes where sun exposure is lower. At lower latitudes this cannot be maintained as skin is damaged by exposure to higher sunlight levels and so selection for darker skin and higher PAE are favoured (Manning *et al.* 2004b). Additionally, men in certain populations characterised by harsh environments at lower latitudes are known to prefer more masculinised women (e.g. Himba), presumably because they are better able to cope and be competitive under demanding conditions than more feminised women (Sorokowski *et al.* 2012). However, the significant relationship was not maintained in the phylogenetic analysis and the prediction that female 2D:4D ratios would be lower in polygynous populations relative to monogamous populations was not supported. The results show that it is key to control for relatedness between populations when carrying out cross-cultural comparative analysis and indicate that ignoring phylogeny could provide false positives, which is possibly what the non-phylogenetically controlled results could have been (Minocher *et al*. 2018).

3.4.1: Summary

I used a PGLS analysis and a phylogenetic tree of human populations to analyse the impact of marriage system on selection for PAE in humans. This study confirmed results from previous research which showed the expected associations between latitude and mating systems and latitude and 2D:4D ratio. However, there were no associations between male or female 2D:4D ratios and marriage system once phylogeny was considered. This suggests that the marriage system practised by a population does not incur considerable selection for higher/lower PAE in either sex in humans, possibly because marriage systems do not predict intrasexual competition, or that intrasexual competition does not select for high PAE in humans. Alternatively, and perhaps more likely, the lack of significant relationships may stem from a limited 2D:4D ratio dataset which was highly biased in favour of monogamous populations. Further research with a more balanced dataset encompassing a wider range of marriage systems and improved 2D:4D ratio data is necessary before the possibility of a relationship between PAE and marriage systems in humans can be completely ruled out. The study lends support to the stipulation that controlling for phylogenetic non-independence in human populations is necessary when carrying out cross-cultural comparative analysis and that future research should aim to do so where ever possible.

- Chapter 4 -

Prenatal androgen effects as a proximate mechanism underpinning variation in social behaviour among female non-human primates

Abstract

The underpinnings of social structure and behaviour in nonhuman primates remains a contentious issue. Explanations concerning species' adaptation to current ecological conditions have taken precedence in the past, but more attention is now being focussed on phylogenetic relationships and the potential role of underlying proximate mechanisms. This study aimed to investigate the relationship between one such proximate mechanism, prenatal androgen effects (PAE), and aspects of social behaviour in female non-human primates using the 2D:4D ratio as a proxy for PAE and phylogenetically controlled methods. In general, female 2D:4D ratios were highest in monogamous species (low inferred PAE) and lowest in polygynandrous and polygynous species (high inferred PAE). 2D:4D ratios also varied with the form of polygyny/polygynandry, potentially with regard to the necessity for competitive over cooperative behaviours and the intensity of female reproductive competition. Species characterised by female dominance had lower 2D:4D ratios than species characterised by male dominance or codominance. Across species of macaques *(Macaca* spp.)*,* female 2D:4D ratio varied according to social style, with species described as more "tolerant" having higher 2D:4D ratios than less tolerant species suggesting that PAE may contribute to this variation. There were no relationships between 2D:4D ratio and either degree of frugivory or group size, although many classic socioecological models regard these variables as key factors determining relationships in female primates. Relationships between 2D:4D ratios and two quantitative measures of female social structure were also nonsignificant but small sample sizes may account for this. Female social relationships are a manifestation of complex competitive and cooperative behaviours and the results suggest that PAE may act as a proximate mechanism underlying the expression of behaviour in female primates in ways that are adaptive to both their social structure and mating system.

4.1 Introduction

4.1.1: Primate socioecology

A 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 thought to be among the most important ecological factors that contribute to the evolution of female social relationships (van Schaik 1989; van Schaik & van Hooff 1983). Predation risk leads diurnal female primates to form groups for safety (van Schaik 1983) which in turn leads to within-group competition for essential resources (van Schaik 1989; Terborg and Janson 1986). Relationships among females are thought to be influenced by the style and strength of the feeding competition that they face within and between their social groups, and this is affected by the distribution of resources (Kappeler & van Schaik 2002; Koenig 2002; Sterck *et al*. 1997; Chapman *et al*. 1995; Isbell 1991).

Food intake can have important effects on a female's survival and lifetime reproductive success and so the ability to dominate and exclude competitors from food resources is advantageous under certain conditions (Sterck *et al*. 1997; Trivers 1972). When resources are evenly distributed or plentiful, indirect (scramble) competition is expected (Kappeler & van Schaik 2002). Display of aggressive behaviour and dominance over others is not expected to be advantageous under this type of competition and so female dominance relations are expected to be ill-defined or not identifiable (Janson & van Schaik 1988; Janson 1985), and consequently, hierarchies (if detectable) are expected to be indistinct and non-linear (Sterck *et al*. 1997). However, when resources are clumped and monopolisable then direct (contest) competition is expected to occur (Janson & van Schaik 1988). This type of competition is likely to result in agonistic interactions between females and the formation of hierarchical social relationships (Sterck *et al*. 1997). Females with despotic relationships have established dominance relations with one another and linear dominance hierarchies (Sterck *et al*. 1997).

Egalitarian relationships are expected between females in folivorous species as the primary food resource (leaves) is thought to be evenly distributed, abundant and, therefore, unmonopolisable (Isbell 1991; but see Koenig *et al*. 1998). Females cannot use aggression or exclusion to gain a larger share of the resources. Frugivory is typically thought to favour despotic relationships because ripe fruits tend to be high-value, unevenly distributed, monopolisable and, therefore, contestable. Some studies have shown that agonism occurs disproportionately during feeding in primates, particularly when feeding on fruits (Klass & Cords 2015; Cords 2000) and previous studies have purported that dietary categories (e.g. degree of frugivory) can provide information as to the contestability and distribution of food and therefore give an indication of the expected level of feeding competition within a social group (Snaith & Chapman 2007; McKenna 1979). However, in a cross-taxa analysis Wheeler *et al*. (2013) found that the expected association between high rates of agonism and frugivory in female primates was not generally supported, while some folivorous female primates show relatively low rates of agonism but still form decided dominance relationships (*Trachypithecus phayrei*: Koenig *et al*. 2004). In addition to the distribution of food, ecology can also indirectly affect female social structure by its effect on group size (Terborgh & Janson 1986). There is notable variation in group size across the primate order (Campbell *et al*. 2011; Kappeler & van Schaik 2002). The intensity of within-group competition levels may increase with group size (Koenig & Borries 2006; Klass & Cords 2015; Terborgh & Janson 1986) and studies have found that primates living in larger groups were characterised by higher rates of agonism (Cowl & Shultz 2017; Wheeler *et al*. 2013).

Another important factor determining female social relationships is whether hierarchies are based on nepotism or individualism. In nepotistic hierarchies female relatives often occupy ranks close together and provide coalitionary support for each other in competitive situations both within- and between-groups (Kappeler & van Schaik 2002). In individualistic hierarchies, female rank tends to be unconnected to the rank of their relatives (Sterck *et al*. 1997). Nepotism is predicted to occur in species where there are high levels of within-group contest competition between females. Where there are also high levels of competition between different groups, dominant females may benefit from subordinate females remaining in the group to help defend resources/territory from females of other groups. This is expected to lead to tolerance on the part of dominant females and an increase in group cohesion-related behaviours such as reconciliation and grooming of subordinates by dominants (Sterck *et al*. 1997). In addition to the ecological factors of feeding competition and predation pressure, the demographic factor, female philopatry, is thought to be involved in the formation of female relationships (Kappeler & van Schaik 2002; Sterck *et al*. 1997). In species where females disperse, female relationships are predicted to be egalitarian. In species where females remain in their natal group, relationships vary depending on the levels of within- and between-group contest competition (see Table 4.1.1 for summary).

Although these broad-scale descriptive classifications of female dominance relationships are useful, there is considerable variation in how these relationships manifest themselves between (and sometimes even within) species (Klass & Cords 2015; Wickberg *et al.* 2013). This observed variation is beyond the descriptive scope of the four categories described in Table 4.1.1 and species do not necessarily conform to every prediction of any socioecological model, leading researchers to position species into the categories which they most closely match. For example, female blue monkey social relationships do not fully correspond to the predictions of any current socioecological model, instead they display an assortment of traits from each of Sterck *et al*. (1997)'s four categories (Klass & Cords 2015). In a study on a population of predominantly folivorous *Colobus vellerosus* (a species with facultative female dispersal: Wickberg *et al.* 2014), occasional foraging on temporally available, clumped foods such as palm nuts and seed pods was sufficient incentive to lead females to form individualistic dominance hierarchies of intermediate strength and high directional consistency (Wickberg *et al*. 2013). Likewise, contrary to the expectations of socioecological models, folivorous mountain gorilla (*Gorilla beringei beringei*) females display relatively low levels of within-group contest competition coupled with female dispersal but still form highly linear dominance hierarchies (Robbins *et al*. 2005) coupled with relatively high rates of female-female agonism (Wheeler *et al.* 2013).

Table 4.1.1: Showing the social categories observed and the factors affecting female dominance relationships (adapted from Sterck *et al*. 1997).

Social category	**Within-group contest competition**	**Between-group contest competition**	**Female Philopatry**	**Female dominance relationship**
Dispersal-Egalitarian	Low	Low	No	Egalitarian
Resident-Egalitarian	Low	High	Yes	Egalitarian
Resident-Nepotistic	High	Low	Yes	Nepotistic & despotic
Resident-Nepotistic-Tolerant	High (potentially)	High	Yes	Nepotistic & despotic but tolerant

4.1.2: Social style in macaques

In addition to differences between more distantly related primate taxa, there can also be great disparity in female social relationships among closely related species (Barton *et al*. 1996; Mitchell *et al.* 1991), and macaques (*Macaca* spp.) are a good example of this variation (Balasubramaniam *et al.* 2012; Thierry & Aureli 2006; Thierry 2000). All species within the *Macaca* genus exhibit similarities in social organisation and some aspects of social structure, in that they live in large permanent mixed-sex groups with male dispersal and female philopatry as the norm (Balasubramaniam *et al*. 2012; Demaria & Thierry 2001). Philopatric females form stable linear dominance hierarchies, but there is considerable varation in dominance relationships and aspects of social interaction between females (and other group members) across macaque species (Balasubramaniam *et al.* 2012; Thierry & Aureli 2006; Thierry 2000). Based on evidence from molecular, morphological and behavioural data, Barbary macaques (*M. sylvanus*) are postulated to be most similar to the ancestral macaque (Thierry *et al*. 2000). *M. sylvanus* females form matrilines with clear dominance hierarchies but relationships between females are tolerant and reconciliation between former opponents is common (Thierry & Aureli 2006). A tolerant social style is even more apparent in the Sulawesi macaques (e.g. *M. hecki, M. nigra*), where counter-aggression and tolerance levels between females are high, even among unrelated individuals (Thierry *et al.* 2008; Abegg *et al*. 1996). Conversely, rhesus (*M. mulatta*) and Japanese macaques (*M. fuscata*) have strict dominance hierarchies characterised by both intense aggression and submission and strong nepotism (Thierry *et al.* 2004).

In light of this remarkable variation in social style, extant macaque species have been graded on a scale from 1 to 4 (grade 1 being the least tolerant and grade 4 being the most tolerant; Thierry 2000). Species are ordered based on their conciliatory tendency, social tolerance, the asymmetry of conflicts, the dominance gradient and kin bias (Thierry 2000). Conflict asymmetry is particularly variable in macaques, with dominance gradients being steepest amongst grade 1 'intolerant' species such as rhesus and Japanese macaques, where the proportion of counter-aggression is less than 15% (Thierry *et al*. 2008; Thierry 2000). In species at the tolerant end of the social style scale, however, dominance gradients are shallower, the intensity of aggression tends to be low and the proportion of counter-aggression can be above 50% (Thierry *et al*. 2008; Thierry 2000). In Sulawesi black-crested macaques (*M. nigra*), retaliation by the initial victim of aggression has been known to occur in over 90% of unrelated dyads and this high conflict asymmetry is a reflection of their more tolerant social style (Petit & Thierry 1994).

Additionally, intense patterns of reconciliation are characteristic of tolerant macaque species and non-kin conciliatory tendency has been observed to be around 50% in Tonkean (*M. tonkeana)* and Sulawesi black-crested macaques (grade 4) and 40% in lion-tailed (*M. silenus)* macaques (grade 3). Comparatively, in rhesus and Japanese macaques (grade 1), non-kin conciliatory tendency is <12% (Thierry *et al*. 2008; Demaria & Thierry 2001; Thierry 2000). High rates of reconciliation are associated with more relaxed dominance hierarchies (e.g. higher asymmetry levels) (Demaria & Thierry 2001; Petit & Thierry 1994) and unlike those of grades 3 and 4, grade 1 species do not show high selective attraction between opponents after conflicts and their patterns of conciliation are limited (Petit & Thierry 1994; de Waal & Yoshihara 1983). Grade 2 macaques (e.g. long-tailed macaques, *M. fascicularis;* pig-tailed macaques, *M. nemestrina*) are more similar to rhesus and Japanese macaques in terms of their aggression and reconciliation patterns. Likewise, Barbary and lion-tailed macaques tend more toward the Sulawesi macaques in their expression of these traits and are assigned to grade 3 on the social style scale (Thierry 2000). Species in grades 3 and 4 display specific tension reducing, affiliative behaviours including the patterns of conciliation described above and elaborate contact behaviours such as clasps and embraces (Thierry 2000; Abegg *et al*. 1996), which are absent in species of grades 1 and 2 (Thierry & Aureli 2006).

Although macaque species inhabit a diverse range of environments, variation in macaque social structure cannot be explained by variation in general ecological factors such as habitat type and predation pressure (Thierry & Aureli 2006; Thierry *et al*. 2000). Macaques are a monophyletic group whose divergence occurred ~5 mya and extant species are split into three phyletic lineages: the *silenus*, *sinica* and *fascicularis* groups (Balasubramaniam *et al*. 2012; Thierry *et al*. 2000). The three phyletic lineages cluster on the 4-grade social style scale which was formulated based on the behaviour of the same species living in a variety of different conditions (captive, free-living and wild). The fact that a given species' behaviour is generally consistent regardless of current living conditions and that social style behavioural traits show significant phylogenetic signal, suggests that phylogeny may be a major factor influencing macaque social behaviour and ecological factors are not acting alone on these traits (Thierry *et al*. 2008; Thierry *et al*. 2000).

The shortcomings of current socioecological models highlight the need for clearer, more comprehensive definitions of dominance categories. These could be derived from quantitative measures of female dominance behaviour (e.g. hierarchical steepness and linearity, directional consistency in dominance interactions and rates of aggression), as these are likely to be more representative of the fine-grained variation we see across primate species (Klass & Cords 2015). Unlike linearity and steepness (Klass & Cords 2011), the directional consistency of female dominance relationships (measured via the directional consistency index: DCI), is not sensitive to unknown relationships and is therefore considered the most accurate measure of despotism (Koenig *et al.* 2013; van Hooff & Wensing 1987). Additionally, because variation in ecology alone is not able to fully explain the observed differences in agonism and dominance patterns among female primates, it is necessary to also consider the effects of phylogeny when examining the effects of ecology on behaviour (Klass & Cords 2015; Thierry 2008).

4.1.3: Patterns of intersexual dominance

Among mammalian species, male dominance over females is the norm and this is true of a large number of primates (Dunham 2008; Kappeler 1993; Pereira *et al*. 1990; Hrdy 1981; Ralls 1976). Males are consistently able to elicit submissive behaviour in all females in dyadic interactions in species displaying male dominance. In some primate species the relationships between the sexes are egalitarian in nature or there is no clear dominance of one sex over the other and the sexes are described as codominant (Petty & Drea 2015; Dunham 2008). Among primates, this pattern is seen in many gibbons (Barelli *et al*. 2011; Reichard & Barelli 2008; Leighton 1987; Carpenter 1940), marmosets and tamarins (Koba *et al*. 2012; Savage *et al*. 1988; Smuts *et al*. 1987). This type of dominance appears to correlate with monogamous and polyandrous mating systems, though this generalisation is not universally applicable (*Eulemur collaris*: Balestri *et al*. 2014; *Brachyteles arachnoides:* Strier 1990).

Female dominance is defined as the ability of adult females in a species to consistently bring about submissive behaviour in males in dyadic agonistic interactions and can take a variety of forms (Kappeler 1993; Pereira *et al*. 1990). Unambiguous female dominance occurs where there are high rates of decided dominance interactions and females of a species are clearly able to dominate their male counterparts. Moderate female dominance describes cases where conflicts between the sexes are not always unidirectional, but females win more often than males. Finally, female feeding priority describes those species in which the appearance of female dominance is limited to feeding contexts (Eichmueller *et al.* 2013). Female dominance over males occurs in some haplorhine primates such as bonobos (*Pan paniscus:* Parish 1994) and some squirrel monkeys (*Saimiri*: Mitchell 1994) but it is most prevalent among strepsirrhine primates, particularly Lemuriformes, and this pattern appears to be the case regardless of species' mating system (Petty & Drea 2015; Kappeler 1993, 1991). Female dominance in Malagasy lemurs is suggested to be the result of these species living in unpredictable and resource poor environments (Wright 1999). Under these circumstances female dominance over male group members provides her and her offspring with priority of access to scarce resources (high quality food and sleeping sites) which can help to mitigate the high costs of reproduction (pregnancy and lactation) and/or increase offspring survival (Eichmueller *et al*. 2013; Dunham 2008). A linked explanation stems from the observed monomorphism in body size between the sexes in many lemurs. Nutritional demands are higher for reproducing females than males, meaning that females have more to lose in terms of fitness by not acquiring essential resources. As a result, females are likely to compete harder to win resources over males and, as males do not have a size advantage, the outcome is female dominance (Dunham 2008 but see Hemelrijk *et al*. 2008). However, male dominance over females is evident in lemur species inhabiting resource poor environments and studies have shown that lemur females do not have abnormally high energetic or reproductive costs in comparison with other primate families (Kappeler 1996b).

4.1.4: Sex hormones and female social relationships

While the hypothesised ecological factors contributing to aspects of social relationships among female primates have been discussed extensively, the role that underlying proximate mechanisms may play in regulating behaviours promoting particular dominance relationships, is poorly understood. In many of the hypotheses that attempt to explain the link between social variation and ecological factors, agonistic behaviour plays an integral part (Klass & Cords 2015; Sterck *et al*. 1997). Dominance and aggression are linked through testosterone in humans and non-human primates (Higley *et al*. 1996). Animal studies implicate prenatal androgen effects (PAE) as having some influence over the shaping of an individual's tendency towards future aggressive behaviour (Mazur & Booth 1998) and higher PAE have been known to increase offspring competitive abilities (Burley & Forster 2004). In species where competition for resources is high, the ability to out-compete challengers is highly advantageous. Therefore, high PAE are likely favourable for enhancing competitive behaviours in female primates which live in large groups (especially those with despotic dominance relationships), and if degree of frugivory is indeed a good proxy for the intensity of direct competition experienced by females, then one might expect greater selection for PAE in females of highly frugivorous species.

The ratio between the lengths of the second and fourth digits of the hands (2D:4D ratio) is a proposed negative correlate of PAE and positive correlate of prenatal oestrogen effects (POE) (Zheng & Cohn 2011). Low 2D:4D ratios (inferred high PAE) are associated with behaviours linked to dominance and aggression in humans and non-human primates (Howlett *et al*. 2015; Howlett *et al*. 2012; Hurd *et al.* 2011; Nelson *et al.* 2010; Bailey & Hurd 2005). Low 2D:4D ratios are associated with high dominance rank in free-ranging adult female rhesus macaques (Nelson *et al*. 2010). Right hand 2D:4D ratio correlates negatively with dominance rank in captive adult female Hamadryas baboons (*Papio hamadryas*) and captive juvenile female chacma baboons (*P. ursinus*) (Howlett *et al*. 2012). In these groups, female dominance rank was found to correlate with 2D:4D ratio, such that low 2D:4D ratio females were more dominant than high 2D:4D ratio females. A females' position in the hierarchy was therefore proposed to be related to PAE on brain patterning and the subsequent expression of dominant behaviours (Howlett *et al*. 2012). The same negative correlation was observed between dominance rank, rates of contact and noncontact aggression and the 2D:4D ratio of both hands in a group of wild adult and adolescent female chacma baboons (Howlett *et al*. 2015). This negative correlation between 2D:4D ratio and female dominance rank may be universal across cercopithecine primates and could be applicable to primates in general (Howlett *et al*. 2012; Nelson *et al*. 2010).

Using Sterck *et al*. (1997)'s classifications of female social relationships, Nelson & Shultz (2010) found that female 2D:4D ratio decreased with increasing intrasexual (feeding) competition levels in 37 species of anthropoid primate. These findings are concurrent with higher PAE being of adaptive value for female primates experiencing high levels of competition (Nelson & Shultz 2010). Because the classifications of female social relationships used by Sterck *et al.* (1997) have received criticism due to inconsistencies between model predictions and observed behaviour (Klass & Cords 2015; Wickberg *et al.* 2013; Thierry 2008) and the 2D:4D ratio measurement methods used by Nelson & Shultz (2010) were not ideal in terms of accuracy or reliability (Ranson *et al*. 2013; Allaway *et al*. 2009; Kemper & Schwerdtfeger 2009; Voracek *et al*. 2007a), a re-examination of the relationship between female social structure and

PAE, preferably using quantitative measures of female dominance behaviour and more reliable 2D:4D ratio data, is desirable.

4.1.5: Sex hormones and social style in macaques

Aspects of macaque dominance relationships and conflict management patterns appear to covary with one another suggesting these may be structurally linked (Balasubramaniam *et al*. 2012; Thierry *et al.* 2008; Thierry 2007). Species with a steep dominance gradient show low conflict asymmetry, high aggression and low reconciliation with the opposite configuration being typical of species with shallow dominance gradients. Correlations between the dominance gradient, conflict asymmetry, aggression intensity and reconciliation rate may be underpinned by proximate mechanisms (Thierry 2000). Behavioural traits are comparatively amenable to evolutionary change (Blomberg *et al*. 2003) and dominant and aggressive tendencies/behaviours are mediated both pre- and postnatally by androgens and affiliative tendencies/behaviours by oestrogen, oxytocin (OT) and vasopressin (VA) (Lim & Young 2006; Bielsky & Young 2004; Razzoli *et al*. 2003; Young *et al*. 1998). Cerebrospinal fluid free OT levels are higher in the more affiliative bonnet macaque (*Macaca radiata*) than in the less affiliative pig-tailed macaque (Rosenblum *et al*. 2002) which is consistent with behavioural and social style differences in the two species. Interindividual differences in serotonin (a monoamine neurotransmitter in control of the neurohormonal stress axis) is under genetic influence and tolerant macaque species with high conciliatory tendencies (grades 3 and 4) are monomorphic for the serotonin transporter gene whereas more intolerant species (grades 1 and 2) are polymorphic for the gene (Wendland *et al*. 2006). Polymorphisms alter the transcriptional activity of the gene and subsequently the function of the corresponding proteins (Newman *et al*. 2005; Lesch 2002; Deckert *et al.* 1999; Denney *et al.* 1999) and variation in serotonergic neurotransmission has been suggested to play a role in key elements of macaque social structure, particularly interspecies variation in aggression-related behaviour (Wendland *et al.* 2006). The central nervous system function of serotonin is decreased by androgen activity and in rhesus macaques (which show the greatest allelic variation in this gene) low levels of serotonin have been associated with unrestrained aggression and a lack of submissive behaviour (Bethea *et al*. 2014; Thierry 2007; Wendland *et al*. 2006; Clark & Henderson 2003).

Behavioural differences relevant to the different social styles of macaques may be influenced by variation in PAE and POE on brain patterning during development, predisposing individuals of particular species to be more competitive or affiliative as appropriate (Coleman *et al*. 2011; Ross & Young, 2009). Therefore, PAE on brain patterning and consequently behaviour, could be a factor contributing to the variation in social behaviour seen in macaques belonging to the different social style grades. However, comparative analyses on social style and PAE in female macaques have yet to be carried out.

4.1.6: Sex hormones and patterns of intersexual dominance

It is not yet known whether PAE play a role in intersexual dominance patterns in primates. Administering androgens to captive infant female rhesus macaques had the effect of increasing their aggressive behaviour to such an extent that they replaced males in the top-ranking positions in their social group (Joslyn 1973). In the female dominant Alaotran gentle lemur (*Hapalemur alaotrensis*), females are more aggressive than males (Waeber & Hemelrijk 2003) and a study on six captive *Eulemur* species found significant differences in the behaviour of females characterised by female dominance and codominance (Petty & Drea 2015). In female dominant species, females directed more dominance and aggressive behaviour towards their male partner than they received. Codominant female lemurs, on the other hand, showed less dominance behaviour than and equal rates of aggression as their male counterparts. Species characterised by female dominance also had more masculine androgen profiles (e.g. higher concentrations of circulating testosterone and androstenedione) than females of codominant species and the authors suggest a hormonal mechanism may underlie the evolution of female dominance (Petty & Drea 2015). Therefore, in comparison to male dominated or codominant species, females belonging to species in which female dominance is the rule could be expected to be more behaviourally masculinised as selection should favour increased expression of aggressive and competitive behaviour.

4.1.7: Sex hormones and mating systems

Most studies investigating sexual competition focus on males, although reproductive competition can also be a strong selective force in females. Studies in primates have revealed associations between the development of female ornamentation and weaponry and the form of reproductive competition between females (Clutton-Brock & Huchard 2013; Clutton-Brock & Harvey 1976). Therefore, when investigating aspects of intrasexual competition between females, it is important to consider the impacts of a species' mating system, alongside ecological factors relating to social structure and dominance relationships. A study in wild female chacma baboons revealed that aggression between females was associated with access to mates (Huchard & Cowlishaw 2011). Females received aggression from other female group members at higher rates when they were reproductively active (swollen or being mate-guarded by a male). Where relationships between females were traditionally considered to be the result of competition for access to resources, this suggests that sexual competition also has some involvement in shaping female social relationships, even in large polygynandrous primate groups with classical sex roles (females are the high investing sex and males are the principal competitors) (Huchard & Cowlishaw 2011).

Aggression between females is typically less frequent and intense than between males (Clutton-Brock & Huchard 2013). However, this general pattern is often not the case for cooperatively breeding primate species, where a single dominant female is able to monopolise reproduction through either behaviourally or hormonally mediated physiological suppression of subordinate helper females (lion tamarins: Garber 1994; marmosets: French *et al.* 1997), infanticide (common marmosets: Saltzman *et al*. 2009), or eviction of potential competitors from the group (pygmy marmosets: Garber 1994). Among primates, the majority of cooperative breeders are the small bodied New World Monkeys which are typically characterised by monogamous or polyandrous mating systems. Variance in reproductive success may be higher among females than males in cooperative breeders and so competition for reproductive sovereignty is likely to be a major selective factor for monogamous and polyandrous females (Garber 1994). In support of this assumption, in many monogamous species both sexes play a role in territory and mate defence and are therefore mostly intolerant of same-sex intruders (Garber 1994). In many polyandrous species, it is typically the breeding female who is intolerant of same-sex competitors and males have a more relaxed approach to each other (French *et al*. 1997; Garber 1994; Garber *et al*. 1993). A polyandrous female has more to lose by tolerating another breeding female in her territory/group in terms of reduced paternal investment and possible mate desertion. These higher stakes for females could explain why females of polyandrous and monogamous species tend to be highly territorial and intolerant of same sex intruders (Garber 1994). Higher PAE could confer fitness benefits on these females via increasing their aggressive and competitive abilities. However, many of the behaviours characteristic of a monogamous mating system such as pair bonding, partner preference and parental care are all facilitated through the action of oestrogen and its associated neuropeptides OT and VA (French *et al*. 2018; Vargas-Pinilla *et al*. 2015; Lee *et al.* 2009; Neumann 2008).

Studies suggest there is a link between high 2D:4D ratios (low inferred PAE) and increased postnatal expression of behaviours associated with oestrogen, OT & VA (Fisher *et al.* 2010; Fink *et al.* 2007a; Williams *et al.* 2003). Therefore, selection for reduced PAE and/or increased POE may temper selection for the aggressive behaviour in monogamous and polyandrous females. Pair-bonded anthropoid primates were found to have generally higher 2D:4D ratios (indicative of lower PAE) than non-pair-bonded species (Nelson & Shultz 2010). In describing species only in terms of pair-bonded or non-pair-bonded, much of the variation in mating systems is lost and as primates display a diverse array of mating systems, distinguishing between these (and the different forms they take) is imperative for understanding how variation in female sexual competition levels may determine the strength of selection for PAE. It is likely to be the case that sexual selection brought about by variation in mating system is likely to have stronger affects in males, especially for those species with classical sex roles (Huchard & Cowlishaw 2011; Nelson & Shultz 2010). Therefore, trait variation with respect to mating system competition in females could result, in part, from correlated response. However, it is likely that PAE on intrasexual competition in both sexes are closely linked as they would confer similar benefits on both male and female competitive abilities (Nelson & Shultz 2010).

4.1.8: Summary of aims

This is the first study to investigate variation in 2D:4D ratio in both strepsirrhine and haplorhine female primates. Applying improved 2D:4D measurement methods and quantitative measures of female social structure, the primary aim of this study is to investigate the relationship between variation in PAE (inferred from 2D:4D ratios) and female intrasexual competition across the Order Primates. Specifically, I aim to:

1) Investigate the relationship between PAE and two factors which have been widely proposed as indicators of female competition levels – diet (degree of frugivory) and group size.
2) Test if a relationship exists between PAE and two quantitative measures of female social structure - DCI and rate of agonism.
3) To determine if there is an association between PAE and the social style grades of macaque species.
4) Explore the potential relationship between PAE and intersexual dominance patterns across primate taxa.
5) Examine the relationship between PAE, mating system categories and the forms of polygyny and polygynandry (mating system subcategories).

4.1.9: Hypotheses and predictions

4a) Based on assumptions regarding the effect of food contestability on female competitive relationships, I would expect females in species that depend on foods which elicit contest competition to face selection for higher PAE.

(i) Highly frugivorous species will display lower 2D:4D ratios than species with lower percentages of fruit in their diet.

4b) Direct competition increases with group size and so females in species characterised by large groups will benefit from the competitive advantages brought about by higher PAE.

(i) Species which live in larger groups will display lower 2D:4D ratios than those that live in smaller groups.

4c) Behavioural traits associated with higher PAE are favoured in females in species characterised by a high degree of despotism.

(i) DCI and 2D:4D ratio will be negatively related.

3d) Behavioural traits associated with higher PAE are advantageous for females in species with high rates of female-female agonism.

(i) There will be a negative relationship between rate of agonism and 2D:4D ratio.

4e) Behavioural differences relevant to the different social styles of macaques are underpinned by differences in PAE, with higher PAE being associated with lower degrees of tolerance.

(i) Macaque species characterised as grade 1 will have lowest 2D:4D ratios and species characterised as grade 4 will have the highest 2D:4D ratios.

4f) PAE play a vital role in the masculinisation of behavioural tendencies and higher PAE may be important for the maintenance of intersexual dominance relationships among primates, particularly female dominance.

(i) Female 2D:4D ratios will be lowest in species in which females are the dominant sex.

4g) Species in which females experience higher competition for mates are likely to benefit from higher PAE.

(i) When considering broad categories of mating system; monogamous females will have the highest 2D:4D ratios, followed by polyandrous females, with females characterised by forms of polygyny and polygynandry having the lowest 2D:4D ratios.

4.2: Methods

4.2.1: Study subjects

Data on the 2D:4D ratios of captive primates were collected between March 2016 and November 2017. Subjects were housed in 29 zoos, wildlife/safari parks and primate research centres in the UK and Europe and one sanctuary in South Africa (see Appendix 2.1). Published 2D:4D ratio data from 25 wild female chacma baboons (*Papio ursinus*) were also included (Howlett *et al.* 2015). Permission to collect data was gained from each institution as described in Chapter 2: Section 2.2.2. Animals included in the study were those of juvenile to adult age. The use of animals which are not fully mature in this study is justified as the 2D:4D ratio is fixed early in prenatal development (Galis *et al*. 2010), is relatively stable during postnatal development (Knickmeyer *et al*. 2011; Lombardo & Thorpe 2008) and does not change appreciably during puberty when there is a marked increase in circulating sex hormone levels (Králík *et al.* 2014; Manning *et al.* 2003, 2004a; Manning 2002).

4.2.2: Data collection

4.2.2.1: 2D:4D ratio measurements

I used the digital photographic and computer-assisted image analysis software method as described in Howlett *et al*. (2015) to obtain 2D:4D ratio measurements of primates. Images of primate hands were collected in two ways***.*** I obtained images using the 'free photo' method as described in Howlett *et al*. (2015) using a Panasonic FZ250 digital camera in 'burst shooting' mode in which the camera is set to take 12 frames per shot. I took 'free photos' from both the dorsal and ventral surfaces of the hands (Figures 4.2.1 a & b). Additionally, occasions when animals were being handled (e.g. for veterinary treatment) were utilised and zoo staff were requested to take photographs of the ventral surface of the animals' hands against a clear Perspex® sheet, with the subjects' palms held flat with fingers straight and fully extended (Figure 4.2.2). For each individual, three photographs per hand were identified in which digits were in the optimal positions (Figures 4.2.1a & b, 4.2.2) and for purposes of data reliability (Allaway *et al*. 2009), I carried out all measurements of 2D:4D ratios from these photographs using the software program ImageJ (Figure 4.2.2). For each individual, I measured the second and fourth digits five times per photograph, giving a total of 15 measurements for each digit and used the mean of these 15 measurements as the measurement for that digit. I calculated the 2D:4D ratio of each hand by dividing the length of the second digit by the length of the fourth digit for each individual. I calculated the mean 2D:4D ratio (M2D:4D) by averaging the right 2D:4D ratio (R2D:4D) and left 2D:4D ratio (L2D:4D). I then took the average of individual within species 2D:4D ratio measurements to obtain R2D:4D, L2D:4D and M2D:4D data for each species. These species averages are the 2D:4D ratio measures used in analyses.

In subsequent analyses, individuals for which 2D:4D ratio data were available for both hands were used**.** One exception was a female Heck's macaque (*M. hecki*) with a missing fourth digit on her right hand. As she was the only female of this species in the dataset, I included her in the macaque social style analysis for L2D:4D only. The final dataset for all other analyses comprised the R2D:4D, L2D:4D and M2D:4D of 513 individual female primates across 71 species (Table 4.2.1; Figure 4.2.3).

4.2.3.2: Anatomical considerations

Variation in primate hand morphology is associated with substrate use (the degree of arboreality versus terrestriality) (Kivell *et al*. 2016; Richmond 2007; Lemelin & Schmitt 1998; Jouffroy *et al*. 1993) and so substrate use data were collated for each species from the published literature and this variable was included as a factor in all analyses. Primates were classified as: arboreal (68-100% arboreal), arboreal/terrestrial (34-67% arboreal) or terrestrial (0-33% arboreal). Where substrate use data were not available as percentages, categorical classifications given by the authors of the publications were used (see Appendix 2.3).

In humans, it has been suggested that men have lower 2D:4D ratios because they have longer digits than women (Lolli *et al*. 2017; Kratochvíl & Flegr 2009; but see Manning 2010), implying that a link exists between 2D:4D ratio and body size. The 2D:4D ratio is fixed early in prenatal development and is generally stable throughout postnatal growth, making it unlikely that allometry has an extensive influence over its development. However, to account for possible effects of body size on 2D:4D ratio, I collected average adult female body mass (in grams) data for each species and controlled for this variable in all analyses (Appendix 4.1).

4.2.3.3: Diet and Group size

To test predictions related to frugivory, I collated data from the literature on the percentage of fruit in each species diet. Percentage of fruit in diet data describes the percentage of time spent feeding/foraging on fruit based on observational data. Nuts, seeds and seed pods are typically high value, patchily distributed and contestable in the same way as fruits and so were also included in this category. I obtained some data from sources using different but equivalent methods and calculated the percentage time spent feeding/foraging on fruit from these data e.g. where data were given as relative frequencies (Table Appendix 4.2). Equivalent methods are those based on scan sampling, where the interval between samples is short relative to the average duration of the behaviour. This method provides estimates of time spent feeding on food items (Martin & Bateson 2007), as do methods in which dietary intake is determined through the proportion of all scan samples in which a food item was recorded as being fed upon (Davies *et al*. 1999).

I obtained data on mean species group size (includes both sexes and all age classes) from the published literature. If more than one value was available for a species (e.g. representing different populations), I took the average of these as the mean group size value for the species as a whole. Where data described the size of mixed-species groups, I only included the number of individuals of the species in question. For some species which live in large multi-level groups, mean group size data describes smaller grouping levels (Appendix 4.3).

4.2.3.4: Female social variables

Data on female social structure were collated from the existing literature and focus on two quantitative variables. DCI describes the proportion of interactions in the more common direction in each dyad among females in a social group and is calculated by subtracting the number of interactions in the rarer direction from those in the more common direction, divided by the total number of interactions. DCI varies on a scale from 0 to 1 (low to high) with a DCI value of 1 meaning there is complete unidirectionality in the outcome of dominant/agonistic interactions across all dyads (van Hooff & Wensing 1987). Data on rates of agonism per hour of observation time (rate of agonism) were also obtained. This was based on data collected through continuous focal sampling of known females. If more than one value was available for a species (representing different groups/populations), I used the average of these as the DCI and rate of agonism values for the species as a whole. Data on DCI and rates of agonism were available for 13 and eight species in the 2D:4D ratio data set respectively (Appendices 4.4 & 4.5).

Figure 4.2.1: Examples of photographs taken using the 'free photo' method from (a) the ventral surface of the hand (buffy-headed capuchin monkey, *Sapajus xanthosternos*) and (b) the dorsal surface of the hand (guinea baboon, *Papio papio*).

Figure 4.2.2: Example of computer-assisted measurement of hands using ImageJ software. Yellow lines indicate the path of measurement for each digit from the basal crease to the tip of the extended digit. The images above present a Perspex® photograph of the left hand of an anaesthetised male coppery titi monkey (*Callicebus cupreus*).

Table 4.2.1: Dataset with female right (R2D:4D), left (L2D:4D) and mean (M2D:4D) 2D:4D with standard deviation (SD) for each species, substrate use (sub use), average female body mass (grams), mean percentage (%) of fruit in diet, mean group size, female rate of agonism (per hour of observation time), female dominance consistency index (DCI) and intersexual dominance patterns. All data based on wild animals unless otherwise stated. See Appendices 2.3 and 4.1-4.6 for the sources of these data.

Species[a]	***n***[b]	**R2D:4D**	**SD**	**L2D:4D**	**SD**	**M2D:4D**	**SD**	**Sub use**[c]	**Body mass (g)**	**% fruit**[d,e]	**Group size**[f]	**Rate of agonism**	**DCI**	**Intersexual dominance**[g]
Eulemur collaris	3	0.722	0.025	0.727	0.020	0.721	0.022	A	2375	78.05	5.0	xxx	xxx	CO
Eulemur coronatus	3	0.708	0.031	0.752	0.024	0.730	0.025	A	1080	70	7.0	xxx	xxx	F
Eulemur flavifrons	1	0.742	0.000	0.730	0.000	0.736	0.000	A	2510	79	8.0	xxx	xxx	F
Eulemur macaco	1	0.693	0.000	0.721	0.000	0.707	0.000	A	2430	73.5	10.0	xxx	xxx	F
Eulemur mongoz	1	0.781	0.000	0.799	0.000	0.790	0.000	A	1560	65	5.5	xxx	xxx	F
Eulemur rubriventer	1	0.811	0.000	0.824	0.000	0.818	0.000	A	1940	80.6	3.0	xxx	xxx	F
Hapalemur alaotrensis	4	0.700	0.036	0.676	0.028	0.688	0.015	A	1600	0	6.0	xxx	xxx	F
Lemur catta	8	0.771	0.025	0.775	0.038	0.773	0.030	A/T	2207	62	14.4	xxx	xxx	F
Prolemur simus	2	0.580	0.006	0.632	0.006	0.606	0.000	A	1300	0.5	8.0	xxx	xxx	M
Varecia rubra	3	0.799	0.043	0.839	0.024	0.819	0.018	A	3520	61	14.3	xxx	xxx	F
Varecia variegata variegata	6	0.828	0.036	0.835	0.049	0.831	0.028	A	3520	67.3	8.0	0.160	*X*	F
Propithecus coronatus	1	0.656	0.000	0.606	0.000	0.631	0.000	A	3738	7.5	5.0	xxx	xxx	F
Microcebus murinus	4	0.728	0.022	0.742	0.022	0.735	0.015	A	62.83	31.33	8.0	xxx	xxx	F
Galago moholi	2	0.598	0.014	0.627	0.006	0.614	0.003	A	173	xxx	4.0	xxx	xxx	M
Alouatta caraya	3	0.873	0.039	0.894	0.011	0.883	0.020	A	4330	19.0	10.1	xxx	xxx	M
Ateles fusciceps rufiventris	12	0.904	0.040	0.883	0.026	0.894	0.021	A	9163	xxx	25.0	xxx	xxx	M
Ateles paniscus	2	0.855	0.036	0.865	0.033	0.860	0.034	A	8440	82.9	15.0	xxx	xxx	M
Callicebus cupreus	2	0.886	0.057	0.892	0.037	0.889	0.047	A	1120	90.35	3.4	xxx	xxx	CO
Pithecia pithecia	6	0.762	0.035	0.784	0.019	0.773	0.016	A	1589	86.35	4.6	xxx	xxx	M
Cebus capucinus	1	0.872	0.000	0.930	0.000	0.901	0.000	A	2540	60	16.4	1.107	*X*	M
Sapajus apella	11	0.938	0.044	0.962	0.056	0.950	0.031	A	2520	17.6	15.5	xxx	*X*	M
Sapajus xanthosternos	7	0.915	0.028	0.903	0.027	0.909	0.014	A	2167	42.7	30.0	xxx	xxx	M

Table 4.2.1 *continued.*

Species[a]	***n***[b]	**R2D:4D**	**SD**	**L2D:4D**	**SD**	**M2D:4D**	**SD**	**Sub use**[c]	**Body mass (g)**	**% fruit**[d,e]	**Group size**[f]	**Rate of agonism**	**DCI**	**Intersexual dominance**[g]
Saimiri boliviensis	16	0.889	0.038	0.885	0.044	0.887	0.036	A	700	93	54.0	xxx	xxx	F
Saimiri sciureus	27	0.915	0.032	0.918	0.039	0.916	0.026	A	675	67.9	23.0	xxx	xxx	F
Callimico goeldii	5	0.888	0.018	0.885	0.017	0.887	0.002	A	468**	29	8.0	xxx	xxx	CO
Callithrix geoffroyi	1	0.964	0.000	0.958	0.000	0.961	0.000	A	190	15	5.0	xxx	xxx	CO
Cebuella pygmaea	4	0.938	0.021	0.939	0.035	0.938	0.028	A	122	0	5.5	xxx	xxx	CO
Leontopithecus chrysomelas	7	0.962	0.015	0.967	0.008	0.965	0.010	A	535	35.1	6.5	xxx	xxx	CO
Leontopithecus rosalia	3	0.946	0.042	0.946	0.024	0.946	0.021	A	598	77	6.5	xxx	xxx	CO
Mico argentatus	3	0.865	0.036	0.853	0.015	0.859	0.010	A	360	36	8.0	xxx	xxx	CO
Mico melanurus	1	0.835	0.000	0.831	0.000	0.833	0.000	A	390	xxx	6.2	xxx	xxx	CO
Saguinus bicolor	1	0.978	0.000	0.965	0.000	0.972	0.000	A	430	39	4.8	xxx	xxx	CO
Saguinus imperator	10	0.941	0.046	0.952	0.036	0.947	0.038	A	475	xxx	5.6	xxx	xxx	CO
Sanuinus oedipus	2	1.003	0.009	0.993	0.030	0.998	0.019	A	404	38	6.0	xxx	xxx	CO
Allenopithecus nigroviridis	2	0.897	0.068	0.824	0.009	0.861	0.029	A/T	3180	xxx	22.0	xxx	xxx	M
Cercocebus chrysogaster	4	0.873	0.005	0.862	0.018	0.868	0.011	A/T	7000	xxx	15.0	xxx	xxx	M
Cercocebus lunulatus	8	0.872	0.025	0.845	0.022	0.858	0.017	A/T	5300	xxx	30.5	xxx	xxx	M
Cercocebus torquatus	3	0.872	0.034	0.872	0.020	0.872	0.024	A/T	5500	80	27.2	xxx	xxx	M
Cercopithecus diana	8	0.864	0.058	0.882	0.040	0.873	0.036	A	3900	59.7	23.9	xxx	xxx	M
Cercopithecus lhoesti	6	0.866	0.052	0.855	0.054	0.861	0.023	A/T	3450	xxx	23.5	xxx	xxx	M
Cercopithecus lowei	1	0.813	0.000	0.847	0.000	0.830	0.000	A/T	3000	xxx	10.0	xxx	xxx	M
Cercopithecus neglectus	5	0.826	0.028	0.844	0.038	0.835	0.029	A/T	4130	xxx	7.8	xxx	xxx	M
Cercopithecus petaurista	1	0.807	0.000	0.794	0.000	0.800	0.000	A	2900	55.5	10.7	xxx	xxx	M
Cercopithecus pogonias	1	0.804	0.000	0.847	0.000	0.825	0.000	A	2900	xxx	18.0	xxx	xxx	M
Chlorocebus pygerythrus	2	0.838	0.004	0.823	0.014	0.830	0.005	A/T	2980	19.6	21.0	xxx	*X*	M
Colobus guereza	2	0.808	0.022	0.766	0.048	0.787	0.035	A	9200	20.8	9.0	xxx	xxx	M
Colobus polykomos	1	0.864	0.000	0.726	0.000	0.795	0.000	A	8300	36.0	13.6	0.600	0.746	M

Table 4.2.1 *continued.*

Species[a]	***n***[b]	**R2D:4D**	**SD**	**L2D:4D**	**SD**	**M2D:4D**	**SD**	**Sub use**[c]	**Body mass (g)**	**% fruit**[d,e]	**Group size**[f]	**Rate of agonism**	**DCI**	**Intersexual dominance**[g]
Macaca fascicularis	24	0.813	0.040	0.827	0.042	0.820	0.036	A/T	3590	76.85	27.7	1.520	1.000	M
Macaca fuscata	11	0.815	0.027	0.851	0.036	0.833	0.019	A/T	8030	51.4	45.5	1.020	*X*	M
Macaca hecki	1	xxx	xxx	0.858	0.000	xxx	xxx	A/T	6800**	xxx	15	xxx	xxx	M
Macaca mulatta	80	0.804	0.055	0.831	0.053	0.817	0.044	A/T	5370	8.5	40.8	xxx	xxx	M
Macaca nemestrina	3	0.805	0.033	0.859	0.033	0.832	0.013	A/T	6500	74.2	18.3	xxx	xxx	M
Macaca nigra	18	0.847	0.038	0.850	0.030	0.848	0.026	A/T	5470	65.4	50.0	*X*	*X*	M
Macaca silenus	19	0.822	0.029	0.842	0.034	0.832	0.022	A	6100	78.1	21.0	xxx	xxx	M
Macaca sylvanus	11	0.821	0.031	0.832	0.037	0.826	0.029	T	5500	32.0	18.3	xxx	*X*	M
Mandrillus leucophaeus	6	0.830	0.023	0.803	0.024	0.817	0.008	A/T	12500	58	58.0	xxx	xxx	M
Mandrillus sphinx	16	0.856	0.049	0.855	0.047	0.851	0.042	A/T	12500	81	52.0	xxx	xxx	M
Papio hamadryas	20	0.863	0.046	0.840	0.060	0.851	0.042	T	9900	54.1	77.4[1]	xxx	xxx	M
Papio papio	17	0.865	0.032	0.862	0.030	0.864	0.023	T	12100	77	62.0[2]	xxx	xxx	M
Papio ursinus	32	0.885	0.037	0.885	0.039	0.885	0.035	T	14800	43.3	48.7	1.558	*X*	M
Theropithecus gelada	7	0.816	0.058	0.838	0.050	0.827	0.047	T	11700	3.5	113.0[1]	xxx	*X*	M
Trachypithecus auratus	5	0.774	0.021	0.762	0.043	0.768	0.030	A	5841	32	14.0	xxx	xxx	M
Trachypithecus obscurus	6	0.769	0.029	0.775	0.019	0.772	0.010	A	6260	35	17.0	xxx	xxx	M
Hylobates agilis	1	1.127	0.000	1.100	0.000	1.113	0.000	A	5820	58	4.4	xxx	xxx	CO
Hylobates lar	1	1.059	0.000	1.096	0.000	1.078	0.000	A	5340	62.7	4.0	xxx	xxx	CO
Hylobates muelleri	1	1.004	0.000	1.013	0.000	1.008	0.000	A	5350	62	3.4	xxx	xxx	CO
Hylobates pileatus	1	1.077	0.000	1.017	0.000	1.047	0.000	A	5440	71	4.1	xxx	xxx	CO
Nomascus leucogenys	2	0.994	0.053	1.021	0.050	1.008	0.001	A	7320	xxx	3.6	xxx	xxx	CO
Symphalangus syndactylus	4	1.071	0.110	1.050	0.058	1.060	0.081	A	10700	46.7	4.0	xxx	xxx	CO
Gorilla gorilla gorilla	4	0.914	0.023	0.911	0.025	0.913	0.023	A/T	71500	48	10.0	xxx	xxx	M
Pan paniscus	2	0.886	0.033	0.932	0.009	0.909	0.012	A/T	33200	55	9.5[3]	xxx	*X*	F
Pan troglodytes	14	0.887	0.038	0.921	0.036	0.904	0.027	A/T	45800	62.5	8.3[3]	0.150	*X*	M

[a] Taxonomy from Groves 2001 with some exceptions (see Appendix 2.3).

[b] Number of individuals.

[c] Substrate use: A = arboreal, A/T = arboreal/terrestrial, T = terrestrial.

[d] Includes fruit, nuts, seeds and seed pods.

[e] Data presented as percentage of time spent feeding on food items or calculated from equivalent methods (see Methods section 4.2.3.3: Diet and Group size).

[f] Includes all animals of the same species in a group e.g. both sexes and all age-sex classes.

[g] Intersexual dominance: M = Males are dominant, F = Females are dominant, CO = Sexes are codominant/there is no clear dominance relationship between the sexes.

[1] Group size here refers to average band size.

[2] Group size here refers to average 3rd level grouping size (analogous to bands).

[3] Group size here refers to average party size.

X Data are from Koenig *et al*. in prep and are withheld at the request of the providing author.

**Data from captive animals.

[xxx] Data not available.

4.2.3.5: Macaque social style

I obtained data on macaque social style grades from Thierry (2000) and included two species from each grade (Table 4.2.2). A species' position on the four-grade scale is determined by their conflict management patterns and other behavioural traits e.g. patterns of nepotism, aggression intensity and asymmetry, steepness of dominance hierarchies and reconciliation tendency.

Table 4.2.2: Four-grade scale of macaque social style and the species used in this analysis.

Social style grade	**1**	**2**	**3**	**4**
Species	*M. mulatta* *M. fuscata*	*M. fascicularis* *M. nemestrina*	*M. sylvanus* *M. silenus*	*M. nigra* *M. hecki*

4.2.3.6: Intersexual dominance patterns

I obtained data on intersexual dominance patterns for all 71 species in the dataset from the published literature (see Appendix 4.6 for a comprehensive list of sources). Species were categorised as either female dominant, male dominant or codominant. Female dominant species are those in which females are consistently able to dominate and/or receive submissive signals from their male counterparts without reversals in these roles. Male dominant describes species which display the opposite condition. Codominant describes those species in which there is no clear dominance pattern between the sexes or where an alpha male and female pair are codominant over other group members of both sexes.

4.2.3.7: Mating system variables

I collated data from various sources on mating system and mating system subcategory for each species. Categories for mating system were: monogamy, polyandry, polygyny and polygynandry. Polygynous and polygynandrous mating systems were then broken down into further subcategories depending on the form in which these systems present in each species (Table 4.2.3). Mating system subcategory data were not available for one species (*C. torquatus*) and so data on mating system and mating system subcategory were available for 71 and 70 species in the 2D:4D ratio data set, respectively (see Appendix 2.5).

As primate mating systems and group size are linked, such that monogamous species often live in smaller groups while the largest groups tend to be associated with polygynandry, I also controlled for group size in the mating system analyses to ensure that any relationships between mating variables and 2D:4D ratios are not a consequence of group size effects.

Table 4.2.3: Forms (subcategories) of polygyny and polygynandry with brief descriptions and the mating patterns of males and females.

Subcategory	Description	Mating pattern
Spatial polygyny	A single agonistically powerful male defends access to a number of females within his range.	Males mate with several females. Females mate with one male.
Harem polygyny	A single male defends exclusive mating access to a group of females.	Males mate with several females. Females mate with one male.
Cooperative defence polygynandry	A group of males cooperatively defend territory/mating access to a group of females.	Males and females mate with multiple partners.
Scramble competition polygynandry	Roving males seek out and mate with females before moving on in search of more mates.	Males and females mate with multiple partners.
Contest competition polygynandry	Species live in permanent mixed-sex groups, males actively compete for access to receptive females, male monopolisation of females is usually not possible.	Males and females mate with multiple partners.

4.2.4: Statistical methods

4.2.4.1 Normality & multicollinearity

I conducted all non-phylogenetically controlled analyses using IBM SPSS Statistical software version 24 and used Shapiro-Wilk tests throughout when assessing normality of the data. Data for female R2D:4D, L2D:4D and M2D:4D were normally distributed, as were percentage fruit in diet and rate of agonism. Female body mass and group size were not normally distributed and so these variables were log-transformed. DCI data were also not normally distributed and so were arcsine transformed. Intersexual dominance, macaque social style, mating system, mating system subcategory and substrate use are categorical variables.

I tested for multicollinearity of the predictor variables in each analysis using the variance inflation factor (VIF). Variance inflation factors (VIF) of between 1 and 1.344 were obtained indicating there is no evidence for multicollinearity among the independent variables.

4.2.4.2: 2D:4D ratio measurement reliability

I used the intraclass correlation coefficient (ICC) set to the 'absolute agreement' definition to test intra-observer reliability. ICC values showed that 2D:4D ratio measurements were highly repeatable for both hands across all species in the dataset and within primate families (Appendix 2.9).

I investigated differences in female R2D:4D and L2D:4D using a paired *t*-test (two-tailed). R2D:4D and L2D:4D in females were not significantly different (t_{70} = -0.754, P = 0.435) and were tightly correlated (Pearson correlation: *r* = 0.954, df = 71, P = <0.001), therefore M2D:4D was also used in subsequent analyses.

4.2.4.3: Phylogenetic signal

I tested for phylogenetic signal in my variables using Pagel' λ and the packages Devtools and Models of Trait Macroevolution on Trees (motmot) in the statistical software program 'R' version 3.4.1 "Single candle" and *10kTrees* (version 3) phylogeny with associated taxonomy from GenBank for the phylogenetic trees (Arnold *et al*. 2010). I found statistically significant Pagel's λ values for all variables other than percentage of fruit in diet, DCI and rate of agonism (Appendix 4.7). Since 2D:4D ratio measures all had significant amounts of phylogenetic signal, the use of phylogenetically controlled methods is justified, and the results reported throughout are those of phylogenetically controlled analysis.

4.2.4.4: Phylogenetically controlled analysis

The 2D:4D ratio is brought about by PAE, which are in turn modulated by the social and ecological environment. Therefore, in all analyses, I assigned 2D:4D ratio measures as the dependent variables and all other variables as the independents. To test for relationships between female 2D:4D ratios and the variables of interest (substrate use, female body mass, percentage of fruit in diet, group size, DCI, rate of agonism, intersexual dominance pattern, mating system and mating system subcategory), I carried out Phylogenetic Generalized Least Squares (PGLS) analysis using the package Comparative Analysis of Phylogenetics and Evolution in R (caper). I ran the analysis across a block of 200 phylogenetic trees for each variable and used the software FigTree (version 1.4.3) to illustrate phylogenetic trees.

Molecular data were not available for five species in *10KTrees* phylogeny (*Callicebus cupreus, Mico melanurus, Cercocebus chrysogaster, Cercocebus lunulatus* and *Propithecus coronatus*) and so, using the R package Analysis of Phylogenetics and Evolution (ape), I added these species into the trees based on their relationships to sister taxa which were present in *10Ktrees* phylogeny. *Callicebus moloch* and *Callicebus cupreus* are sister species which diverged approximately 3.65 mya (Byrne *et al.* 2016; Perelman *et al.* 2011). *Mico melanurus* is in the *Mico* subgenus and I treated it as monophyletic with other *Mico* species and included it using information on phylogeny from Garbino (2015). I incorporated *Cercocebus chrysogaster* using *Cercocebus torquatus* which it diverged from ~ 3.33 mya. I integrated *Cercocebus lunulatus* using its sister species, the Sooty mangabey (*C. torquatus atys*). *C. lunulatus* was widely considered a subspecies of *C. t. atys* (Groves 2001) until recent taxonomic reassessment elevated it to species level (Oates *et al*. 2016; Mittermeir *et al.* 2013). Genetic data suggests that *P. coronatus* and *P. deckenii* are in fact the same subspecies and so I substituted *P. deckenii* for *P. coronatus* in the phylogeny (Pastorini *et al*. 2001; Tattersall 1988 but see Thalmann *et al.* 2002). I then pruned species which were used to incorporate missing taxa but were not relevant to subsequent analyses (no 2D:4D ratio data) from the final trees prior to analysis.

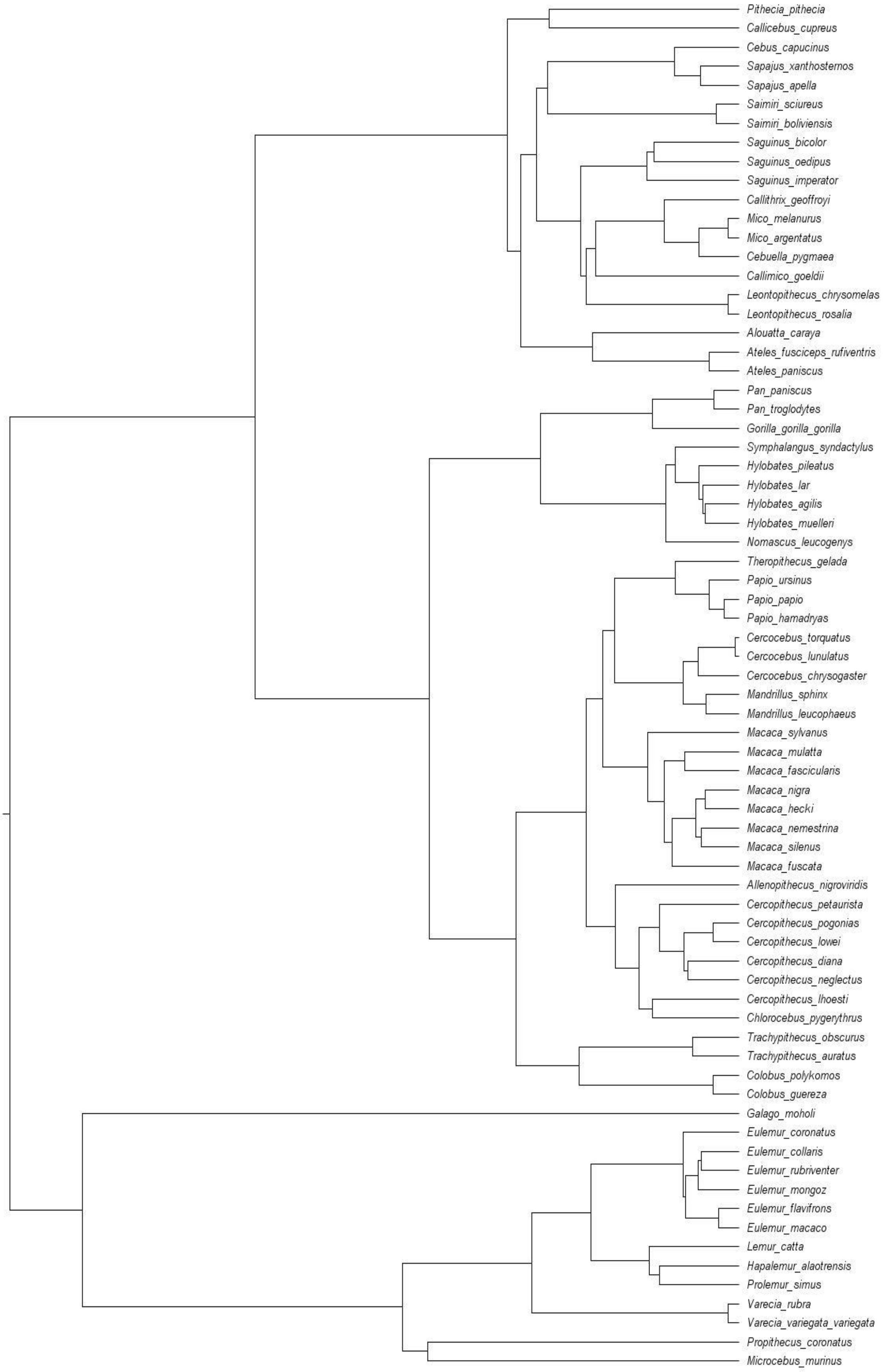

Figure 4.2.3: Phylogenetic tree with all 72 primate species represented.

4.3: Results

4.3.1: Anatomical considerations

There were no significant relationships between substrate use and any of the 2D:4D ratio measures. There were no significant relationships between female body mass and any of the 2D:4D ratio measures (Table 4.3.1). However, due to the variation in hand morphology and allometry that exists between species, female body mass and substrate use were included as factors in all analyses.

Table 4.3.1: Results of the PGLS regression testing for an effect of substrate use and female body mass on female 2D:4D ratio.

Variables	***t***	***p***	**Estimate**	**± s.e**	**df**	**λ**	**Adj.r^2**
Female R2D:4D & Substrate use	0.477	0.635	0.395	0.834	66	0.993	-0.011
Female L2D:4D & Substrate use	0.709	0.481	0.580	0.817	66	0.963	-0.007
Female M2D:4D & Substrate use	0.638	0.526	0.533	0.834	66	0.963	-0.009
Female R2D:4D & Female body mass	-0.117	0.894	-0.169	1.442	66	1.000	-0.016
Female L2D:4D & Female body mass	-0.481	0.630	-0.744	1.536	66	1.000	-0.013
Female M2D:4D & Female body mass	-0.321	0.742	-0.505	1.561	66	1.000	-0.015

4.3.2: Other control variables

Both mating variables were significantly related to group size (Table 4.3.2) and so group size was also included as an additional factor in analysis on mating sytems.

Table 4.3.2: Results of the PGLS regression testing for an effect of group size on mating system and mating system subcategory (subcat.) in female primates while controlling for substrate use and female body mass. Model variables are indicated in bold with the control variables taken into account, parameters for individual control variables are displayed below these. Significant results are indicated in bold.

Variables	***t***	***p***	**Estimate**	**± s.e**	**df**	**λ**	**Adj.r^2**
Mating system & Group size	**3.050**	**0.003**	**0.198**	**0.065**	**66**	**0.880**	**0.164**
Substrate use	1.301	0.198	0.207	0.158			
Body mass	1.366	0.176	0.109	0.081			
Mating system subcat. & Group size	**3.936**	**<0.001**	**0.131**	**0.033**	**66**	**0.808**	**0.249**
Substrate use	1.709	0.093	0.261	0.152			
Body mass	0.571	0.570	0.044	0.077			

4.3.3: Diet and Group size

There were no significant associations between the percentage fruit in diet or group size and any of the 2D:4D ratio measures (Table 4.3.3).

Table 4.3.3: Results of the PGLS regression testing for an effect of percentage (%) of fruit in diet and average group size on female 2D:4D ratio while controlling for substrate use and female body mass. Model variables are indicated in bold with the control variables taken into account, parameters for individual control variables are displayed below these.

Variables	*t*	*p*	Estimate	± s.e	df	λ	Adj.r^2
Female R2D:4D & % fruit in diet	1.402	0.166	75.591	53.744	55	0.813	0.004
Substrate use	-0.958	0.342	-8.107	8.440			
Body mass	0.934	0.354	2.812	4.089			
Female L2D:4D & % fruit in diet	1.665	0.102	87.695	52.891	55	0.752	0.018
Substrate use	-1.037	0.304	-8.568	8.238			
Body mass	1.048	0.299	4.113	3.934			
Female M2D:4D & % fruit in diet	1.548	0.127	85.394	54.986	55	0.786	0.012
Substrate use	-1.000	0.322	-8.362	8.343			
Body mass	0.996	0.323	3.991	4.013			
Female R2D:4D & Group size	-0.375	0.709	-0.422	1.125	67	0.952	0.014
Substrate use	0.987	0.328	0.183	0.185			
Body mass	1.474	0.145	0.135	0.092			
Female L2D:4D & Group size	-0.677	0.501	-0.806	1.189	67	0.957	0.016
Substrate use	0.975	0.335	0.181	0.185			
Body mass	1.434	0.157	0.132	0.092			
Female M2D:4D & Group size	-0.550	0.584	-0.666	1.215	67	0.954	0.015
Substrate use	0.993	0.325	0.185	0.185			
Body mass	1.458	0.150	0.134	0.092			

4.3.4: Female social variables

There were no significant associations between either DCI (Figure 4.3.1) or rate of agonism and any of the 2D:4D ratio measures (Table 4.3.4).

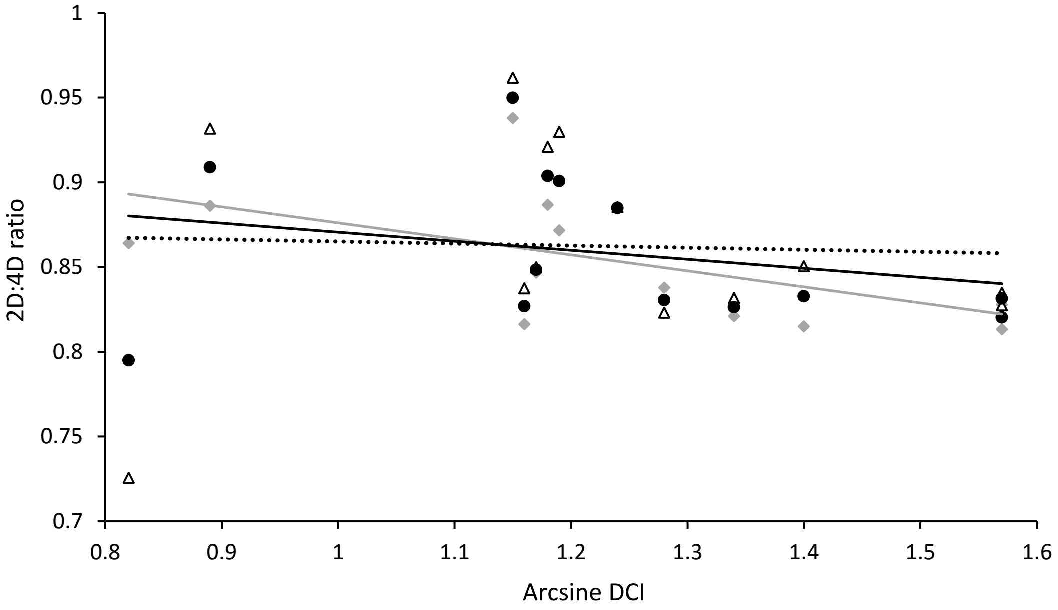

Figure 4.3.1: Association between arcsine DCI and female 2D:4D ratio measures. R2D:4D (grey diamonds, grey solid trendline), L2D:4D (white triangles, black dotted trendline), M2D:4D (black circles, black solid trendline).

Table 4.3.4: Results of the PGLS regression testing for an effect of female DCI and rate of agonism on female 2D:4D ratio while controlling for substrate use and female body mass. Model variables are indicated in bold with the control variables taken into account, parameters for individual control variables are displayed below these. Significant results are indicated in bold.

Variables	*t*	*p*	Estimate	± s.e	df	λ	Adj.r^2
Female R2:D4D & DCI	-1.699	0.130	-2.896	1.700	9	0.078	0.238
Substrate use	0.113	0.912	0.012	0.104			
Body mass	-1.184	0.266	-0.082	0.068			
Female L2D:4D & DCI	0.361	0.729	0.423	1.162	9	0.634	0.074
Substrate use	0.820	0.433	0.096	0.120			
Body mass	-1.398	0.197	-0.115	0.084			
Female M2D:4D & DCI	-0.271	0.776	-0.431	1.600	9	0.540	-0.056
Substrate use	0.896	0.396	0.101	0.114			
Body mass	-1.336	0.216	-0.109	0.081			
Female R2D:4D & Rate of agonism	1.132	0.320	6.773	5.980	4	0.000	0.544
Substrate use	3.161	**0.034**	0.774	0.244			
Body mass	-2.680	0.055	-0.520	0.194			
Female L2D:4D & Rate of agonism	0.006	0.952	0.016	2.658	4	0.491	0.399
Substrate use	2.340	0.081	0.689	0.284			
Body mass	-2.370	0.078	-0.419	0.177			
Female M2D:4D & Rate of agonism	0.224	0.835	0.930	4.177	4	0.217	0.450
Substrate use	2.593	0.061	0.675	0.265			
Body mass	-2.349	0.079	-0.417	0.174			

4.3.5: Macaque social style

I found a significant positive relationship between R2D:4D and social style in female macaques (Figure 4.3.2). Females in species belonging to grade 4 had higher R2D:4D than females in other grades. However, the trend between social style and L2D:4D and M2D:4D in female macaques was nonsignificant (Table 4.3.5).

Table 4.3.5: Results of the PGLS regression testing for an effect of social style on female 2D:4D ratio while controlling for substrate use and female body mass. Model variables are indicated in bold with the control variables taken into account, parameters for individual control variables are displayed below these. Significant results are indicated in bold.

Variables	t	p	Estimate	± s.e	df	λ	Adj.r^2
Female R2D:4D & Macaque social style	**3.109**	**0.049**	**55.476**	**18.582**	**3**	**0.900**	**0.628**
Substrate use	0.228	0.835	0.115	0.541			
Body mass	-1.201	0.319	<-0.000	<0.000			
Female L2D:4D & Macaque social style	2.369	0.099	121.791	51.408	4	0.998	0.292
Substrate use	0.642	0.555	0.556	0.864			
Body mass	-1.199	0.296	<-0.000	<0.000			
Female M2D:4D & Macaque social style	2.726	0.072	99.751	36.607	3	0.731	0.485
Substrate use	0.854	0.456	0.448	0.524			
Body mass	-1.951	0.146	<-0.000	<0.000			

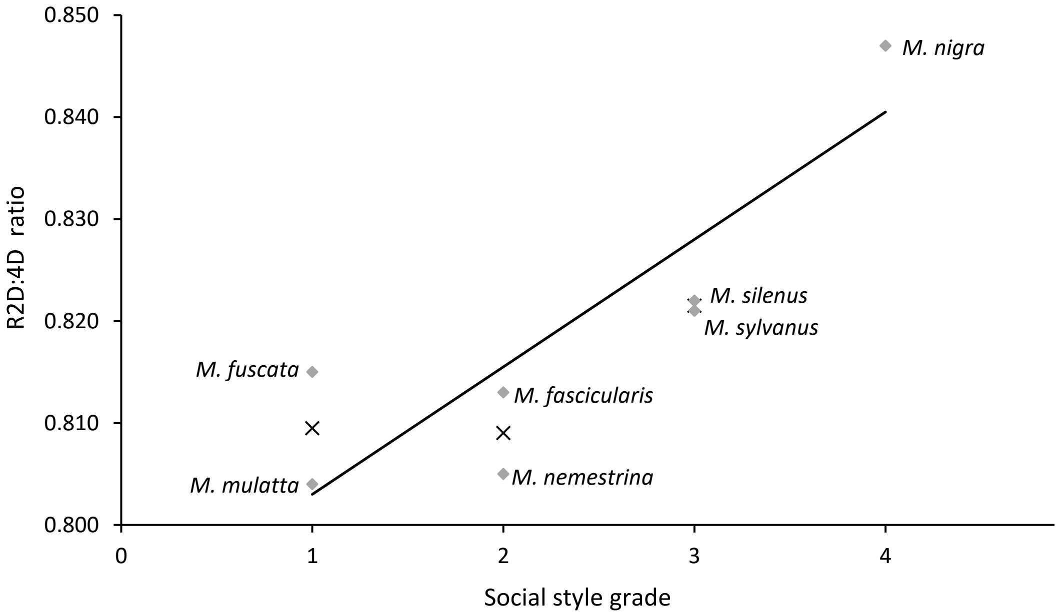

Figure 4.3.2: Relationship between social style grade and female R2D:4D (grey diamonds) in each macaque species. Black crosses denote average R2D:4D for species within each grade.

4.3.6: Intersexual dominance relationships

There were significant relationships between all 2D:4D ratio measures and intersexual dominance pattern (Table 4.3.6). Species in which females are the dominant sex had consistently lower female R2D:4D, L2D:4D and M2D:4D, followed by females in male dominated species with females in codominant species having the highest 2D:4D ratios (Figure 4.3.3).

Table 4.3.6: Results of the PGLS regression testing for an effect of intersexual dominance relationships (intersexual dom.) on female 2D:4D ratio while controlling for substrate use and female body mass. Model variables are indicated in bold with the control variables taken into account, parameters for individual control variables are displayed below these. Significant results are indicated in bold.

Variables	*t*	*p*	Estimate	± s.e	df	λ	Adj.r^2
Female R2D:4D & Intersexual dom.	**3.106**	**0.003**	**3.217**	**1.036**	**67**	**0.974**	**0.112**
Substrate use	0.177	0.860	0.024	0.132			
Body mass	0.020	0.862	0.002	0.078			
Female L2D:4D & Intersexual dom.	**2.619**	**0.011**	**2.919**	**1.115**	**67**	**0.977**	**0.078**
Substrate use	0.163	0.871	0.022	0.133			
Body mass	-0.001	0.892	<0.000	<0.000			
Female M2D:4D & Intersexual dom.	**3.025**	**0.004**	**3.388**	**1.120**	**67**	**0.979**	**0.106**
Substrate use	0.153	0.878	0.021	0.132			
Body mass	0.029	0.883	0.002	0.078			

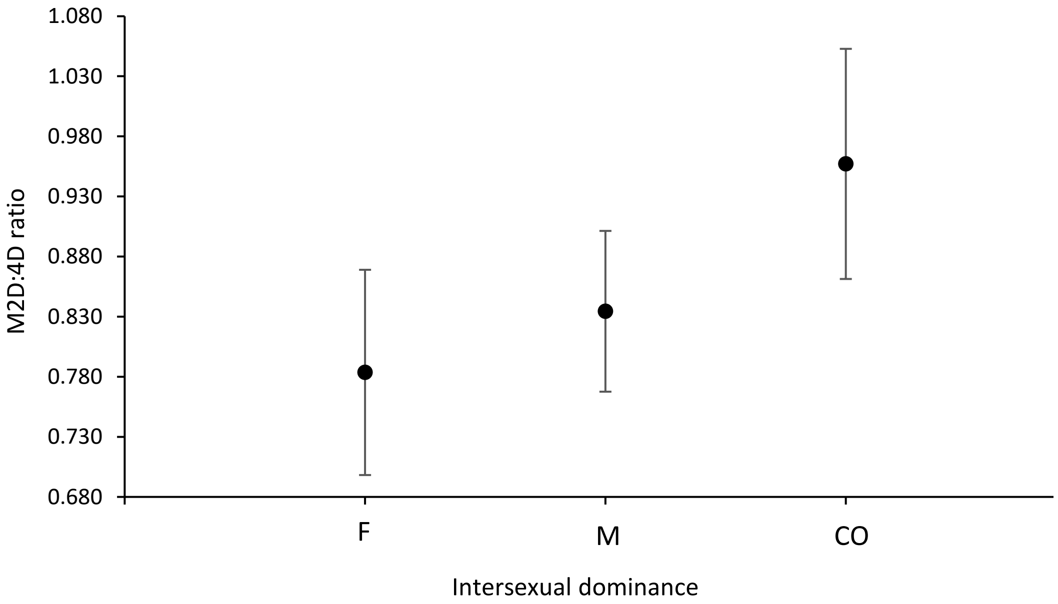

Figure 4.3.3: Association between intersexual dominance patterns and female M2D:4D (mean ± standard deviation). F = Female dominant, M = Male dominant, CO = Sexes are codominant.

4.3.7: Mating system variables

There were significant associations between mating system and female R2D:4D and M2D:4D but not L2D:4D (Table 4.3.7). Species characterised by polygyny had the lowest 2D:4D ratios, followed by polygynandrous species, then polyandrous species, and finally monogamous species which had the highest 2D:4D ratios (Figure 4.3.4). There were also significant associations between mating system subcategory and female R2D:4D and M2D:4D but not L2D:4D (Table 4.3.7). Monogamous females had the highest 2D:4D ratios, followed by those characterised by cooperative defence polygynandry, polyandry, contest competition polygynandry, harem polygyny and finally scramble competition polygynandry (Figure 4.3.5). There were no examples of species characterised by spatial polygyny in this dataset.

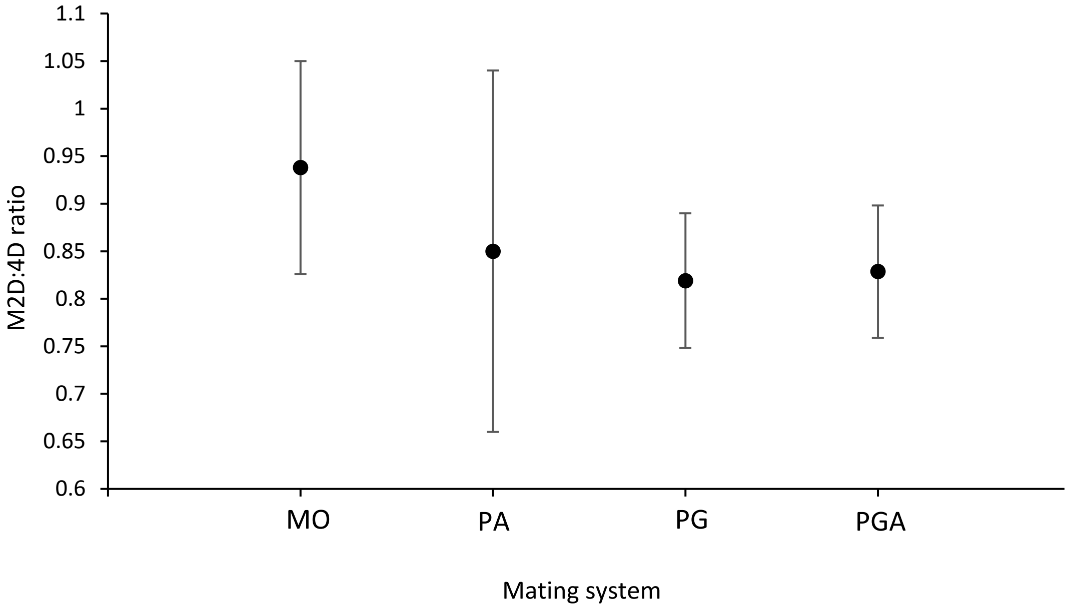

Figure 4.3.4: Relationship between female M2D:4D (mean ± standard deviation) and species mating system. MO = Monogamy, PA = Polyandry, PG = Polygyny and PGA = Polygynandry.

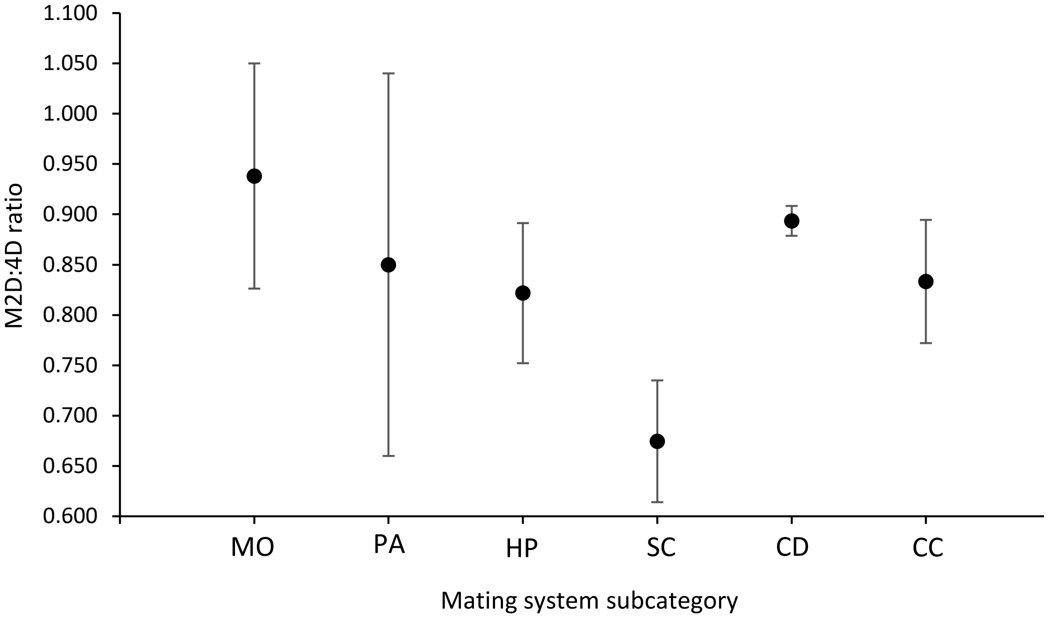

Figure 4.3.5: Relationship between female M2D:4D ratio (mean ± standard deviation) and mating system subcategory (MO = monogamy, PA = polyandry, HP = harem polygyny, SC = scramble competition polygynandry CD = cooperative defence polygynandry, CC = contest competition polygynandry.

Table 4.3.7: Results of the PGLS regression testing for an effect of mating system variables on female 2D:4D ratio while controlling for substrate use, female body mass and average group size. Model variables are indicated in bold with the control variables taken into account, parameters for individual control variables are displayed below these. Significant results are indicated in bold.

Variables	***t***	***p***	**Estimate**	**± s.e**	**df**	**λ**	**Adj.r^2**
Female R2D:4D & Mating system	**-2.650**	**0.010**	**-4.773**	**1.794**	**66**	**1.000**	**0.143**
Substrate use	1.118	0.268	0.296	0.265			
Body mass	0.286	0.775	0.045	0.155			
Group size	**2.423**	**0.018**	**0.460**	**0.192**			
Female L2D:4D & Mating system	-1.836	0.072	-3.610	1.972	66	1.000	0.098
Substrate use	1.108	0.272	0.302	0.272			
Body mass	0.218	0.824	0.035	0.161			
Groups size	**2.278**	**0.026**	**0.445**	**0.195**			
Female M2D:4D & Mating system	**-2.436**	**0.018**	**-4.810**	**1.977**	**66**	**1.000**	**0.130**
Substrate use	1.153	0.253	0.308	0.272			
Body mass	0.236	0.811	0.037	0.157			
Group size	**2.327**	**0.023**	**0.446**	**0.193**			
Female R2D:4D & Mating system subcategory	**-2.970**	**0.006**	**-8.328**	**3.305**	**65**	**0.687**	**0.363**
Substrate use	1.019	0.742	0.040	0.484			
Body mass	2.447	**0.033**	0.534	0.227			
Group size	4.313	**<0.001**	1.448	0.343			
Female L2D:4D & Mating system subcategory	-1.898	0.062	-6.148	3.182	65	0.789	0.284
Substrate use	0.315	0.759	0.160	0.510			
Body mass	2.005	0.054	0.484	0.243			
Group size	3.887	**<0.001**	1.399	0.360			
Female M2D:4D & Mating system subcategory	**-2.458**	**0.017**	**-7.911**	**3.190**	**65**	**0.777**	**0.314**
Substrate use	0.289	0.780	0.144	0.496			
Body mass	2.129	**0.042**	0.501	0.236			
Group size	3.968	**<0.001**	1.399	0.351			

4.4: Discussion

The support for variation in primate socioecology being underpinned by variation in PAE was mixed. Predictions regarding the relationship between PAE and macaque social style grade, patterns of intersexual dominance and female reproductive competition were all met. However, I did not find the expected relationships between PAE and degree of frugivory, group size or the two quantitative measures of female dominance behaviour. This study demonstrates that PAE may act as a proximate mechanism underlying variation in certain aspects of social behaviour in female non-human primates but may not be associated with the (potential) effects of diet and group size on social structure. Alternatively, these two factors which are often used to formulate the hypotheses on which classic socioecological theory is based may not, in fact, be reliable predictors of female intrasexual competition levels.

Variation in PAE/POE may be the mechanism underpinning the differences in affiliative and competitive behaviours observed in macaque species. Macaque species characterised as grade 4 (most tolerant) had the highest 2D:4D ratios (lowest PAE) and the greatest disparity in 2D:4D ratios occurred between grade 4 and the other grades. The 2D:4D ratios of grade 1 and 2 species were similar to each other and although 2D:4D ratios of grade 3 species were higher than grades 1 and 2, they were still considerably lower than those of grade 4 species. Species at intermediate grades have been noted to vary inconsistently on several of the social measures contributing to their position on the scale (Balasubramaniam *et al.* 2012) with more overlap in social style between those of more or less tolerant grades. It is those species at the extreme ends of the scale which are the most behaviourally distinct from one another (Duboscq *et al*. 2013) and also appear to differ most in their exposure to PAE as inferred from their 2D:4D ratios. Individuals of lower grades display more overt, severe aggressive behaviours such as bites, behaviour which is rarely observed in species of more tolerant grades (Thierry 2000; Thierry 1985). There may therefore be increased selection for higher PAE and associated aggressive behaviours in species of the more despotic grades to whom it is beneficial to display these characteristics. The facilitation of the tolerant and conciliatory behaviours that characterise species of the higher social style grades, on the other hand, would call for a reduction in PAE and/or increase in POE.

There was a significant relationship between female 2D:4D ratios and intersexual dominance patterns. Female 2D:4D ratios were lower in species characterised by female dominance than those characterised by both male dominance and codominance. The low 2D:4D ratios in species characterised by female dominance may be due to selection for higher PAE which could result in behavioural masculinisation necessary for dominating males in these species (Dunham 2008; Waeber & Hemelrijk 2003; Joslyn 1973). The results lend support to prenatal sex hormones acting as a proximate mechanism underlying the evolution of female dominance in nonhuman primates (Petty & Drea 2015). Codominant species have the highest 2D:4D ratios (lower PAE) and this could be due to their mating systems as species in which the sexes are codominant (e.g. gibbons, titi monkeys, marmosets and tamarins) are often characterised by monogamy or polyandry (Koba *et al*. 2012; Smuts *et al*. 1987; Kinzey 1981, 1997; Carpenter 1940), though this is not a universal pattern (e.g. collared brown lemurs; Balestri *et al.* 2014).

As predicted, monogamous females had the highest 2D:4D ratios, likely as a result of selection for many of the key behaviours underpinning monogamous relationships in primates also requiring selection for reduced PAE and/or increased POE (French *et al*. 2018). Polyandrous females had lower 2D:4D ratios than monogamous females, but higher 2D:4D ratios than females characterised by polygyny or polygynandry. Interestingly, females of species characterised by polyandry tended to have lower 2D:4D ratios than their male counterparts. Although sample sizes were insufficient for formal testing, differences in intrasexual tolerance between males and females may explain why 2D:4D ratios were lower in females than males in these species. For example, polyandrous females are involved in the active defence of territories and are intolerant of and aggressive towards same-sex competitors and there is generally only one dominant breeding female within a group (Garber 1994; French & Inglett 1989). Polyandrous males, on the other hand, tend to be tolerant and cooperative with one another (Garber 1994; van Hoof & van Schaik 1994) and can be indifferent or welcoming to the presence of other females (French & Inglett 1989).

Females of species characterised by polygynous mating had the lowest 2D:4D ratios, followed by polygynandrous females. It is not clear why 2D:4D ratios would differ in polygynous and polygynandrous females but the pattern may be a manifestation of variation in 2D:4D ratios within the subcategories of the mating systems. Females characterised by scramble competition polygynandry had the lowest 2D:4D ratios but these values are based on two strepsirrhine species only and data from haplorhine females characterised by this mating system are needed before any conclusions can be made as to the relationship between PAE and this mating system. Female 2D:4D ratios in species characterised by harem polygyny and contest competition polygynandry were very similar, with harem polygyny 2D:4D ratios being very slightly lower. This is perhaps unsurprising as group formation in species characterised by these mating systems is likely to be very similar, meaning that females have similar competitive relationships with one another. Although small sample sizes precluded formal analysis, among polygynandrous species there was a tendency for female 2D:4D ratios to be highest in species characterised by cooperative defence polygynandry and even polyandrous female 2D:4D ratios were lower than those of females characterised by this mating system. This could be a reflection of differences in intra-sexual tolerance and mating competition between polyandrous and cooperative defence polygynandrous females. There is evidence that the formation of platonic social bonds is associated with OT in adult primates (Zeigler & Crockford 2017). The species characterised by cooperative defence polygyny (chimpanzee and howler monkey species), are likely to experience increased selection for cooperative and affiliative behaviours (moderated by oestrogens and associated neuropeptides) as females in these species disperse from their natal groups at maturity and need to form relationships with other (usually) unrelated females in the groups they migrate into. Conversely, higher PAE would be favoured in polyandrous females because mating competition is intense and females can gain substantial fitness benefits by achieving reproductive sovereignty and having several males to help with offspring care (French *et al*. 1997; Garber 1994).

There were no significant relationships between female 2D:4D ratios and either of the measures of female dominance behaviour. Species which showed higher rates of female-female agonism did not have lower 2D:4D ratios than those with lower rates, and indeed no trend was observable. Likewise, the associations between DCI and the 2D:4D ratio measures were not significant, although a slight trend was discernible in the predicted direction; females with higher DCI tended to have lower 2D:4D ratios (higher inferred PAE), although this trend was weak and limited to the right hand. As DCI is perhaps the most reliable way to quantify the degree of despotism characterising a given primate group, this trend is consistent with previous studies which noted associations between levels of female intrasexual competition and 2D:4D ratios in anthropoid primates (Nelson & Shultz 2010). Quantitative measures of female dominance are better able to represent the fine-grained variation we see in female social relationships across primate species than the broad classifications of traditional socioecological models. However, sample sizes were small for both of these variables and so the lack of relationship may result from a lack of statistical power in the analysis. Further research into the relationship between quantitative female dominance measures and 2D:4D ratios with larger sample sizes could prove productive.

Contrary to prediction, females with a higher percentage of fruit in their diet did not have lower 2D:4D ratios. The hypothesised greater contestability of fruit relative to other food types led to the suggestion that feeding competition should be greatest amongst highly frugivorous species and lowest amongst highly folivorous species (see discussion in Clutton-Brock & Janson 2012; Snaith & Chapman 2007), a supposition which has been corroborated by some studies (Steenbeek & van Schaik 2001; Janson & Goldsmith 1995), but not others. For example, within-group contest competition was not elevated by increased feeding on fruits in Assamese macaques (*M. assamensis*) (Heesen *et al*. 2013) and no association was found between rates of agonism in female primates and the percentage of fruit in their diet (Wheeler *et al*. 2013). Folivorous species display a preference for young, tender leaves which can be patchily distributed and therefore contestable (Yeager & Kool 2000; Koenig *et al.* 1998). The fact that folivores may also experience high levels of contest competition is supported by the observation that female dominance relationships in a highly folivorous colobine monkey were substantially affected by occasionally feeding on high-quality contestable foods which were only available on a seasonal basis (Wickberg *et al*. 2013). The results lend support to dietary categories (or degree of frugivory) not being good predictors of female intrasexual competition in primates. Other resources may be more important for some species, such as reproduction (French & Inglett 1989), territory (Schülke & Kappeler 2003) or even safe positions within the social group (Ron *et al*. 1996), and competition between females may occur in reference to these rather than just food.

Females of species characterised by larger group sizes did not have lower 2D:4D ratios than females of species which live in smaller groups. This is somewhat surprising as females living in larger groups have a greater number of within-group competitors and an increased likelihood of experiencing contest competition (Koenig and Borries 2006) which can result in the higher rates of agonism that are observed among females living in larger groups (Wheeler *et al.* 2013). A possible explanation for the lack of relationship could be that between-group competition in smaller primate groups, for example over territory in pair-living and solitary species, also generates selection for higher levels of PAE, particularly in species where females are actively involved in territory defence (Lazaro-Perea 2001; Azenberger 1992; Raemaekers & Raemaekers 1985). Additionally, there is likely to be substantial selection for cooperative and affiliative behaviours to facilitate the coexistence of primates in large groups and this is likely to moderate selection for higher PAE (French *et al*. 2018). Further, depending on relationships between females, larger group sizes could result in increased within-group scramble competition and, unlike direct contest competition, scramble competition is not likely to result in stronger selection for behaviours associated with higher PAE (e.g. dominance), although there is evidence to suggest that within-group contest competition also increases with increasing group size (Wheeler *et al*. 2013; Koenig & Borries 2006). These factors, together with the fact that dietary composition and group size cannot fully predict female intrasexual competition within and between groups, likely explains the lack of a relationship between these variables and PAE.

4.4.1: Summary

The variables percentage of fruit in diet and group size are not associated with 2D:4D ratio (and therefore PAE) and cannot satisfactorily explain variation in levels of female intrasexual competition. The quantitative dominance measures of rate of agonism and DCI do not appear to be related to PAE in female primates, although future analysis with larger sample sizes may provide further insights. Prenatal sex hormones may contribute to the variation observed in macaque social style through the important roles of PAE and POE on the expression of aggressive and affiliative behaviour. Species characterised by female dominance had lower 2D:4D ratios than male dominant and codominant species. This pattern is likely due to increased PAE in female dominant species resulting in masculinisation of particular behaviours which are conducive to dominating males (e.g. aggression). Female 2D:4D ratios were highest in monogamous species (low inferred PAE), followed by polyandrous, polygynandrous and polygynous species (high inferred PAE) and 2D:4D ratios varied with the form of polygyny and polygynandry, potentially with regard to the necessity for competitive over cooperative behaviours.

This study has improved on previous work in terms of having more reliable 2D:4D ratio measurements, using quantitative measures to investigate female intrasexual competition, including mating systems as a measure of female reproductive competition and investigating intersexual dominance relationships. The hormones underlying competitive and cooperative behaviours are largely conserved across all mammals and PAE may act as a proximate mechanism underlying the expression of behaviour in female primates in ways that are adaptive to their social system. The results stress that, in order to fully understand the relationship between PAE and competition in female non-human primates, it is necessary to consider reproductive competition and intersexual dominance relationships alongside ecological factors and female sociality.

- Chapter 5 –

***Prenatal androgen effects and personality in ring-tailed lemurs* (Lemur catta)*, robust capuchin monkeys* (Sapajus spp.) *and human children* (Homo sapiens)**

Abstract

Individual differences in behaviour can often be attributed to variation in prenatal androgen effects (PAE), suggesting that prenatal exposure to sex hormones may play important roles in the expression of personality traits in animals. By measuring behavioural variables under experimental conditions, this study explores the association between PAE (inferred from 2D:4D ratios) and personality traits (boldness, exploration tendency/curiousness, persistency, competitiveness) in three species of primate: ring-tailed lemurs (*Lemur catta*), robust capuchins (*Sapajus* spp.) and human children (*Homo sapiens*). The 2D:4D ratio was not a good predictor of persistency in any of these species, suggesting that expression of this trait and/or behaviours associated with this trait may not be influenced by PAE. The 2D:4D ratio was not associated with boldness or exploration tendency in ring-tailed lemurs, or with curiousness in robust capuchins, although the captive condition of these animals may have influenced their responses in some experiments. Boldness and exploration tendency in boys correlated negatively with 2D:4D ratios, as did competitiveness in robust capuchins, suggesting that in these species, PAE play a significant role in the expression of these personality traits. The 2D:4D ratio was a better predictor of behaviour in boys than girls, possibly as a result of sex differences in the evolutionary significance of the traits investigated and/or the possibility that in girls exposed to PAE within the normal range for their sex, PAE have a limited ability to influence personality traits over which female sex hormones may also have a regulatory role. Correlations between personality traits and 2D:4D ratio in boys became non-significant when one male participant with a comparatively feminised 2D:4D ratio was removed from the analysis suggesting that PAE on personality, although less apparent in individuals exposed to PAE within the typical range for their sex, may be detectable in individuals exposed to PAE outside of this range.

5.1: Introduction

5.1.1: Personality

In its most general sense, personality can be described as "…the internal organisation of behaviour that is stable over considerable time-periods in the individual yet varies among the individuals of a population on latent dimensions…" (Uher 2008, pg. 476). Personality traits are highly variable both across and within populations (Pederson *et al*. 2005) and across individuals (Sih & Bell 2008) and influence population dynamics as well as individual survival (Iwanicki & Lehmann 2015). Personality traits are moderately heritable, have fitness consequences (Iwanicki & Lehmann 2015; Dammhahn 2012; Seyfarth *et al*. 2012; Weiss *et al*. 2012; Koski 2011) and can affect various life-history measures such as dispersal (Dammhahn & Almeling 2012; Cote *et al*. 2010) and reproductive output (Morton *et al*. 2015). It is postulated that the development and expression of personality have both a physiological and genetic basis, as well as being influenced by the external environment (Burton *et al*. 2013).

5.1.2: Prenatal sex hormones and personality

Sex differences in personality are common (Dammhahn 2012; Schuett *et al.* 2010), suggesting that these may result from the organising influence of prenatal sex hormones on brain patterning. Higher prenatal androgen effects (PAE) are implicated in the expression of a number of personality traits in humans and other animals including dominance, assertiveness and aggressiveness (Ribeiro *et al*. 2016; Wacker *et al*. 2013), whereas higher prenatal oestrogen effects (POE) are associated with increased prosocial behaviour (Williams *et al*. 2003) and higher scores in personality factors such as agreeableness and privateness (Lindová *et al*. 2008). Increased extraversion in humans and boldness in other animals has been shown to facilitate mating success and, in a variety of species, individuals who avoid conflict are less desirable as mates (Lewis 2015). In non-human species, exploratory and bold behaviour can result in increased predation risk and in humans could result in increased risk of injury (Lewis 2015). In non-human primates, males tend to explore further in unfamiliar territories than females (Ellis *et al*. 2008). Older male grey mouse lemurs (*Microcebus murinus*) were found to be consistently bolder than females (Dammhahn 2012); however, individual risk-taking in grey mouse lemur males was not altered by changes in circulating sex hormone levels, despite increases in testosterone during the mating seasons. The males showed consistent risk-taking behaviour over time, suggesting that their personality may be influenced by PAE on brain patterning and behaviour rather than circulating androgen levels (Dammhahn & Almeling 2012). In a study on chimpanzees (*Pan troglodytes*), however, no sex difference in the personality trait boldness was found. It is unclear if this finding is an artefact of the testing methods used in which whole social groups took part in the experimental procedures, as the presence of group mates may have caused some individuals to behave more boldly than they would have had they been tested alone (Šlipogor *et al.* 2016; Massen *et al.* 2013). Additionally, in a study of adult robust capuchins, sex was not associated with the majority of personality constructs tested, excepting two traits which are widely linked to PAE - aggressiveness and dominance, in which males scored higher than females (Uher *et al*. 2013). However, many of the constructs tested by Uher *et al.* (2013) are unlikely to be influenced by PAE (e.g. self-cleanliness and food orientation), and so observable sex differences with regards to these would not be expected.

In humans, men have been reported to be bolder and less fearful than women (Jeon *et al*. 2016; Speltz & Bernstein 1976). Circulating testosterone levels are associated with higher novelty seeking and sensation seeking in human males (Määtänen *et al*. 2013; Voracek *et al*. 2010). Sensation seeking has a strong genetic basis and is generally higher in men than women, suggesting that sex hormones, particularly androgens, play a part in the expression of this trait (Voracek *et al.* 2010). Human females that have a fraternal twin brother show higher disinhibition (Resnick *et al*. 1993), experience seeking (Slutske *et al*. 2011; Resnick *et al*. 1993), thrill and adventure seeking (Slutske *et al*. 2011) and sensation seeking (Resnick *et al*. 1993) in comparison with females with same-sex twins (Tapp *et al*. 2011). Additionally, females from male-female twin pairs were rated as more verbally aggressive than females with same-sex twins (Cohen-Bendahan *et al*. 2005). This pattern is believed to be caused by the transfer of the brother's androgens having masculinising effects on the female foetus in utero (Tapp *et al*. 2011; Knickmeyer *et al*. 2005).

5.1.3: The 2D:4D ratio and personality

There is evidence for associations between psychological traits/behaviours and physical features in humans and other animals (Lindová *et al*. 2008). For example, facial-width-to-height ratio (FWHR) is linked with testosterone (Lefevre *et al*. 2013) and facial characteristics are structured prenatally by testosterone in human men and likely in other primates (Neave *et al*. 2003; Kasperk *et al*. 1997), suggesting that FWHR may act as a biomarker for traits associated with high PAE. FWHR predicted individual differences in assertiveness and dominance in robust capuchins (*Sapajus* spp*.;* Lefevre *et al*. 2014a; Wilson *et al*. 2014) and self-reported dominance and aggression in both sexes in humans (Lefevre *et al.* 2014b). Another morphological trait influenced by PAE is the second to fourth digit (2D:4D) ratio (Manning *et al.* 1998). Male animals are typically exposed to higher PAE than females and this stimulates the growth of the fourth digit, the result being a lower (more masculine) 2D:4D ratio. In contrast, prenatal oestrogen effects (POE) are generally higher in females and this results in reduced growth of the fourth digit, leading to a higher (more feminine) 2D:4D ratio. Thus, lower 2D:4D ratios indicate that an individual developed in an environment higher in PAE (Manning & Fink 2018; Manning 2011; Zheng and Cohn 2011). For example, in addition to being masculinised in their expression of personality traits as described above, girls with twin brothers also have lower 2D:4D ratios than girls with twin sisters, again a likely consequence of the masculinising effects of androgens originating from the male foetus (Tapp *et al.* 2011; Voracek & Dressler 2007; van Anders *et al*. 2006).

In humans, close links between low 2D:4D ratios (high PAE) and masculine personality types in both sexes have been observed (Kim *et al.* 2014). Low 2D:4D ratio individuals tend to display higher dominance (Manning & Fink 2008; Neave *et al*. 2003), higher aggression (Hampson *et al*. 2008; Benderlioglu & Nelson 2004, 2007) and increased sensation seeking (Voracek *et al.* 2010; Hampson *et al.* 2008; Resnick *et al.* 1993). Women who described themselves as more assertive and competitive have lower 2D:4D ratios (Wilson 1983) and women with higher right hand 2D:4D ratios were found to score lower on the trait social boldness (assertiveness) (Lindová *et al.* 2008). Individual differences in risk-taking behaviour in the financial domain are also associated with lower 2D:4D ratios in men and women (Kim *et al.* 2014). Individuals of both sexes with higher 2D:4D ratios had a higher perception of financial risk and displayed less risky behaviour than lower 2D:4D ratio individuals (Kim *et al.* 2014). This suggests that, in addition to traits such as aggression, competitiveness and sensation seeking, aspects of risk-taking and risky behaviour are influenced by PAE in humans. Low 2D:4D ratios have also been associated with greater susceptibility to boredom (Hampson *et al*. 2008), greater need for novelty and aversion to repetitive experience in both sexes (Tapp *et al*. 2011) and higher impulsivity (Hanoch *et al*. 2012) and impulsive sensation seeking in human men (Wacker *et al*. 2013).

Similar findings have been reported in studies of non-human primates for some behaviours linked to high PAE. Female cercopithecine primates with lower 2D:4D ratios were found to hold higher positions in the dominance hierarchy than those with higher 2D:4D ratios (Hamadryas baboon [*Papio hamadryas*]: Howlett *et al*. 2012; chacma baboon [*P. ursinus*]: Howlett *et al*. 2015, 2012; rhesus macaque [*Macaca mulatta*]: Nelson *et al*. 2010) and female chacma baboons with lower 2D:4D ratios also displayed higher rates of both contact and non-contact aggression than those with higher 2D:4D ratios (Howlett *et al*. 2015). However, the relationship between 2D:4D ratios/PAE and personality traits in the majority of primate species remains understudied.

5.1.4: Questionnaire-based personality research

Data from previous studies suggest that the behaviour of individuals exposed to higher PAE (as inferred by exhibiting lower 2D:4D ratios) is likely to be bolder (less inhibited, less risk-averse), more aggressive, more dominant, more competitive and assertive, more exploratory/curious (more experience and sensation seeking), more distractible and less persistent (more prone to boredom) than those exposed to lower PAE (higher 2D:4D ratios). Much human personality research in general and research investigating associations between 2D:4D ratio and personality have relied on data from self-report or observer reported questionnaires based on ‘Cattell’s 16PF’, the ‘Big 5’, ‘HEXACO’ personality factor models or some variation on these

(Shaw 2013; Lippa *et al.* 2006; Fink *et al.* 2004b; Eysenck & Eysenck 1985; Cattell *et al.* 1970). These inventories result in a number of broad personality dimensions often labelled 'super traits' (Lindová *et al*. 2008) which are measured via a series of questions designed to rate an individual on the levels of each dimension/factor (Ashton 2015). Similar methods have been adapted and applied to non-human primates (Brosnan *et al.* 2015; Lewis 2015; Weiss *et al.* 2015, 2012; King *et al.* 2008) and although useful in terms of convenience, reducing research time and gaining large sample sizes (Ashton 2015), questionnaire or survey-based data collection methods have their shortcomings. Main criticisms stem from the fact that surveys are reliant on the accuracy of one person's opinion of themselves and/or others and also the reality that animals can often behave differently around different people (Highfill *et al.* 2010), which is particularly relevant where surveys involve people providing ratings of animal behaviour (e.g. keepers describing the behaviour of their charges). It is also necessary to consider context when investigating relationships between 2D:4D ratio and personality (Ribeiro *et al.* 2016; Manning & Fink 2018) and this is not possible using lexical questionnaire-based methods (Uher 2018; Uher 2015). This highlights that more reliable personality trait data is needed in studies of 2D:4D ratio, and this could be gained through quantifiable behavioural variables collected under experimental conditions.

5.1.5: Summary of aims

Individual differences in behaviour can often be attributed to variation in PAE and POE (Knickmeyer *et al.* 2005) suggesting that prenatal exposure to sex hormones may play important roles in the expression of personality traits in animals (Shaw 2013), including humans and non-human primates. Using data gained from behavioural variables measured under experimental conditions, I will explore the association between PAE (inferred from 2D:4D ratios) and personality in three species of primate. These include a strepsirrhine primate, the ring-tailed lemur (*Lemur catta*), a New World monkey, the robust capuchin (*Sapajus* spp.) and an ape, human children (*Homo sapiens*). Personality traits present in primates and other animals include 'competitiveness', 'boldness', 'exploration tendency/neophilia/curiousness' (hereafter exploration tendency) and also 'persistency' (Massen *et al*. 2013;

Dammhahn 2012; Neumann *et al.* 2013; Uher *et al.* 2013; Koski 2011; Nettle 2006; Parke *et al.* 2004). Individual expression of these traits could be influenced by differences in prenatal exposure to sex hormones and these traits will thus be the focus of this study. I aim to shed light on the potential role of PAE as a neuroendocrinological mechanism underlying differences in the expression of personality traits in individuals.

5.1.6: Hypotheses and predictions

5a) Greater exposure to PAE causes individuals to display higher levels of boldness.

(i) In ring-tailed lemurs and human children, individuals with lower 2D:4D ratios will score higher in behaviours associated with boldness.

5b) Higher PAE may cause individuals to exhibit increased exploratory/curious behaviours.

(i) In ring-tailed lemurs and human children, individuals with lower 2D:4D ratios will score higher in behaviours associated with exploration tendency than those with higher 2D:4D ratios.

(ii) Robust capuchin monkeys with lower 2D:4D ratios will score higher for curiousness than those with higher 2D:4D ratios.

5c) Exposure to higher PAE is likely to increase competitive behaviour in individuals.

(i) Robust capuchin monkeys with lower 2D:4D ratios will show higher levels of competitiveness than higher 2D:4D ratio individuals.

5d) High PAE individuals are likely to be less persistent and have increased susceptibility to boredom. Therefore, individuals exposed to lower PAE are more likely to score higher for behaviours associated with persistency in tasks without an immediate reward.

(i) In all three species, individuals with lower 2D:4D ratios will have lower persistency scores than individuals with higher 2D:4D ratios.

5.2: Methods

5.2.1: Study sites and subjects

5.2.1.1: Ring-tailed lemurs

Study subjects comprised a captive group of 11 ring-tailed-lemurs housed at Yorkshire Wildlife Park, Doncaster, UK. The group consisted of a breeding pair and their offspring and animals ranged from one to 11 years of age (six adult males, 1 adult female, two adolescent females, one juvenile male and one juvenile female). Animals were housed in a one-acre naturalistic outdoor enclosure made up of mixed woodland. The enclosure is also shared with two black and white ruffed lemurs (*Varecia variegata*) not included in this study, which had coexisted with the ring-tailed lemur group for six years at the time of this study. This is a walk-through exhibit with public access during Park opening hours. The lemurs also have access to an indoor house overnight and in cold weather conditions. The house is separated into three 2m (length) x 1.5m (width) x 2.5m (height) pens by wire mesh and sliding doors, each pen also has a door for outdoor access into an outdoor pen and the main enclosure. Pens contain sleeping shelves and tree branches. Two of these pens served as experimental pens in which all research was carried out. All animals were individually recognised.

5.2.1.2: Robust capuchin monkeys

Study subjects comprised 10 captive adult robust capuchin monkeys (five males and five females) between the ages of eight and 33 years, studied at the Primate Centre of the ISTC-CNR, housed at the Bioparco of Rome, Italy. Individuals belonged to four groups containing between five and 11 individuals which live in naturalistic outdoor enclosures (18-127 m^2) with access to indoor pens. The indoor pens served as the testing area for personality experiments conducted by and described in Uher *et al*. (2013).

5.2.1.3: Human Children

Study participants comprised 18 girls and 17 boys aged three to five years, taking part in research at the Kent Child Development Unit, University of Kent, Canterbury, UK.

Children were volunteered for this study by their parent/guardian. Two rooms in the Unit were used in this study; a waiting room in which participants spent time until they are called for testing, and an experimental room. All testing sessions took place in the experimental room with two cameras set-up for video recording. The room was furnished with a table and chair at which the child sat at the beginning of each test and another chair in the opposite corner for their parent/guardian. A 50cm high stool was positioned in the centre of the room at 1m distance from the child.

5.2.2: Data collection

5.2.2.1: 2D:4D ratio measurements

To obtain 2D:4D ratio measurements, I used the digital photographic and computer-assisted image analysis software method as described in Howlett *et al*. (2015). For the human children study group, participants were asked to place their hands against the Perspex sheet and I took three photographs of each participant's hands (Figure 5.2.1a). Hand images of the robust capuchin monkey study group were collected when animals were anaesthetised for their annual health assessments (Figure 5.2.1b). Staff at the institution were provided with an instruction sheet detailing the protocol, the position that the primate hands and fingers must be presented in and example photographs with information on the landmarks used to measure the digits (see Appendix 2.2). Each hand was photographed three times for each animal and any images which did not adhere to the criteria outlined in the protocol were discarded. All members of the ring-tailed lemur study group were habituated to human presence inside their enclosure and so hand images were obtained whilst the animals were fully alert. Each lemur was encouraged to walk onto the Perspex sheet which was positioned next to their sleeping shelf by means of a food reward and photographs of the palms of their hands held flat against the sheet were taken from underneath (Figure 5.2.1c). For each individual, I identified three photos for each hand in which digits were in optimal positions (i.e. in a flat and straight position with the entire length of the digits and measurement landmarks visible) and used these images to measure 2D:4D ratios.

For purposes of data reliability (Allaway *et al*. 2009), I carried out all measurements of 2D:4D ratios from these photographs using the computer-assisted image analysis software program Image Processing and Analysis in Java (ImageJ). I measured the second (2D) and fourth (4D) digits five times for each photograph, giving a total of 15 measurements per digit for each individual. I used the mean of these 15 measurements as the measurement for that digit. I calculated the 2D:4D ratio of each hand by dividing the length of the 2D by the length of the 4D for each individual. I calculated the mean 2D:4D ratio (M2D:4D) by averaging the right 2D:4D ratio (R2D:4D) and left 2D:4D ratio (L2D:4D).

5.2.2.2: Personality traits

I carried out my own series of tests to quantify personality in the ring-tailed lemur and human children study groups and utilised personality data from Uher *et al.* (2013) for the robust capuchin study group. In the ring-tailed lemur and human children study groups, boldness is defined as a non-fearful response to a threat that is not predatory. I chose not to include predator simulations as subjects have been shown to display a variety of personality behaviours in response to such stimuli (such as anxiety) which are not necessarily indicative of boldness (Carter *et al.* 2012). Exploration tendency is described here as a neophilic response to novel stimuli (Massen *et al*. 2013). Persistency is described as the continued exploration of an object without an immediate reward (Koski & Burkart 2015). Some of these traits may have similar behavioural outcomes and so I recorded the same variables across experiments (where appropriate), with additional variables specific to certain experiments (see Table 5.2.1 for summary). Ring-tailed lemurs are a good choice of strepsirrhine in which to carry out experimental studies of these three non-social personality traits as this species' qualitative cognitive abilities are similar to many haplorhine primates in terms of their physical cognition (Kittler *et al*. 2015; Fichtel & Kappeler 2010).

Personality traits previously described by Uher *et al*. (2013) were used for the robust capuchins. I chose three traits which were complementary to those being studied in the other species and which were likely to be related to individual prenatal androgen exposure: competitiveness, curiousness and persistency (see Uher *et al*. 2013 supplementary material for a full description of the behavioural measures applicable to these traits). For the robust capuchin study group, the personality construct ‘curiousness’ is analogous with ‘exploration tendency’ in ring-tailed lemurs and human children.

Figure 5.2.1: Examples of Perspex photographs of non-human primate and human hands used to measure 2D:4D ratios: (a) human boy, (b) adult female robust capuchin monkey and (c) adolescent female ring-tailed lemur.

5.2.2.3: Personality experiments with ring-tailed lemurs

I carried out multiple experiments to test boldness, exploration tendency and persistency. Each test lasted five minutes. I video recorded each individual test using a Panasonic DMC-FZ150 digital camera which I reviewed later. I repeated the tests twice, approximately two months apart, over a three-day period on 5-7th April and 7-9th June 2016. In order to mitigate habituation in the repeat session, I randomised all tests as much as possible and observed animals in random order. Experiments were conducted one hour after the animals had received their morning feed and so their performance in tests involving food rewards should reflect the personality traits under investigation and not motivation to feed based on hunger level.

As having a social audience could influence the responses of the focal animals (Šlipogor *et al.* 2016; Koski & Burkart 2015; Massen *et al*. 2013), I avoided interference from audience effects or social facilitation, by having focal animals enter the experimental pen one at a time. Each test began when the focal animal voluntarily entered the experimental pen. Lemurs were free to move around the entire pen for the duration of the test and at the end were released into the outdoor enclosure. The test was then reset for the next animal which entered through the adjoining indoor pen. If individuals did not approach/touch the apparatus in any of the tests, latencies were set at the maximum (Uher *et al.* 2013; Dammhahn 2012).

5.2.2.3.1: Boldness-exploration tendency tests - Novel object 1 & Novel object 2

These tests aimed to assess individual boldness and exploration tendency in terms of response to a novel object. The novel objects were represented by a child’s pink push powered ride-on toy car (Figure 5.2.2a) and a brown leather bean bag (Figure 5.2.2b). I observed animals in random order and exposed them to one novel object at a time. I randomised the order of novel object presentation in all sessions. The novel object was positioned in the centre of the pen. I measured: latency to approach the object, number of approaches, latency to touch the object, time spent in proximity to the object (within a 30cm radius), time spent manipulating (sniffing, touching, biting, moving) the object and the frequency of moderate-arousal ‘click’ series vocalisations (Macedonia 1993).

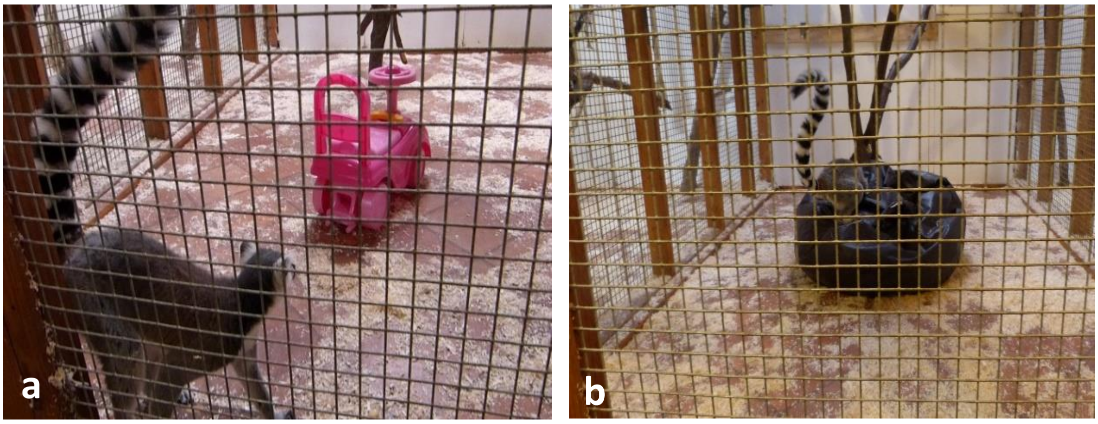

Figure 5.2.2: (a) Novel object 1 and (b) novel object 2 photographed during the ring-tailed lemur experimental sessions.

5.2.2.3.2: Exploration tendency test – Exploration cubes

I used the 'exploration cubes' apparatus which was made up of many cubes linked together (Figure 5.2.3) to test individuals' exploratory and bold behaviour. The front of these cubes was blocked leaving a small hole giving the animals a restricted view of the contents. Animals had to reach inside to access the contents of the cubes. The contents of the 16 cubes were both novel and familiar to the lemurs and varied between those which the animals would find stimulatory (e.g. dried apricots) and those to which they would be averse or uninterested (e.g. dish of water). Six cubes contained one of the following categories of food (six dried apricots, six cubes of raw sweet potato, six dog biscuits, six raw mushrooms, six slices of raw chilli pepper, six raw garlic cloves), six cubes contained one of the following categories of object (green feather, yellow feather, dish of water, shells, beads, a woolly toy), and four cubes contained nothing. The contents of the cubes were rearranged at the repeat session, so individuals could not learn the location of preferred items and had to explore all of the cubes again. The cubes were placed in the centre of the pen with the access holes facing the door through which the animals entered.

I measured the variables: latency to approach, number of approaches, time spent in proximity to the cubes (within a 30cm radius), latency to touch the cubes, time spent manipulating the cubes (sniffing, touching, biting, moving, peering into holes), the number of cubes explored visually, number of cubes explored tactilely and the frequency of moderate-arousal 'click' series vocalisations (Table 5.2.1). After each experiment the cubes were reset before the next animal entered the pen.

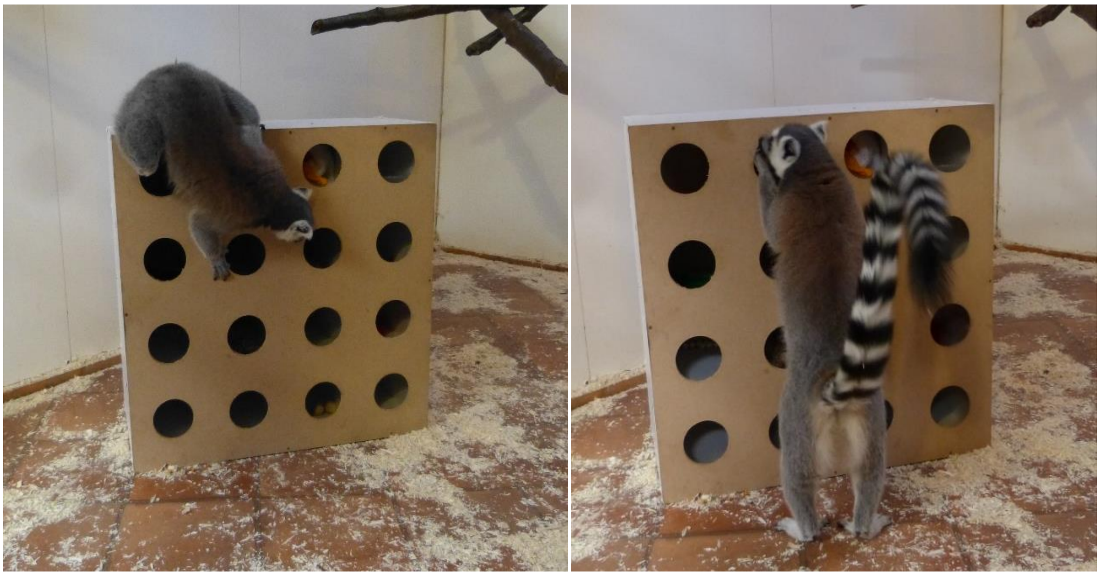

Figure 5.2.3: Photographs of the ‘exploration cubes’ as they were presented to the study subjects during the ring-tailed lemur experimental sessions. Each cube contained a different stimulus except four that contained no stimulus.

5.2.2.3.3: Persistency test – Banana bottle

To measure persistency, I used a 150 ml bottle made of clear plastic with a drip nozzle and filled this with banana puree that was clearly visible to the lemurs from the outside. I then placed this bottle inside a cylindrical wire bird feeder which prevented the animals gaining direct access to the bottle (Figure 5.2.4a). The banana bottle was hung from a branch in the animals’ indoor pen at a point furthest from the entrance door in order to maximise the visibility of the food reward within (Figure 5.2.4b). The lemurs had to manipulate the object to cause small amounts of the puree to drip out and reach the food reward (Figure 5.2.4c). I measured: latency to approach banana bottle, number of approaches, latency to detect food reward, time spent in proximity to the banana bottle (within a 30cm radius), latency to touch the banana bottle, frequency of moderate-arousal ‘click’ series vocalisations, time spent trying to reach reward, number of attempts and average time spent trying per attempt.

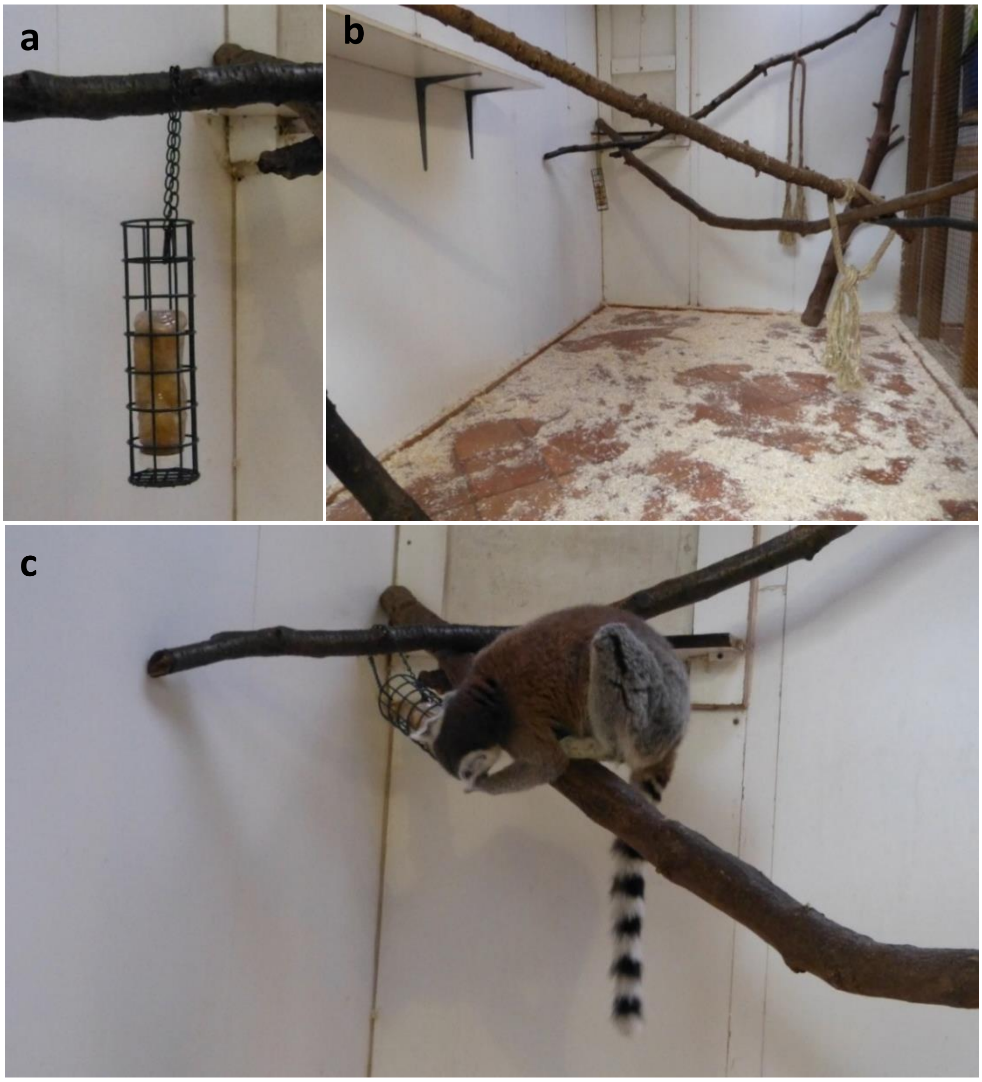

Figure 5.2.4: (a) the experimental set-up of the 150 ml plastic bottle with the food reward visible inside, (b) position of banana bottle during ring-tailed lemur experimental session and (c) ring-tailed lemur manipulating the bottle in order to reach the reward within.

5.2.2.4: Personality experiments with robust capuchin monkeys

Existing data on robust capuchin personality traits formulated based on behavioural data collected under similar experimental conditions by Uher *et al.* (2013) were used in this study. The traits of interest are: competitiveness, curiousness (analogue of exploration tendency) and persistency.

5.2.2.5: Personality experiments with human children

I carried out multiple experiments to test boldness, exploration tendency and persistency in human children. Each individual test was recorded using a Cannon

FS200 digital video camera and reviewed at a later date. Experiments were repeated twice, two to three weeks apart, over the period of the 26th July 2016 - 14th October 2016 depending on the availability of the participants. To avoid possible social audience effects on the behaviour of the children, they took part in the tests one at a time and I (the researcher) was not present in the room during the tests. A parent or guardian was present in the room but was instructed to keep their interaction with the child minimal. Each test lasted two minutes and began when I had deposited the relevant apparatus and exited the experimental room. Children were free to move around the entire room for the duration of the tests. If participants did not approach/touch the apparatus in any of the tests, latencies were set at the maximum.

5.2.2.5.1: Boldness-exploration tendency tests - Novel objects

I aimed to assess boldness and exploration tendency in terms of each individual's response to four novel objects. Novel object A is a cardboard cylinder covered in purple wrapping paper with three bells and an electronic toy which lights up and makes a sound when pressed attached to the inside (Figure 5.2.5a). Novel object B is a black plastic ball encased in a rubber surround (Figure 5.2.5b). The black ball has a smaller ball inside which makes a rattling sound when the object is moved. Novel object C is a rubber dog toy (Figure 5.2.5c). The blue and pink wheels can be spun around the central tube. Novel object D is a glittery purple rubber tube (Figure 5.2.5d). It has harder plastic inside which makes a crackle sound when squeezed. Participants were exposed to one novel object at a time which was positioned on the stool in the centre of the room at the beginning of each test. See Table 5.2.1 for a description of the variables measured in these tests.

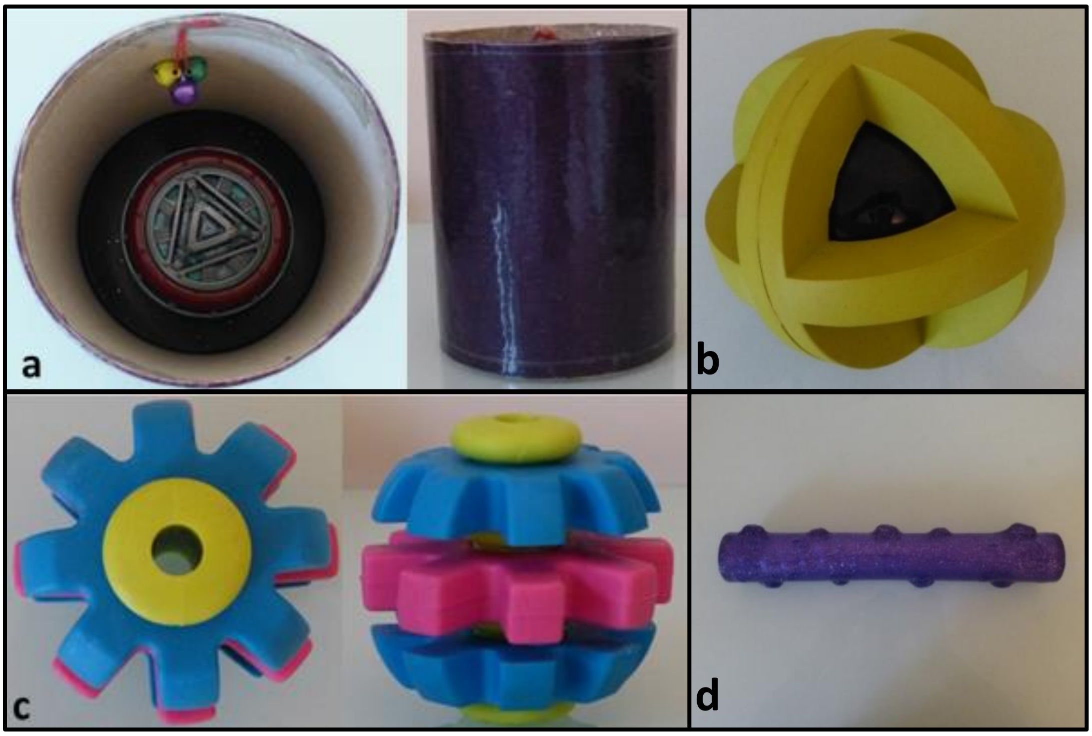

Figure 5.2.5: (a) novel object A overhead view and front view, (b) novel object B overhead view, (c) novel object C overhead view and front view and (d) novel object D overhead view.

5.2.2.5.2: Exploration tendency test – Exploration cubes

I used the ‘exploration cubes’ as described above (Figure 5.2.3) to measure the exploratory and bold behaviour of each individual. The contents of the 16 cubes were both novel and familiar to the children and varied between those which the children would find stimulatory (e.g. boiled sweets) and those to which they would be uninterested (e.g. empty plastic container). Six cubes contained one of the following categories of food (three dried apricots, three jelly sweets, three raw mushrooms, three boiled sweets, three raw garlic cloves, three raw green beans), six cubes contained one of the following categories of object (green feather, yellow feather, empty plastic container, shells, crayons, a brightly-coloured piece of fabric), and four cubes contained nothing. Contents of the cubes were rearranged at the repeat session so that individuals could not learn the location of preferred items and had to explore all of the cubes again. The cubes were placed at the opposite side of the room to where the child sat with the access holes facing the child. See Table 5.2.1 for the variables measured in this test.

5.2.2.5.3: Persistence test – Puzzle ball

To measure persistency, a soft clear rubber puzzle ball measuring 40cm in circumference with a green plastic maze inside was used and a shiny animal sticker reward was placed inside (Figure 5.2.6). This reward was clearly visible to the child from the outside of the ball and was positioned inside the ball at the farthest point from the 3cm wide dispenser hole which prevented the participant gaining immediate access to the reward. Participants were shown the reward inside the puzzle ball and told that they could keep the reward if they were able to extract it. The puzzle ball was then positioned on the stool in the centre of the room at the beginning of the test. Participants needed to manipulate the ball in order to move the reward through the maze and gain access to it at the dispenser hole. At the end of the session children were given a different shiny animal sticker reward to alleviate any frustration experienced by not reaching the sticker inside the puzzle ball. Table 5.2.1 provides a description of the variables measured in this test.

Figure 5.2.6: The puzzle ball in which the shiny animal sticker reward was placed. Participants must manipulate the ball in order to reach the reward inside.

Table 5.2.1: Summary of the personality traits measured, the behavioural variables relevant to each trait and the experimental set-ups (tests) that examined them in the ring-tailed lemur and human children study groups. Some tests measure more than one personality trait. All latencies and times measured in seconds.

Personality trait	Test	Behavioural variables
Boldness	Novel objects, exploration cubes, banana bottle/puzzle ball.	Latency to approach (within a 30cm radius), number of approaches, time spent in proximity (within a 30cm radius), frequency of moderate-arousal 'click' series vocalisations (ring-tailed lemurs only).
Exploration tendency	Novel objects, exploration cubes, banana bottle/puzzle ball.	Latency to touch, latency to detect reward (ring-tailed lemurs only), time spent manipulating novel object/exploration cubes, number of cubes visually explored, number of cubes tactilely explored.
Persistency	Banana bottle/puzzle ball.	Time spent trying to reach the reward, number of attempts on the banana bottle/puzzle ball, average time spent trying to reach the reward per attempt.

5.2.3: Formulation of personality traits from raw behavioural data

Using the behavioural data gained from the personality experiments I followed the method described in Uher *et al.* (2013) to formulate individual personality trait scores for boldness, exploration tendency and persistency in the ring-tailed lemur and human children study groups. First, the raw data for each behavioural variable was Z-standardised within each experimental set-up (test), separately for each of the two sessions, to provide contextualised behavioural measurements. Some of these Z-scores were subsequently reversed depending on how they related to a particular personality trait (see Appendices 5.1-5.3). Within tests, I then averaged the Z-scores of those variables examining the same personality traits, again separately for each session (see Table 5.2.1). This provided a single Z-score for each personality trait within each test and session (e.g. obtaining one persistency score for each ring-tailed lemur in session one of the Banana bottle test is achieved by averaging the Z-scores of the three behavioural variables used to measure this trait) and this score is referred to as the 'contextualised composite construct measure' by Uher *et al.* (2013). I then averaged these contextualised composite construct measures across each test to achieve a single value for each personality trait per session (e.g. one boldness value per individual in session one based on the average of contextualised composite measures across all tests). Finally, I averaged these scores across the two sessions to give one overall score per individual for each personality trait. Uher *et al*. (2013) describes these scores as 'decontextualised composite construct measures' (hereafter termed 'personality traits' in this study) as the scores represent behavioural data pertaining to a personality trait gained across several different situations (tests) and provide a measure that better reflects the temporal stability of individual behaviour (see Uher *et al*. 2013 glossary for a comprehensive description of these terms). Decontextualized composite construct measures for competitiveness, curiousness and persistency in the individual robust capuchins were provided by Uher *et al*. (2013).

5.2.4: Statistical analysis

I conducted all statistical analysis using IBM SPSS Statistical software for Windows version 24. One ring-tailed lemur male was missing the 4th and 5th digits of his left hand and so data were available on the R2D:4D of this individual only. Likewise, data on R2D:4D only were obtainable for two males and one female in the robust capuchin study group due to these individuals having injuries to or missing key digits on their left hands.

5.2.4.1: Normality

I used Shapiro-Wilk tests throughout when assessing skew of data. Data for R2D:4D, L2D:4D and M2D:4D were all normally distributed for ring-tailed lemur, robust capuchin and human children study subjects. All personality variables were normally distributed for robust capuchins, ring-tailed lemurs and boys. Data for boldness and persistence were normal for girls but exploration tendency data were not. Exploration tendency data in girls were robust to transformation and so non-parametric tests were used in analysis of this variable.

5.2.4.2: 2D:4D ratio measurement reliability

The intraclass correlation coefficient (ICC) set to the 'absolute agreement' definition showed that 2D:4D ratio measurements were highly repeatable for both hands in all three study groups (Appendix 5.1).

5.2.4.3: 2D:4D ratio comparisons

I investigated within sex differences in R2D:4D and L2D:4D using a paired *t*-test (two-tailed) and between sex differences in R2D:4D and L2D:4D using independent samples *t*-tests (two tailed). In all three study groups R2D:4D and L2D:4D within sexes were not significantly different so I also used M2D:4D in subsequent analyses. There were no significant differences between the sexes for either R2D:4D or L2D:4D in ring-tailed lemurs or robust capuchin monkeys. Human children however showed significant intersexual differences in R2D:4D but not L2D:4D (Table 5.2.2) and so the sexes were analysed separately. As sample sizes for the non-human primate study groups were small and 2D:4D ratios were not significantly different, the sexes were analysed together for the non-human primates.

Table 5.2.2: Results of paired *t*-tests comparing 2D:4D ratios within sexes and independent samples *t*-tests comparing 2D:4D ratios between the sexes in the three study groups. Significant results indicated in bold.

Digit ratios compared	*t*-test (two-tailed)
Ring-tailed lemurs R2D:4D & L2D:4D (males only)	t_5 = -1.665, P = 0.157
Ring-tailed lemurs R2D:4D & L2D:4D (females only)	t_3 = 0.073, P = 0.946
Ring-tailed lemurs R2D:4D & R2D:4D (males vs females)	t_9 = 0.069, P = 0.946
Ring-tailed lemurs L2D:4D & L2D:4D (males vs females)	t_8 = 1.480, P = 0.177
Robust capuchin R2D:4D & L2D:4D (males only)	t_2 = -0.699, P = 0.557
Robust capuchin R2D:4D & L2D:4D (females only)	t_3 = -0.759, P = 0.530
Robust capuchin R2D:4D & R2D:4D (males vs females)	t_8 = -0.812, P = 0.440
Robust capuchin L2D:4D & L2D:4D (males vs females)	t_5 = -0.454, P = 0.669
Human children R2D:4D & L2D:4D (boys only)	t_{16} = -0.167, P = 0.870
Human children R2D:4D & L2D:4D (girls only)	t_{17} = 1.537, P = 0.143
Human children R2D:4D & R2D:4D (boys vs girls)	**t_{33} = 3.660, P = <0.001**
Human children L2D:4D & L2D:4D (boys vs girls)	t_{33} = -1.273, P = 0.212

5.2.4.4: Test-retest reliability

To determine whether there was individual consistency across time in the contextualised behavioural measurements and the three personality traits themselves in the ring-tailed lemur and human children study groups, I analysed individual test-retest reliability across the two experimental sessions using either Pearson or Spearman rank correlations depending on whether the assumptions of the Pearson correlation were met. These analyses had already been carried out for the robust capuchin monkey study group (see Uher *et al*. 2013 for details).

5.2.4.5: Personality trait data

2D:4D ratio data are classified as the independent variable and personality trait data as dependent variables. Relationships between each personality trait and the personality traits and 2D:4D ratios were analysed using either Pearson or Spearman Rank correlations depending on whether the assumptions of the Pearson correlation were met.

5.3: Results

5.3.1: Test-retest reliability

5.3.1.1: Ring-tailed lemurs

With the exception of two variables, individuals showed significant moderate to high correlations across the two sessions in all contextualised behavioural measurements (Appendix 5.2). Nine of the 11 individuals displayed significant moderate-high test-retest reliability in all 29 contextualised behavioural measurements across the two sessions (Table 5.3.1). Ring-tailed lemurs showed significant positive correlations between their personality trait scores in the two sessions (boldness – *r* = 0.852, df = 11, P = 0.001; exploration tendency – *r* = 0.876, df = 11, P = <0.001; persistency – *r* = 0.663, df = 11, P = 0.026, Figure 5.3.1).

Table 5.3.1: Pearson correlations (*r)* showing individual ring-tailed lemur temporal reliability in the 29 contextualised behavioural measurements (*n*) across all tests.

Individual	*r*	*p*	*n*
LM1	**0.422**	**0.016**	29
LM2	0.304	0.159	29
LM3	**0.555**	**0.002**	29
LM4	**0.429**	**0.047**	29
LM5	**0.699**	**<0.001**	29
LM6	**0.696**	**<0.001**	29
LM7	**0.668**	**<0.001**	29
LF1	**0.526**	**0.003**	29
LF2	**0.582**	**0.001**	29
LF3	**0.734**	**<0.001**	29
LF4	0.320	0.090	29

5.3.1.2: Human children

There was significant test-retest reliability for 22 of the 35 participants in all 34 contextualised behavioural measurements across the two sessions (Table 5.3.2). Seven of the ten contextualised behavioural measurements showed significant low-moderate correlation across the two sessions in boys (Appendix 5.3). Significant moderate to high correlations were observed between the personality traits boldness (*r* = 0.704, df = 17, P = 0.002) and exploration tendency (*r* = 0.690, df = 17, P = 0.002) in the two sessions in boys. However, there was no correlation between boys' scores for persistency across the two sessions (*r* = 0.193, df = 17, P = 0.457, Figure 5.3.2a). There were significant correlations ranging from low to high across the two sessions in six out of ten of the contextualised behavioural measurements in girls (Appendix 5.4). Moderate correlations were observed across the two sessions for boldness (*r* = 0.542, df = 18, P = 0.020) and exploration tendency (*r* = 0.496, df = 18, P = 0.036). The correlation between persistency scores across the two sessions was moderate but not significant (*r* = 0.406, df = 18, P = 0.095; Figure 5.3.2b).

Table 5.3.2: Temporal reliability (SR = Spearman Rank correlations, P = Pearson correlations) of individual human children's contextualised behavioural measurements (*n*) across all tests. Significant correlations are indicated in bold.

Participant (boys)	**Correlation**	***r***	***p***	**Participant (girls)**	**Correlation**	***r***	***p***	***n***
M1	P	**0.536**	**0.007**	**F1**	P	**0.563**	**0.004**	34
M2	P	0.395	0.117	**F2**	SR	**0.403**	**0.047**	34
M3	P	0.226	0.351	**F3**	SR	**0.314**	**0.035**	34
M4	P	**0.486**	**0.016**	**F4**	P	**0.729**	**<0.001**	34
M5	P	**0.407**	**0.048**	**F5**	P	0.174	0.416	34
M6	P	-0.141	0.511	**F6**	SR	0.227	0.286	34
M7	P	**0.429**	**0.037**	**F7**	SR	0.135	0.530	34
M8	P	**0.406**	**0.049**	**F8**	P	0.269	0.281	34
M9	P	**0.424**	**0.043**	**F9**	P	0.367	0.122	34
M10	SR	0.296	0.161	**F10**	P	**0.412**	**0.046**	34
M11	SR	0.312	0.138	**F11**	SR	**0.466**	**0.022**	34
M12	P	**0.540**	**0.006**	**F12**	SR	-0.340	0.154	34
M13	P	0.186	0.383	**F13**	P	**0.464**	**0.038**	34
M14	SR	0.278	0.188	**F14**	P	**0.410**	**0.042**	34
M15	P	**0.519**	**0.009**	**F15**	P	**0.519**	**0.027**	34
M16	P	**0.552**	**0.005**	**F16**	P	**0.611**	**0.002**	34
M17	P	**0.450**	**0.027**	**F17**	P	**0.522**	**0.018**	34
				F18	P	**0.508**	**0.011**	34

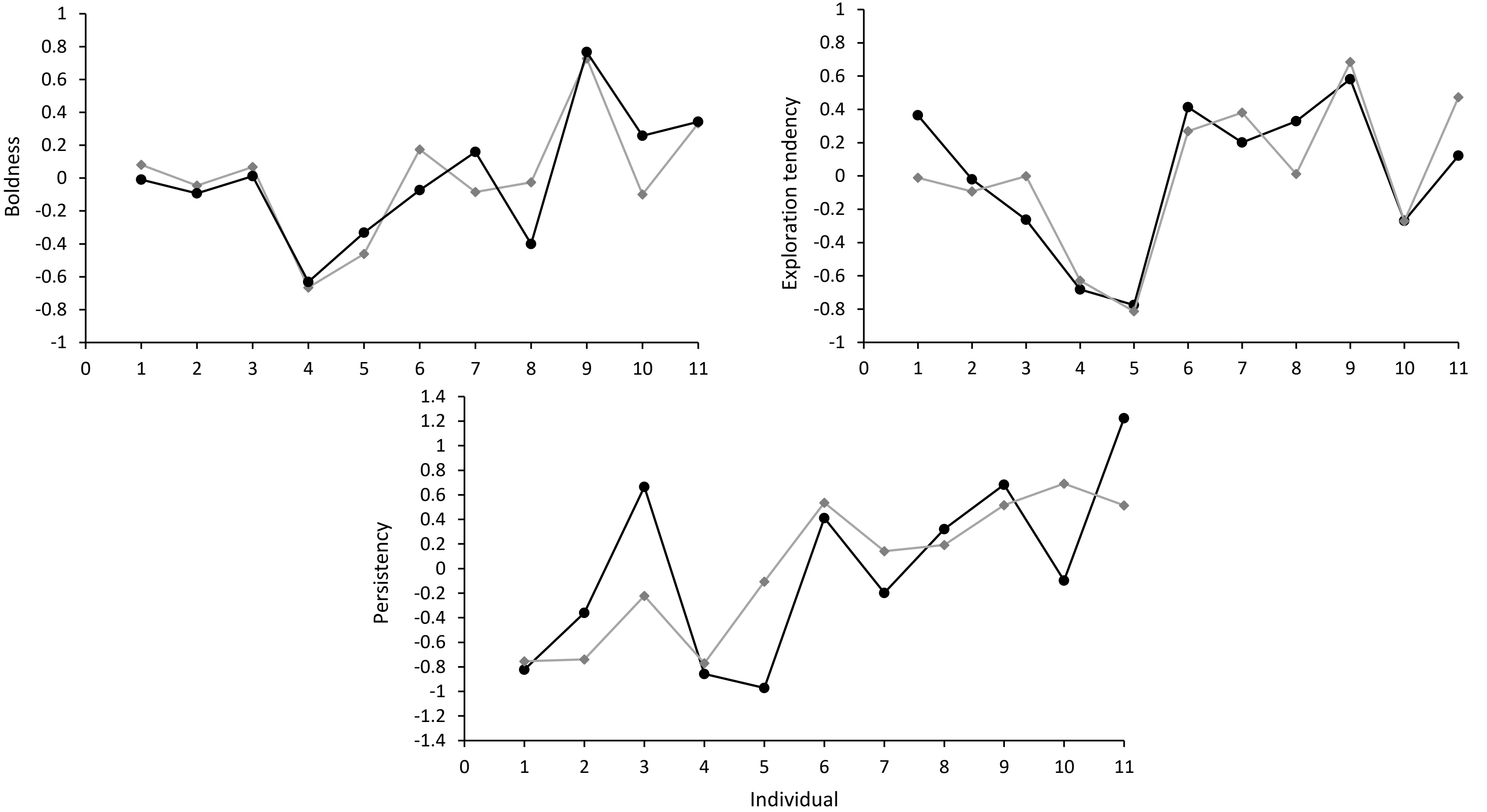

Figure 5.3.1: Depicting differences in individual ring-tailed lemur personality trait scores in the first session (black circles, black solid line) and the second (repeat) session (grey diamonds, grey solid line).

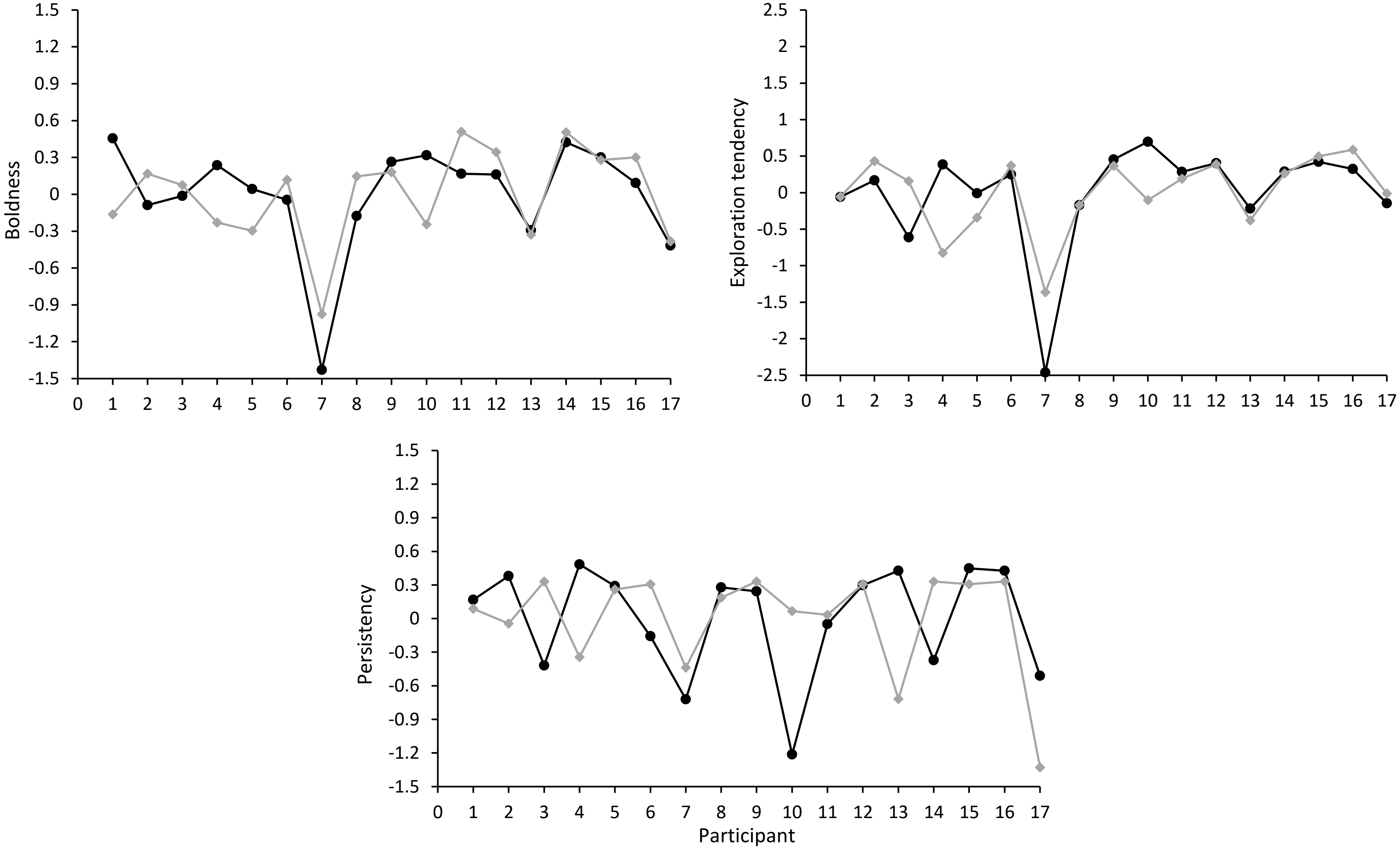

Figure 5.3.2a: The personality trait scores of individual boys in the first session (black circles, black solid line) and the second (repeat) session (grey diamonds, grey solid line).

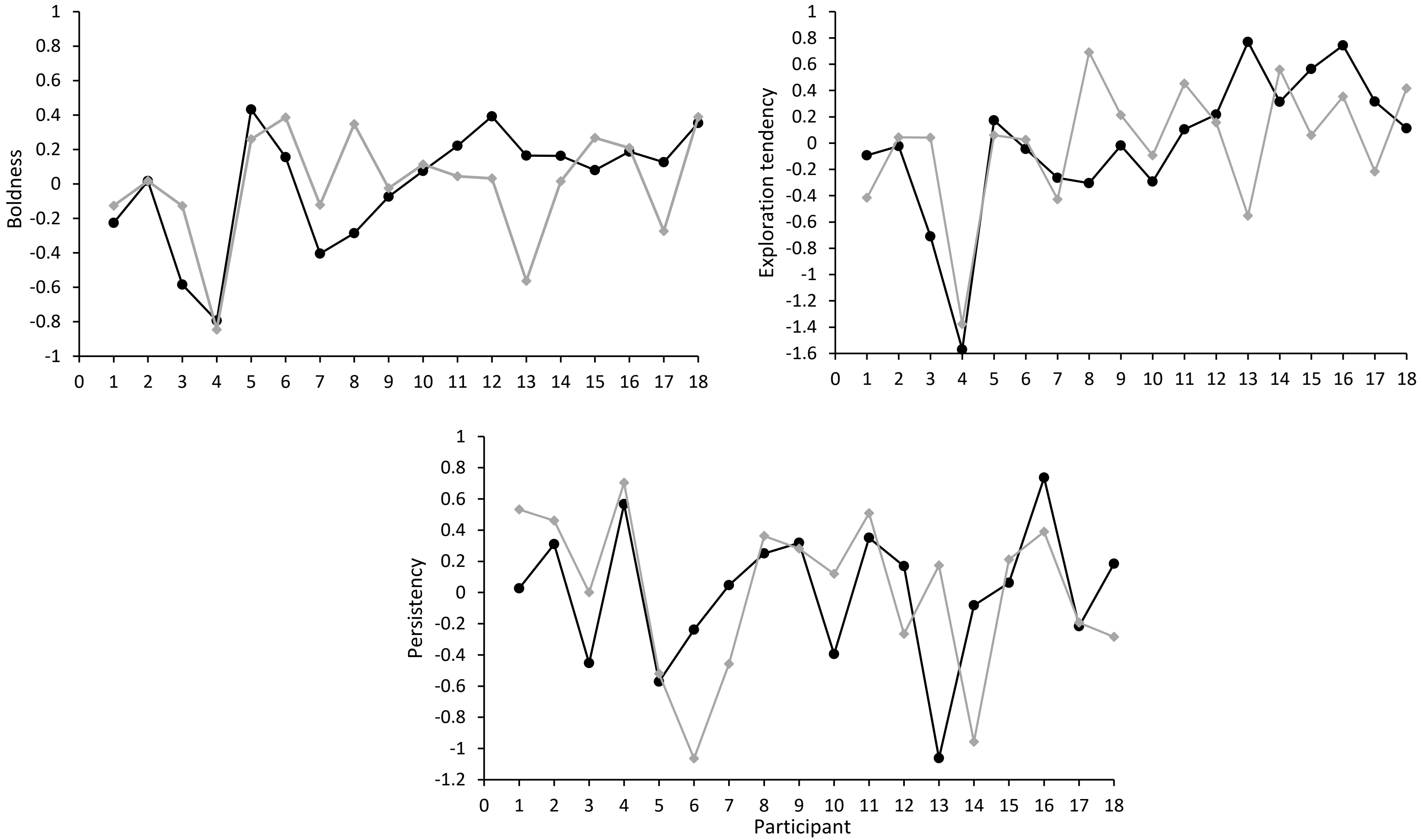

Figure 5.3.2b: Individual girl's personality trait scores in the first session (black circles, black solid line) and the second (repeat) session (grey diamonds, grey solid line).

5.3.2: Ring-tailed lemurs

5.3.2.1: Boldness

There were no significant correlations between any of the 2D:4D ratio measures and boldness in this group of ring-tailed lemurs (R2D:4D - *r* = 0.354, df = 11, P = 0.286; L2D:4D – *r* = -0.129, df = 10, P = 0.723; M2D:4D – *r* = 0.054, df = 10, P = 0.882, Figure 5.3.3).

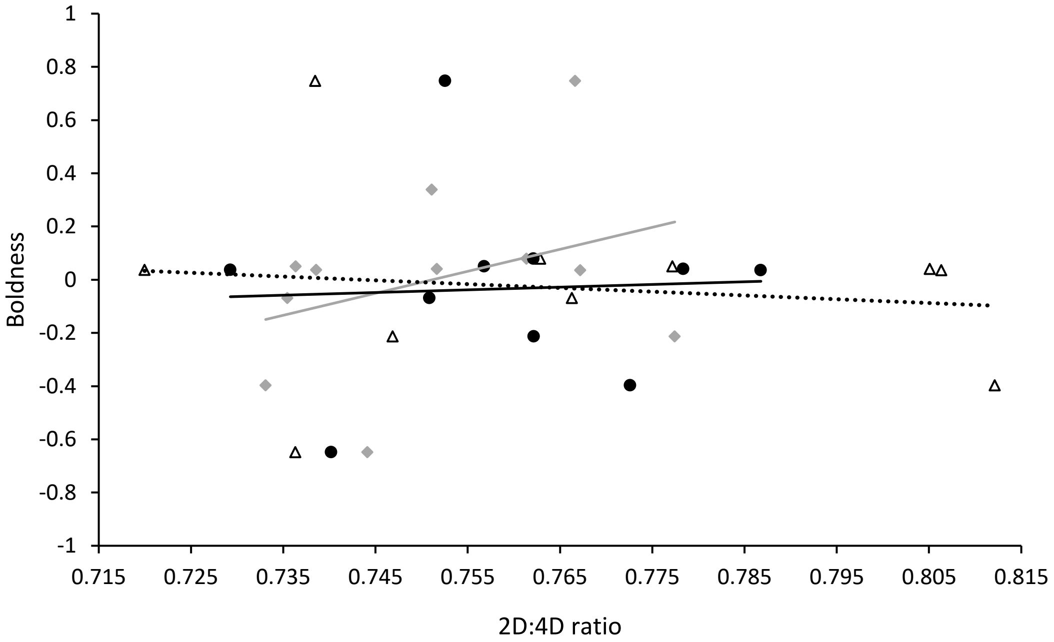

Figure 5.3.3: Relationship between R2D:4D (grey diamonds, grey solid trendline), L2D:4D (white triangles, black dotted trendline) and M2D:4D (black circles, black solid trendline) and boldness in ring-tailed lemurs.

5.3.2.2: Exploration tendency

Exploration tendency was not significantly correlated with any of the 2D:4D ratio measures (R2D:4D - *r* = 0.390, df = 11, P = 0.235; L2D:4D – *r* = -0.339, df = 10, P = 0.338; M2D:4D – *r* = -0.131, df = 10, P = 0.718, Figure 5.3.4).

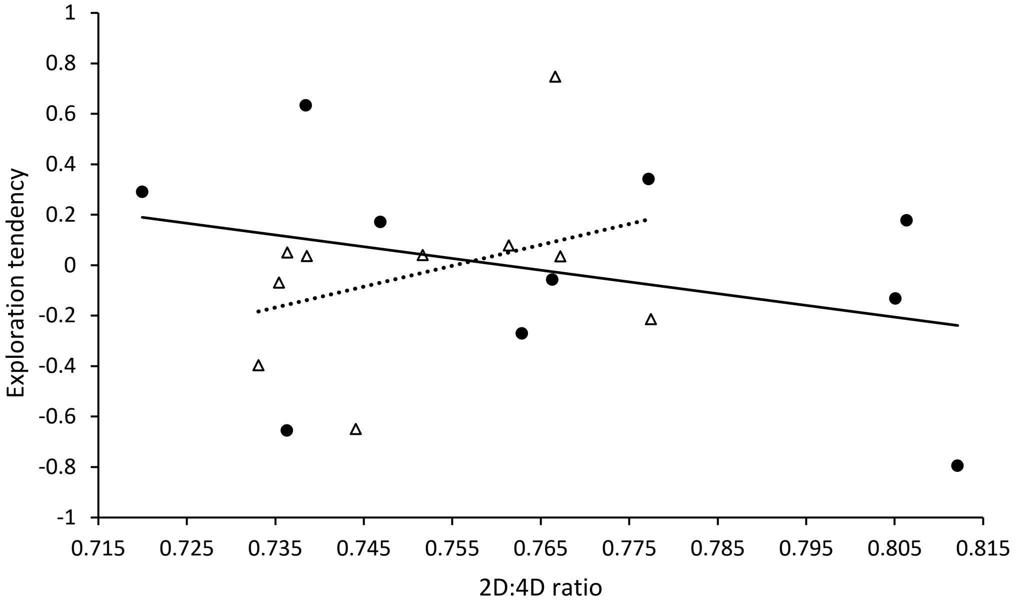

Figure 5.3.4: Relationship between exploration tendency and R2D:4D (grey diamonds, grey solid trendline), L2D:4D (white triangles, black dotted trendline) and M2D:4D (black circles, black solid trendline) in ring-tailed lemurs.

5.3.2.3: Persistency

Persistency did not significantly correlate with any of the 2D:4D ratio measures in ring-tailed lemurs (R2D:4D - *r* = 0.275, df = 11, P = 0.414; L2D:4D – *r* = -0.245, df = 10, P = 0.495; M2D:4D – *r* = -0.088, df = 10, P = 0.809, Figure 5.3.5).

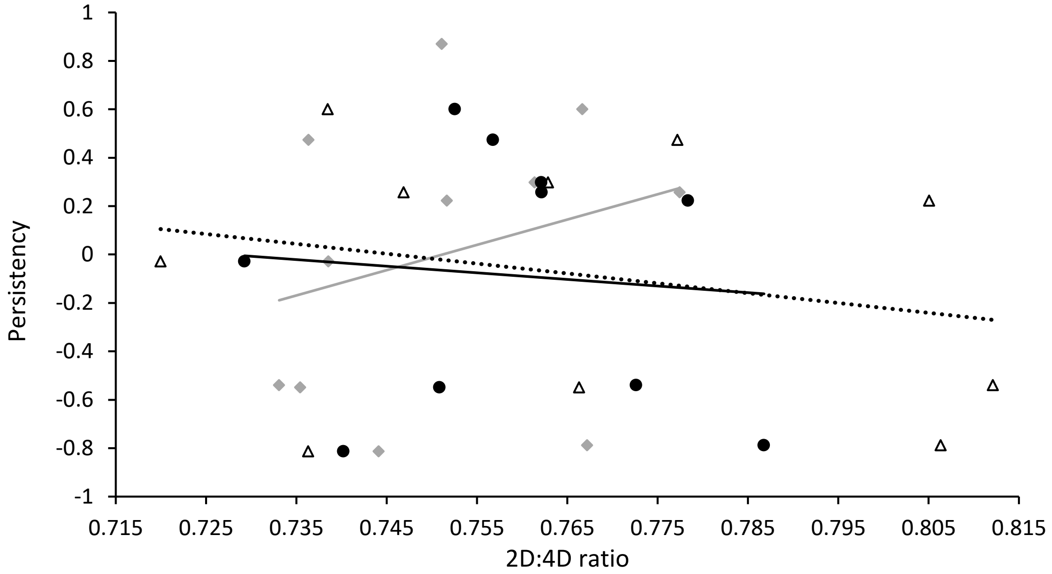

Figure 5.3.5: Relationship between persistency and R2D:4D (grey diamonds, grey solid trendline), L2D:4D (white triangles, black dotted trendline) and M2D:4D (black circles, black solid trendline) in ring-tailed lemurs.

5.3.3: Robust capuchin monkeys

5.3.3.1: Competitiveness

Competitiveness was significantly negatively correlated with L2D:4D (r = -0.786, df = 7, P = 0.036) and M2D:4D (r = -0.857, df = 7, P = 0.014) but not R2D:4D (*r* = -0.575, df = 10, P = 0.082) in robust capuchins (Figure 5.3.6).

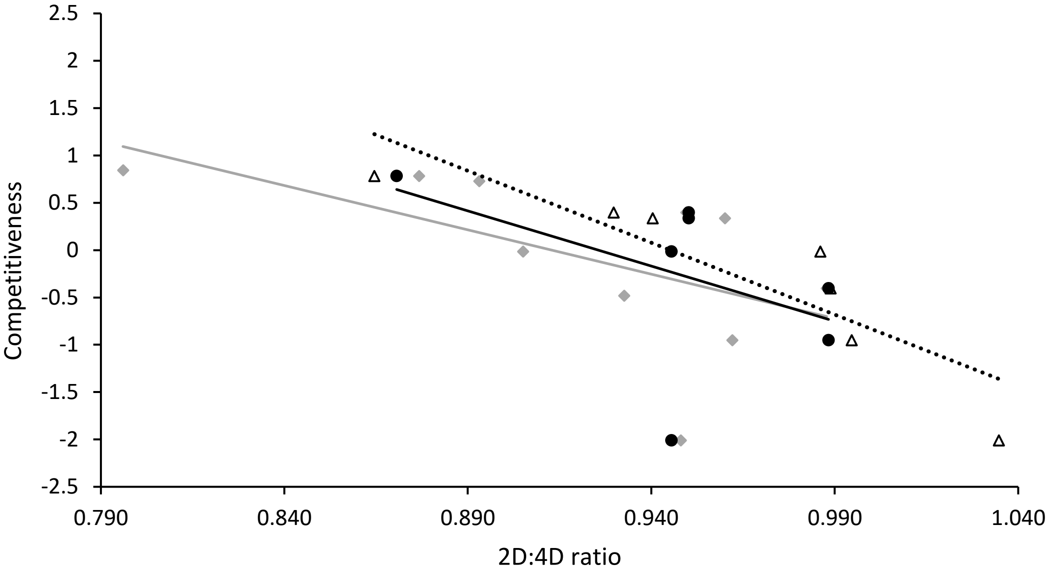

Figure 5.3.6: Relationship between R2D:4D (grey diamonds, grey solid trendline), L2D:4D (white triangles, black dotted trendline) and M2D:4D (black circles, black solid trendline) and competitiveness in robust capuchins.

5.3.3.2: Curiousness

Curiousness was not significantly correlated with any of the 2D:4D ratio measures in robust capuchins (R2D:4D - *r* = -0.222, df = 10, P = 0.538; L2D:4D – *r* = -0.276, df = 7, P = 0.550; M2D:4D – *r* = -0.198, df = 7, P = 0.671, Figure 5.3.7).

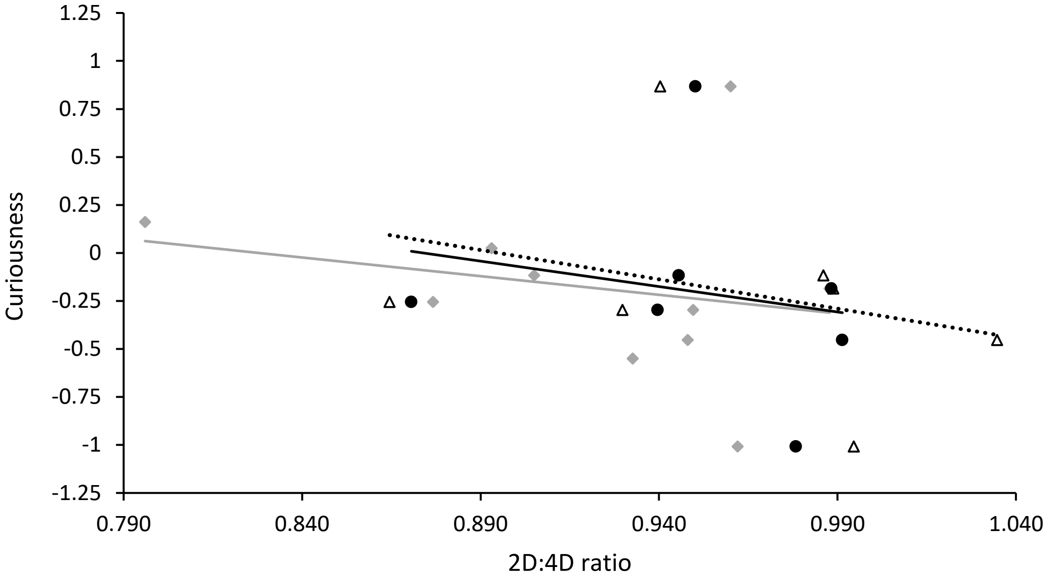

Figure 5.3.7: Relationship between curiousness and R2D:4D (grey diamonds, grey solid trendline), L2D:4D (white triangles, black dotted trendline) and M2D:4D (black circles, black solid trendline) in robust capuchins.

5.3.3.3: Persistency

There were no significant correlations between persistency and any of the 2D:4D ratio measures in robust capuchins (R2D:4D - $r = 0.004$, df = 10, P = 0.991; L2D:4D – $r = -0.248$, df = 7, P = 0.592; M2D:4D – $r = -0.276$, df = 7, P = 0.549, Figure 5.3.8).

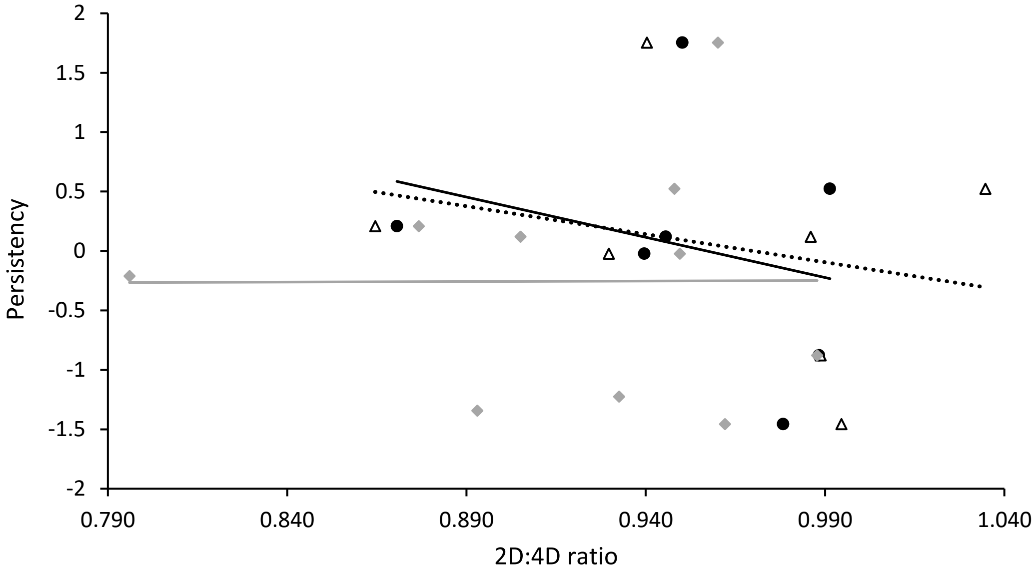

Figure 5.3.8: Relationship between persistency and R2D:4D (grey diamonds, grey solid trendline), L2D:4D (white triangles, black dotted trendline) and M2D:4D (black circles, black solid trendline) in robust capuchins.

5.3.4: Human children

5.3.4.1: Boldness

Correlations were not significant for boldness and R2D:4D (*r* = -0.077, df = 18, P = 0.762) or M2D:4D (*r* = -0.371, df = 18, P = 0.130) in girls. The negative correlation between boldness and L2D:4D in girls was near significance (*r* = -0.468, df = 18, P = 0.050, Figure 5.3.9). Boldness correlated significantly and negatively with R2D:4D (*r* = -0.631, df = 17, P = 0.007), L2D:4D (*r* = -0.494, df = 17, P = 0.044) and M2D:4D (*r* = -0.600, df = 17, P = 0.011, Figure 5.3.10) in boys. The significant correlations were not maintained however, when a male participant with comparatively higher 2D:4D ratios than other members of the cohort was removed from the analysis (R2D:4D - *r* = -0.134, df = 16, P = 0.622; L2D:4D – *r* = -0.097, df = 16, P = 0.722; M2D:4D – *r* = -0.131, df = 16, P = 0.630).

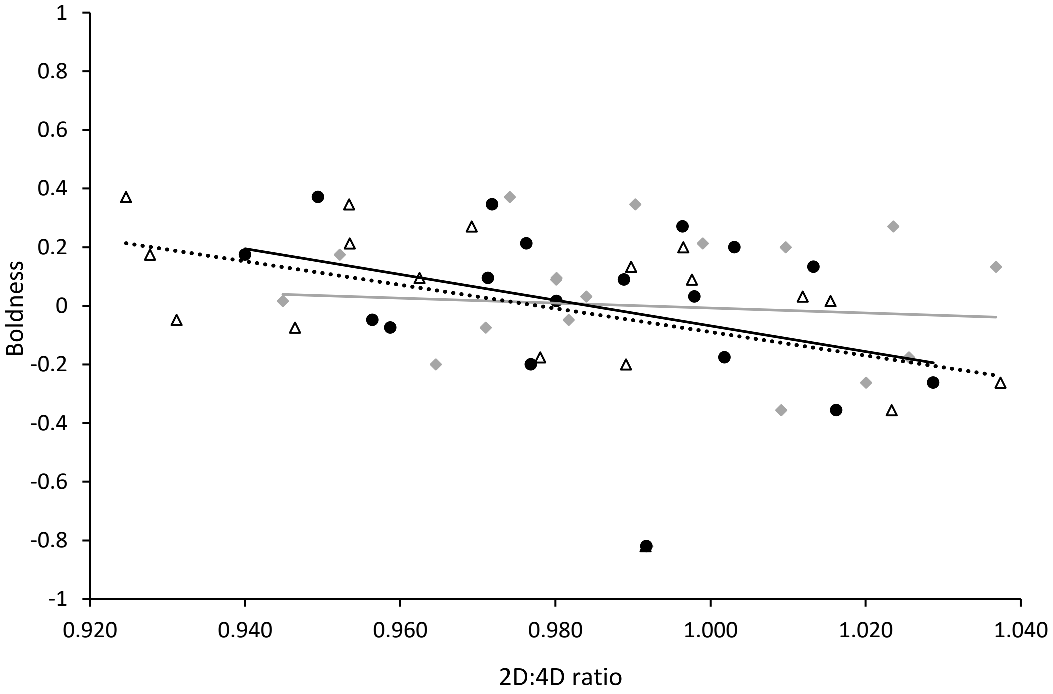

Figure 5.3.9: Relationship between R2D:4D (grey diamonds, grey solid trendline), L2D:4D (white triangles, black dotted trendline) and M2D:4D (black circles, black solid trendline) and boldness in girls.

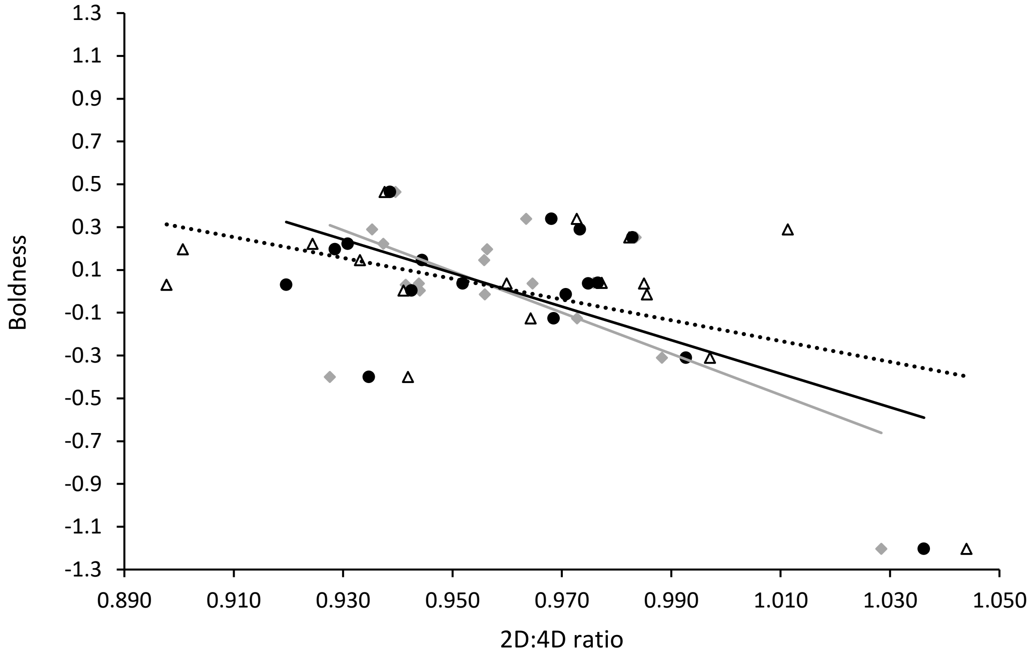

Figure 5.3.10: Relationship between R2D:4D (grey diamonds, grey solid trendline), L2D:4D (white triangles, black dotted trendline) and M2D:4D (black circles, black solid trendline) and boldness in boys.

5.3.4.2: Exploration tendency

There were no significant correlations between exploration tendency and any of the 2D:4D ratio measures in girls (R2D:4D - *r* = -0.210, df = 18, P = 0.402; L2D:4D – *r* = -0.269, df = 18, P = 0.280; M2D:4D – *r* = -0.265, df = 18, P = 0.287, Figure 5.3.11). Exploration tendency correlated significantly and negatively with R2D:4D (*r* = -0.651, df = 17, P = 0.005) and M2D:4D (*r* = -0.579, df = 17, P = 0.015) in boys but not L2D:4D (*r* = -0.499, df = 17, P = 0.070; Figure 5.3.12). Again, no significant correlations were apparent when the higher 2D:4D ratio male was removed from the analysis (R2D:4D - *r* = -0.094, df = 16, P = 0.728; L2D:4D – *r* = 0.076, df = 16, P = 0.779; M2D:4D – *r* = 0.016, df = 16, P = 0.953).

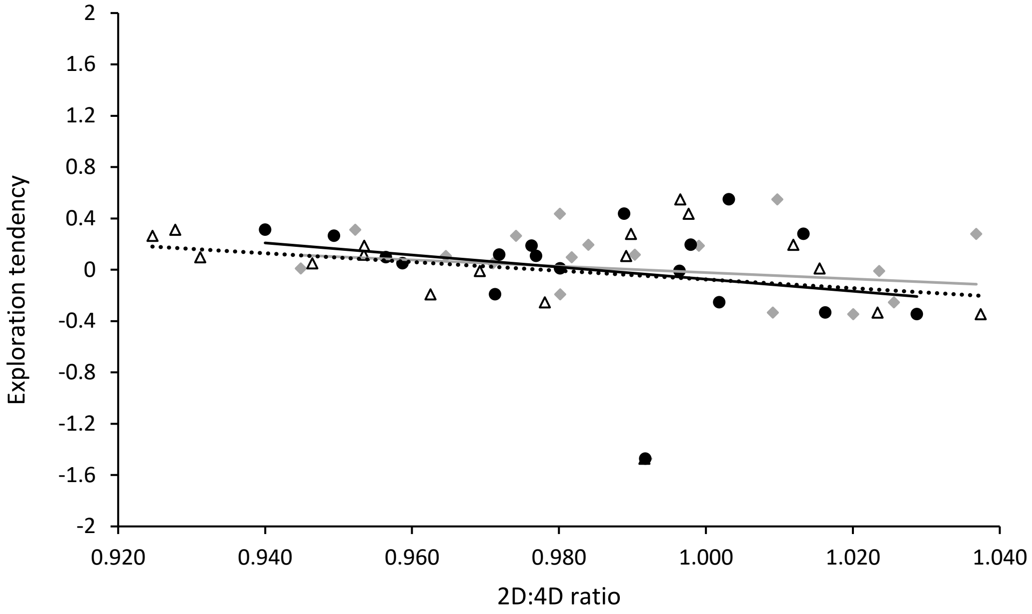

Figure 5.3.11: Relationship between R2D:4D (grey diamonds, grey solid trendline), L2D:4D (white triangles, black dotted trendline) and M2D:4D (black circles, black solid trendline) and exploration tendency in girls.

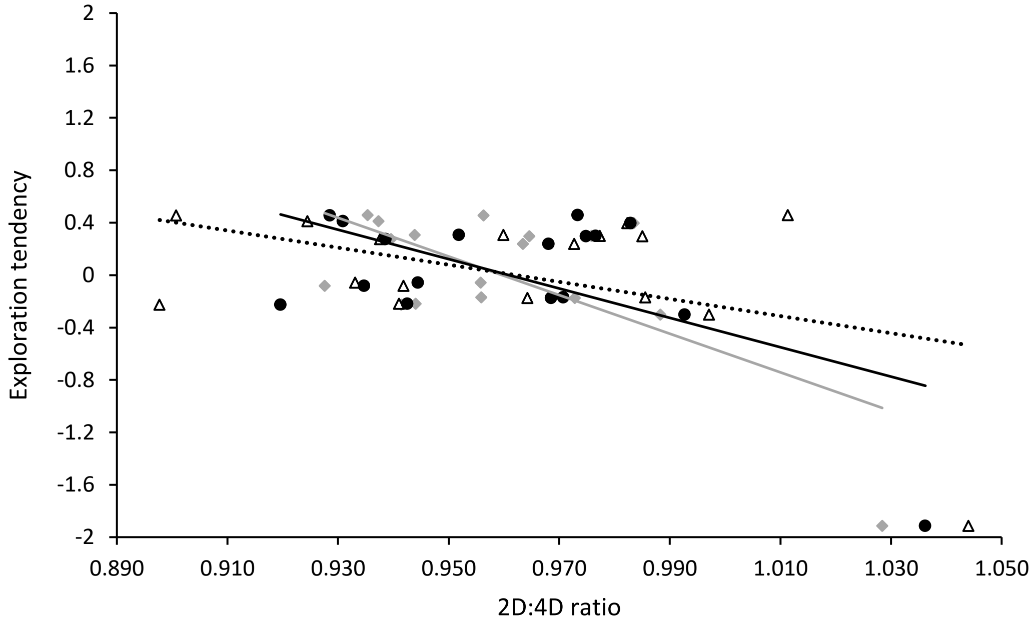

Figure 5.3.12: Relationship between R2D:4D (grey diamonds, grey solid line), L2D:4D (white triangles, black dotted trendline) and M2D:4D (black circles, black solid trendline) and exploration tendency in boys.

5.3.4.3: Persistency

There were no significant correlations between persistency and any of the 2D:4D ratio measures in girls (R2D:4D – *r* = 0.031, df = 18, P = 0.904; L2D:4D – *r* = 0.101, df = 18, P = 0.690; M2D:4D – *r* = 0.082, df = 18, P = 0.746) or boys (R2D:4D – *r* = -0.160, df = 17, P = 0.539; L2D:4D – *r* = -0.221, df = 17, P = 0.393; M2D:4D – *r* = -0.214, df = 17, P = 0.410, Figure 5.3.13a & b).

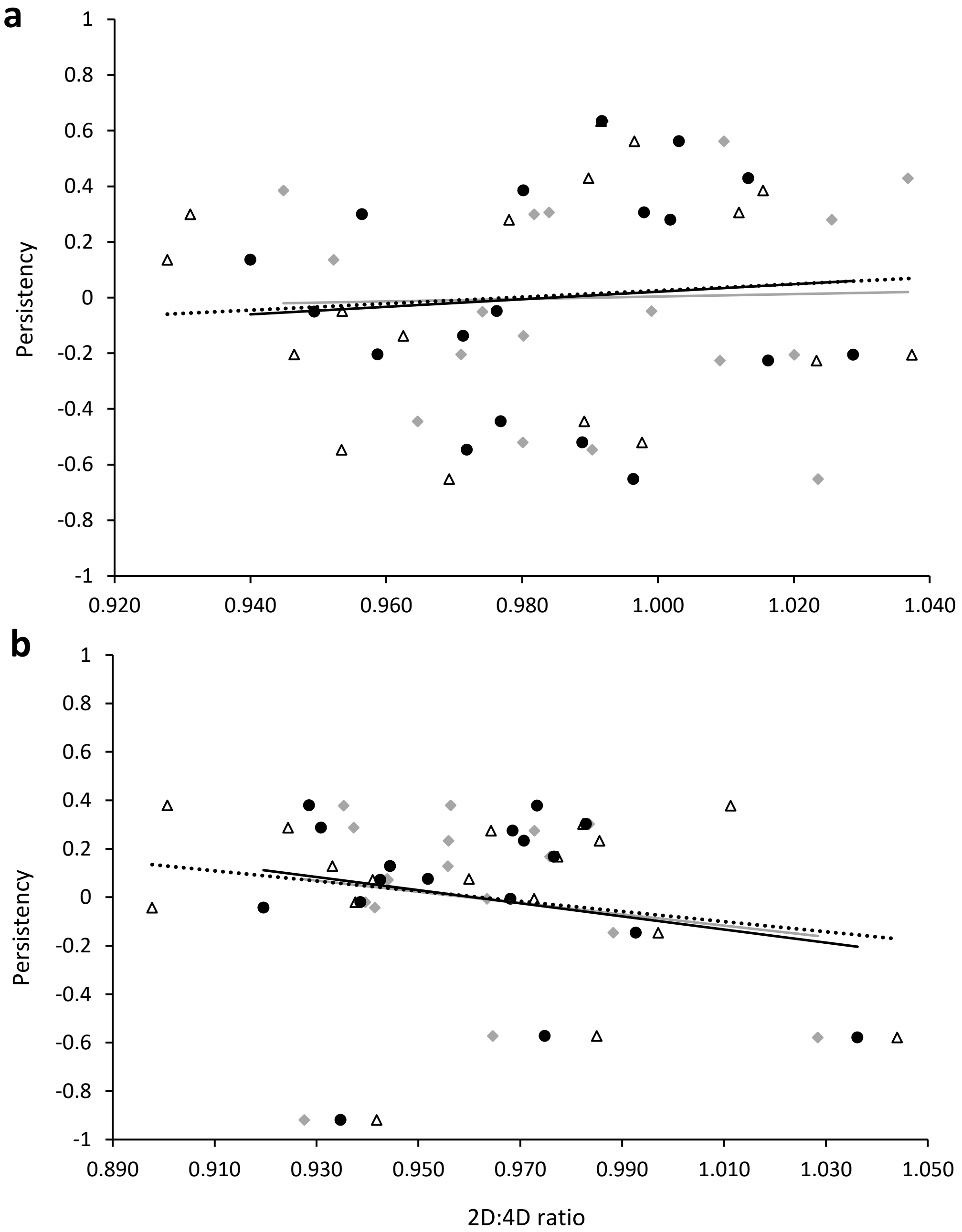

Figure 5.3.13: Relationship between R2D:4D (grey diamonds, grey solid trendline), L2D:4D (white triangles, black dotted trendline) and M2D:4D (black circles, black solid trendline) and persistency in (a) girls and (b) boys.

5.4 Discussion

This study demonstrates that PAE (as inferred from 2D:4D ratios) correlate with some but not all of the investigated personality traits, and the results varied across the three species of primate. 2D:4D ratio correlated negatively with boldness and exploration tendency in human boys and with competitiveness in robust capuchins. No other personality traits correlated with 2D:4D ratios in any taxa, including no significant relationships between any personality traits and 2D:4D ratios in ring-tailed lemurs and human girls. In humans, it appears that PAE may have a greater capacity to influence the expression of behavioural traits in males than in females. This may be the case in other non-human primates, but small sample sizes precluded the ability to explore the possibility in this study. Overall, these results suggest that there is a relationship between PAE and personality in humans and other haplorhine primates but that the association is limited to particular traits, the expression of which are influenced by the predisposing effects of prenatal androgens on brain patterning and possibly where postnatal androgens also play a regulatory role. In many human 2D:4D ratio and personality studies which rely on questionnaires/ratings to assess personality in individuals, significant correlations between variables tend to be weak (Kim *et al*. 2014; Hampson *et al*. 2008; Lindová *et al.* 2008; Lippa *et al.* 2006; Fink *et al*. 2004b). In this study the significant 2D:4D ratio-personality trait correlations in children and robust capuchins ranged from moderate to strong suggesting that an experimental approach using quantifiable behavioural variables is superior for identifying associations between personality traits and PAE in primates.

There were no significant correlations between any of the 2D:4D ratio measures and any of the personality traits in ring-tailed lemurs and data for R2D:4D and L2D:4D tended to trend in opposite directions for each trait in this species. Low 2D:4D ratio individuals were not bolder than high 2D:4D ratio individuals in this group of ring-tailed lemurs but the trends were in the predicted direction for L2D:4D. Contrary to prediction, I found no associations between exploration tendency and any of the 2D:4D ratio measures in ring-tailed lemurs but again, the trends were in the predicted direction for L2D:4D and M2D:4D in that individuals with lower L2D:4D and

M2D:4D had higher exploration tendency scores. I found no relationship between persistency and any of the 2D:4D ratio measures and the data trended in the predicted direction for R2D:4D only. Individuals with higher R2D:4D showed generally (though not significantly) higher persistency scores than those with lower R2D:4D but the opposite pattern was observed between this personality trait and L2D:4D and M2D:4D.

The ring-tailed lemur sample size was small and the lack of association between the 2D:4D ratio measures and the three personality traits may be a result of low statistical power or due to several individuals with 'middling' 2D:4D ratios scoring high on all three personality traits whereas those with higher or lower 2D:4D ratios did not display a discernible pattern in the traits. Additionally, the captive condition and management of these animals should be acknowledged as a potential factor influencing their behaviour under experimental conditions. For example, these animals regularly receive 'enrichment' (e.g. food hidden in logs, different scents) and although the lemurs had not had previous contact with any of the apparatus used in this study, their past experience with enrichment generally could have affected their reactions in some of the tests. Differences in expression of personality between captive and wild animals have been observed in other animals, including the spotted hyena (*Crocuta crocuta*) where captive animals were found to be less neophobic and more explorative than their wild counterparts (Benson-Amram *et al.* 2013). Wild animals face different selective pressures to those living in captivity and study into associations between the 2D:4D ratio and personality traits in wild animals may provide different results. Replicating the required comparable experimental conditions in a wild environment, however, would be challenging.

There were significant associations between 2D:4D ratios and competitiveness in robust capuchins; monkeys with lower L2D:4D and M2D:4D displayed higher competitiveness. The correlation between R2D:4D and competitiveness was not significant, but the trend of the data was in the expected direction with lower R2D:4D individuals displaying higher competitiveness. PAE are known to increase competitive abilities in humans (Hönekopp & Schuster 2010; Hönekopp *et al.* 2006; Pokrywka *et al*. 2005) and other animals (Burley & Foster 2004; Schwabl & Lipar

2002) and considering the role of both pre- and postnatal androgens in the expression of dominant and aggressive behaviour (Mazur & Booth 1998; Higley *et al*. 1996; Christiansen & Knussmann 1987), this negative relationship in robust capuchins is perhaps not surprising. Additionally, the way in which the trait competitiveness was measured in robust capuchins was via a dyadic food competition test (Uher *et al.* 2013), in which an item of food was placed equidistant between two individuals in the same cage (Uher *et al*. 2013 supplementary material). This experimental set-up could have been viewed by the animals involved as a challenge situation and many of the associations between 2D:4D ratio and personality traits/behaviours in humans are found where experiments are conducted under challenge conditions (Ribeiro *et al.* 2016; Crewther *et al.* 2015; Manning *et al*. 2014; Kilduff *et al*. 2013). The 2D:4D ratio, therefore, may correlate not just with the organising effects of prenatal androgens on brain patterning, but also on the endocrine system, postnatal hormone reactivity and its associated behavioural outcomes (Crewther *et al*. 2015; Manning *et al*. 2014).

As in the ring-tailed lemurs, captive management practises of the robust capuchins may have affected these individuals' expression of exploratory behaviours and there were no significant associations between curiousness and any of the 2D:4D ratio measures in robust capuchins. The trends were all in the predicted direction however, such that individuals with lower 2D:4D ratios had higher scores for curiousness. There were no significant correlations between persistency and any of the 2D:4D ratio measures in robust capuchin monkeys and the data trends for L2D:4D and M2D:4D were in the opposite direction to prediction. Data showed a negative rather than positive trend so individuals with lower left and mean 2D:4D ratios scored higher for persistency than those with higher 2D:4D ratios. There was, however, no discernible relationship between this trait and the R2D:4D ratio in robust capuchins, the trendline presenting as near flat. I found no sex difference in 2D:4D ratio among robust capuchins and Uher *et al*. (2013) in their study on this group found no age or sex differences in the three personality traits examined here, so these factors cannot explain any lack of relationship. The fact that I did not find a relationship between certain 2D:4D measures and personality traits may be due to the small sample size of ten individuals and subsequent low statistical power. Although this could be the case for boldness and exploration tendency, the failure to detect an association between 2D:4D ratio measures and persistency seems unlikely to be an artefact of low power. A more likely explanation is that the expression of this trait may not be influenced by PAE in the same way that traits like competitiveness and possibly curiousness/exploration tendency are.

Human boys displayed moderate negative correlation between their scores for boldness and all 2D:4D ratio measures, suggesting that PAE influence the expression of this trait in boys. Conversely, although the data trended in the same direction for girls, the correlations were not significant for this trait and any of the 2D:4D ratio measures. Exploration tendency correlated negatively with R2D:4D and M2D:4D in boys but not with any of the 2D:4D ratio measures in girls. This suggests that PAE on brain patterning may have an influence over the postnatal expression of these traits in boys but not in girls. Although the trend in the data was in the predicted direction, girls with lower 2D:4D ratios did not have significantly higher exploration tendencies than girls with higher 2D:4D ratios. Although nonsignificant, trends were in the predicted direction for girls in that those with higher 2D:4D ratios also had higher scores for persistency. However, in boys the trends were consistently contrary to prediction with higher 2D:4D ratio boys having lower persistency scores. As this trait showed low test-retest reliability the results could be an indication of habituation of the children. If they had been unsuccessful at the first attempt to extract the reward inside the puzzle ball this could have made them averse to trying a second time. Additionally, as experience had taught them that they were likely to receive a reward afterwards regardless of whether they were successful in retrieving the reward inside the puzzle ball, their motivation in the second session may have been reduced in some cases. Another explanation is that, as in ring-tailed lemurs and robust capuchins, the 2D:4D ratio is not a good predictor of this trait in human children. It is highly probable that, unlike the 2D:4D ratio, expression of this trait is not under the organisational influence of PAE or that this trait is not of biological significance to these species and therefore not subject to evolved mechanisms as other traits are.

Sexual differentiation of the mammalian brain occurs in utero where it is driven by the production of gonadal steroid hormones, the concentrations of which differ between the sexes. The 2D:4D ratio appears to be a better predictor of behaviour in boys than in girls and boys also had on average lower 2D:4D ratios than girls. This sex difference is likely due to the fact that males develop in an environment which is comparatively higher in prenatal androgens than females, meaning that traits over which androgens may have an organisational influence are more apparent in boys or moderated by higher POE in girls. Aggression is a sexually dimorphic behaviour in humans (males tending to be more aggressive than females) and is proposed to be related to the organisational effects of prenatal androgens (Bailey & Hurd 2005). Consistent with this, high physical aggression has been associated with low 2D:4D ratio (high PAE) in men but not in women (Bailey & Hurd 2005). Another sexually dimorphic trait associated with the organisational effects of prenatal androgens is risk-taking. This has been found to be consistently higher in men than in women across various contexts (e.g. financial, social, recreational, ethical and health) and low 2D:4D ratios are associated with increased risk-taking behaviour in men but not in women (Stenstrom *et al.* 2011). The fact that male but not female 2D:4D ratios correlated with the traits mentioned above and with boldness and exploration tendency here may be due to the evolutionary significance of these traits for males. Expression of behaviour associated with these traits would be adaptive in males, in terms of mating competition, traditional roles in hunting, warfare and exploration of the physical environment, which may have led to stronger selection for these personality traits and the underlying proximate mechanisms regulating their expression in males than in females (Hampson *et al.* 2008). Additionally, as all girls involved in this study were free of any hormonal disorders and can be assumed to have been exposed to PAE within the normal range for their sex, it is possible that associations between 2D:4D ratios and behaviours/traits associated with more masculine hormonal profiles (e.g. boldness and exploration tendency) are not as evident in normal girls as they are in boys. POE are higher in girls compared to their male counterparts and this may have affected the expression of behaviours associated with boldness and exploration tendency in girls, possibly by making them more risk-averse. Indeed, Lindová *et al*. (2008) suggest that since significant correlations between 2D:4D ratio and personality traits were only found in their female cohort, this draws attention to the involvement of POE, as well as PAE, in the association between 2D:4D ratio and certain personality traits.

There was one male participant in the human children study group with comparatively high 2D:4D ratios who also had very low scores for both boldness and exploration tendency compared to the other male participants, and correlations between 2D:4D ratios and boldness and exploration tendency became non-significant when this individual was removed from the analysis. One interpretation of this result is that relationships between 2D:4D ratio and personality traits may be more apparent in the expression of traits known to be affected by PAE on brain patterning and behaviour e.g. dominance, aggression, competitiveness. Alternatively, or additionally, for traits which are influenced by other factors, including other pre- and postnatal hormones, their relationship with 2D:4D ratio may not be perceptible unless individuals experienced a prenatal hormonal environment in which PAE/POE were outside the typical range for their sex. Both the feminised 2D:4D ratio and behaviour of this participant are suggestive of a prenatal environment higher in POE than PAE, possibly outside of the typical range for human boys. The lasting behavioural effects of atypical prenatal sex hormone exposure have been observed in artificially androgenised juvenile female rhesus macaques (*Macaca mulatta*) which showed a reduction in interest in infants compared to controls (Wallen 2005). In wild non-hormonally manipulated female chacma baboons (*Papio ursinus*), however, no association was observed between a female's exposure to PAE (inferred from 2D:4D ratios) and her interest in infants, lower 2D:4D ratio (higher PAE) females were not less interested in infants than higher 2D:4D ratio (lower PAE) females (Howlett *et al*. 2015). Further evidence of behavioural consequences arising as a result of exposure to unusual sex hormone levels comes from studies of human girls with congenital adrenal hyperplasia (CAH), a condition in which disruption of the glucocorticoid synthesis pathway in the adrenal glands during development causes androgens to be produced at unusually high levels and, as a result, CAH affected girls are exposed to prenatal androgen levels comparable to those of normal boys (Wallen & Hassett 2009). In comparison to controls, girls with CAH have lower 2D:4D ratios

(Brown *et al*. 2002), masculinised patterns of aggression (Nielssen *et al.* 2011) and display a reduced interest in infants (Leveroni & Berenbaum 1998). Boys with CAH on the other hand, are exposed to prenatal androgen levels largely similar to boys without CAH (Pang *et al.* 1980) and show no appreciable increase in male-typical behaviours, being behaviourally similar to control boys (Hines *et al.* 2016; Pasterski *et al.* 2011, 2005; Berenbaum & Hines 1992). The masculinisation described for CAH girls can therefore be attributed to exposure to usually high PAE for their sex. Although this individual affected the strength of the correlation between 2D:4D ratio and boldness and exploration tendency in boys, the fact that an individual with a very feminised 2D:4D ratio (low inferred PAE) also displayed very low scores for these traits (where higher scores would be indicative of higher PAE) and that the data trended in the same direction among girls, suggests that the relationship is a true one and PAE can affect an individual's bold and exploratory behaviour. A larger sample size of children in order to increase the breadth of 2D:4D ratio measurements in both sexes would be advantageous in further investigating these relationships.

5.4.1: Summary

This study is the first to investigate correlations between 2D:4D ratio and personality traits in multiple primate species using quantitative behavioural variables and an experimental approach. Much stronger correlations were obtained between personality traits and 2D:4D ratios in comparison to more traditional questionnaire-based methods, and this suggests that using quantitative behavioural data measured under experimental conditions may be a more suitable way to study prenatal sex hormone effects on behaviour in primates, including humans.

The 2D:4D ratio was not a good predictor of any of the three personality traits in ring-tailed lemurs or of curiousness in robust capuchins, although their captive condition may have influenced their responses in some experiments. The 2D:4D ratio was not a good predictor of the personality trait persistency in these primates suggesting that expression of this trait and/or behaviours associated with this trait may not be influenced by PAE on brain patterning. Alternatively, this trait may not lead to variation in fitness in these species and therefore would not be under selective pressure. Competitiveness, boldness and exploration tendency correlated negatively with 2D:4D ratio measures suggesting that PAE play a significant role in the expression of these personality traits in robust capuchin monkeys and humans and perhaps also in other haplorhine primates. The 2D:4D ratio appears to be a better predictor of behaviour in boys than girls, perhaps as a result of sex differences in the evolutionary significance of these traits and/or the possibility that in females exposed to the usual range for their sex, PAE have a limited ability to influence behaviours/personality traits over which female sex hormones may also have a regulatory role. Additionally, the fact that the correlations between personality traits and 2D:4D ratio in boys were rendered non-significant by the removal of one male participant with a very feminised 2D:4D ratio suggests that PAE on personality, although not as apparent in individuals which have been exposed to prenatal sex hormones within the typical range for their sex, may be more detectable in individuals which have been exposed to PAE/POE outside of this range.

- Chapter 6 -

General discussion

6.1: Summary and main findings

The ultimate causes contributing to variation in primate behaviour and social systems have been well studied (Koenig *et al.* 2013; Przybyta 2013; Kappeler & van Schaik 2004; van Schaik 1989; Sterck *et al*. 1997; Trivers 1972), but their evolutionary foundations are still not completely known (Thierry 2008; Koenig & Borries 2009; Sussman *et al.* 2005; Sussman & Garber 2004). In particular, the role that proximate mechanisms and phylogenetic constraints may play in the expression of primate behaviour and sociality are poorly understood. The objective of this thesis was to determine whether prenatal androgen effects (PAE) may act as a proximate mechanism affecting the expression of primate behaviour in ways that are ultimately adaptive. Here I return to the overall aims of the thesis and discuss whether these have been achieved.

1) To investigate the relationship between PAE and mating behaviour and intrasexual competition in male non-human primates.

In general, monogamous and polyandrous males had the highest second-to-fourth digit (2D:4D) ratios (low inferred PAE) while polygynandrous and polygynous males had the lowest 2D:4D ratios (high inferred PAE). Male 2D:4D ratios varied with the form of polygyny and polygynandry relative to the requirements for males to display competitive behaviours over cooperative behaviours within each mating system. The results indicate that PAE may act as a proximate mechanism underpinning the expression of behaviour in male primates in ways that appear adaptive to their mating system and show that distinguishing between different mating systems (and the forms these take) is crucial if analyses are to accurately encompass variation in male intrasexual competition and the strength of selection for PAE. Cooperation, competition and the proximate mechanisms which underlie their expression are closely linked, and through improved mating system terminology and more in-depth categorisations, this study has revealed that understanding the relationship between PAE and mating behaviour in male non-human primates relies on considering the strength of selection for cooperative behaviours facilitated by prenatal oestrogen effects (POE), in addition to competitive behaviours. Relationships between 2D:4D ratios and anatomical traits associated with male intrasexual competition (male canine crown height [MCCH] and canine crown height [CCH] dimorphism) were non-significant, as were relationships between 2D:4D ratios and male reproductive skew and mating skew. Small sample sizes meant that I was unable to fully explore the impact that PAE may have on the latter two quantifiable measures of male sexual competition, and these, in addition to sexually selected anatomical traits such as testis size, are worthy of further investigation. The results thus provide mixed support for the hypothesis that PAE may act as a proximate mechanism underpinning the expression of behaviour in male primates in ways that are adaptive to their mating system.

2) To explore the potential relationship between PAE and marriage systems in humans.

Studies in non-human primates imply that selection for higher PAE is stronger in both sexes where intrasexual competition is higher (Chapter 2; Nelson & Shultz 2010). Whether or not this observation holds true for humans was not fully understood. Although there was some support for this premise in non-phylogenetically controlled analysis, this study found no associations between male or female 2D:4D ratios and marriage system once the patterns of relatedness among the study populations were considered. This brought to light the vulnerabilities incurred by ignoring phylogeny when carrying out cross-cultural analysis in human populations. As males are the competing sex, there may still be strong selective pressure for high PAE regardless of the marriage system being practised. Additionally, as higher PAE impact negatively on female fertility, sexual selection may favour lower PAE and higher POE in females, again, irrespective of the marriage system. The results suggest that the marriage system practised by a population does not incur considerable selection for higher/lower PAE in either sex in humans, perhaps because marriage systems do not predict intrasexual competition, or that intrasexual competition does not select for high PAE in humans. However, when considering that evidence suggests an association between PAE and mating systems and non-human primates and the bias in the dataset towards monogamous human populations, further research is necessary before the possibility of a relationship between PAE and marriage systems in humans can be completely ruled out. The results support the recommendation that shared ancestry should be controlled for when carrying out cross-cultural comparative analysis in human populations.

3) To investigate the relationship between PAE and aspects of social behaviour and intrasexual competition in female non-human primates.

While the last decades have seen considerable attention given to the potential for ecological variation to explain variation in the behaviour of female primates at an ultimate level, the proximate mechanisms that underpin this variation have received far less attention. This study has shown that PAE may underlie some of this variation, although the evidence points towards PAE being more associated with aspects of intersexual competition (intersexual dominance patterns) and female reproductive competition (mating systems) suggesting these factors may be more important than generally assumed. Species characterised by female dominance over males had lower 2D:4D ratios than species characterised by male dominance or codominance, suggesting that PAE may be important for the maintenance of intersexual dominance relationships among primates, particularly female dominance. In terms of mating systems, monogamous females generally had highest 2D:4D ratios and polygynandrous and polygynous species had the lowest. As was the case in males, female 2D:4D ratios varied with the form of polygyny/polygynandry, possibly with regard to selection for competitive over cooperative behaviours and/or variation in the intensity of female reproductive competition. However, it must be acknowledged that the pattern could arise, in part, from correlated response as a result of selection for higher PAE in species in which males experience high intrasexual competition for mates (Nelson 2011). However, correlated response does not explain the pattern of polyandrous females having lower 2D:4D ratios than their male counterparts and it is likely that PAE on intrasexual competition in both sexes are closely linked as they confer similar benefits on male and female competitive abilities (Nelson & Shultz 2010; Nelson 2011).

Although there was no evidence that variation in female-female dominance interactions are associated with variation in PAE across the primate order as evidenced by the lack of relationships between 2D:4D ratio and rate of agonism or DCI, a more taxonomically-narrow analysis conducted with macaque species showed associations between 2D:4D ratios and social style in female macaques. Species characterised as more tolerant had higher 2D:4D ratios than less tolerant species indicating that the influence that PAE and POE have on the expression of aggressive and affiliative behaviour in this genus may underly the variation in macaque social systems.

Group size and diet, two factors which are often used to formulate the hypotheses on which classic socioecological theory is based, were not associated with PAE and may not be reliable predictors of female intrasexual competition levels. The lack of association between degree of frugivory and female 2D:4D ratios is not wholly unexpected as a number of studies over the last decades have not supported the idea that broad dietary categories reflect the levels of various modes of competition (Heesen *et al*. 2013; Wheeler *et al*. 2013; Yeager & Kool 2000; Koenig *et al.* 1998). The lack of association between group size and 2D:4D ratios is somewhat surprising as the empirical evidence generally supports the contention of increasing female-female competition with increasing group size (Wheeler et al. 2013; Koenig & Borries 2006). However, this increase in competition could manifest as either scramble or contest competition (or both) and it is only in the latter where an increase in PAE would be advantageous. Additionally, between-group competition in smaller primate groups (e.g. over territory in pair-living and solitary species) are likely to incur selection for higher PAE (Lazaro-Perea 2001; Azenberger 1992; Raemaekers & Raemaekers 1985), and in larger primate groups there is likely to be selection for behaviours associated with POE (cooperation and affiliation) in order to facilitate coexistence (French *et al*. 2018). It is not possible to determine the form or intensity of female intrasexual competition using variables such as dietary category and group size, suggesting that quantitative measures of female social structure should be used in preference to broad socioecological categories.

4) To examine the role of PAE as a neuroendocrinological mechanism underlying variation in the expression of individual personality traits in primates.

Interspecific behavioural differences arise from how individuals of those species behave, and personality traits are highly variable both across and within populations (Pederson *et al*. 2005) and across individuals (Sih & Bell 2008). If interspecific variation in PAE are associated with variation in some aspects of primate social systems, then it is also expected that variation in PAE within species will be associated with individual differences in behaviour (Howlett *et al*. 2012, 2015; Nelson *et al*. 2010; Knickmeyer *et al.* 2005). I explored the potential role that PAE may have on the expression of behaviour at the individual level by examining the relationship between 2D:4D ratios and personality traits in ring-tailed lemurs (*Lemur catta*), robust capuchins (*Sapajus* spp.) and human children (*Homo sapiens*). There were no associations between 2D:4D ratios and any of the personality traits in ring-tailed lemurs. The 2D:4D ratio was not associated with persistency scores in any species suggesting that the expression of this trait may not be influenced by PAE on brain patterning. Boldness and exploration tendency in boys correlated negatively with 2D:4D ratios, as did competitiveness in robust capuchins, suggesting that in these species and perhaps also in other haplorhine primates, PAE play a role in the expression of these traits. The results suggest that the relationship between PAE and personality may be limited to particular traits, the expression of which are influenced by behavioural predispositions arising from PAE and possibly those traits in which postnatal androgens also play a regulatory role. Sex differences in personality are common, and associations between personality traits and 2D:4D ratios were more apparent in boys than in girls. This lends support to sex differences in certain personality traits in humans being underpinned by variation in PAE that the sexes are exposed to. This observation could possibly be a result of sex differences in the evolutionary significance of the traits investigated and/or the possibility that, unless present at levels above the normal range for the female sex, PAE have a limited ability to influence personality traits over which female sex hormones may also have a regulatory role. The personality traits boldness, exploration tendency/curiousness and competitiveness have fitness consequences (Dammhan & Almeling 2012; Smith

& Blumstein 2008) and this study has shown that PAE may act as a proximate mechanism underlying the expression of such adaptive traits.

6.1.1: Conclusions

I conclude that the aims of the thesis have been met. 2D:4D ratios provide an indication of PAE on brain patterning and its subsequent behavioural predispositions which, in some cases at least, are specific and conducive to the social system and the level of inter- and intrasexual competition experienced by female non-human primates and the level intrasexual competition incurred by mating systems in male non-human primates. These observations may or may not be mirrored in humans, but further research is required before this can be ascertained. As well as having broad cross-species influences, PAE also appear to underlie inter-individual differences in the expression of some adaptive behavioural traits within species. This series of studies provides new and valuable insights into the role of PAE as a proximate mechanism underlying the expression of primate behaviour in ways which are ultimately adaptive, at higher taxonomic levels and at the individual level. The thesis as a whole highlights the importance of considering proximate as well as ultimate causes in studies of primate behaviour.

6.2: Study strengths

6.2.1: The non-human primate dataset

The non-human primate dataset encompassed 2D:4D ratio data from a total of 920 individuals (406 males and 514 females) from 80 species. These included individuals from 64 species of haplorhine primate and 16 species of strepsirrhine primate (Table 2.2.1 and 4.2.1). This study has improved on previous work by including both strepsirrhine and haplorhine primates in the dataset and containing a larger number of haplorhine species (Nelson 2011; Nelson & Shultz 2010). This is the first study to explore the relationship between 2D:4D ratios and aspects of male and female social behaviour in both suborders.

6.2.2: 2D:4D ratio measurement method

The digital photographic and computer-assisted image analysis software measurement method has been shown to be superior to all other 2D:4D measurement methods in terms of intra- and inter-measurer reliability (Ranson *et al*. 2013; Allaway *et al.* 2009; Kemper & Schwerdtfeger 2009; Appendix 2.9) and measurement precision (Kemper & Schwerdtfeger 2009). Intraclass correlation coefficient (ICC) values showed that intra-measurer reliability was very high across all primate families. The lowest ICC values were obtained for Cheirogaleidae (0.884 for the right hand and 0.903 for the left hand) suggesting that hand size may impact on measurement accuracy (Nelson 2011; Appendix 2.9). However, these ICC values are still well above what are considered acceptable levels of agreement (Koo & Li 2016) and the measuring of very small digits is aided by features of computer-assisted software such as zooming (Kemper & Schwerdtfeger 2009; Voracek *et al*. 2007a). I have shown that it is feasible to implement this method on large datasets and would recommend, as others have, that this method be used to measure 2D:4D ratios in humans, non-human primates and other animals wherever possible (Allaway *et al.* 2009; Kemper & Schwerdtfeger 2009).

A key benefit of the digital photographic data collection method is quality control. Even the most explicit instructions (Appendix 2.2) can be open to individual interpretation and this is evidenced by some of the Perspex® sheet hand images which I received (Figure 6.2.1). The 'free photo' and Perspex® sheet data collection methods allow the observer to view the digital images of the hands themselves and then accept or reject them based on whether they adhere to criteria making them suitable for measuring 2D:4D ratios. Conversely, I would be unable to vet the raw data if I had received it in the form of a list of primate digit measurements and ascertaining whether the fingers had been measured from the correct landmarks or in a fully extended position would not be possible.

Figure 6.2.1: Examples of rejected Perspex® hand images which did not adhere to the criteria making them unsuitable to measure 2D:4D ratios from: a) aye-aye (*Daubentonia madagascariensis*), palm is not flat against the Perspex® sheet and digits are in a curved position, b) black howler monkey (*Alouatta caraya*) the tip of the second digit is in a curved position, c) rhesus macaque (*Macaca mulatta*), palm is not flat against the Perspex® sheet and as a result the digits are not fully extended.

One drawback of this method concerns researcher time. Measuring digits from photographs using the computer-assisted image analysis software method can be more time-consuming than other measurement methods (Kemper & Schwerdtfeger 2009). However, this shortcoming is offset by the improved reliability, precision and quality control this method affords to the 2D:4D ratio data in comparison to other, less time-consuming methods. Additionally, the inclusion of the ‘free photo’ method of collecting hand images allowed for a larger sample size to be obtained as I was not reliant on the rare instances when animals were being handled for other reasons (e.g. veterinary treatment). As the ‘free photo’ method is opportunistic and non-invasive (the observer must await the opportunity to photograph hands when they are in optimum positions as the animal goes about its usual movements), data collection can take longer than if invasive methods (e.g. catching and handling animals) are used. However, the fact that this method is non-invasive is one of its great strengths as it allows for data to be collected without affecting the animals and as such is likely to be well within the ethical and animal welfare guidelines of most institutions. Additionally, as these images can be obtained from public viewing areas, the researcher does not impact on the time of the institution staff and these factors play a role in increasing the likelihood that organisations such as zoos will support research projects employing this, as opposed to more invasive methods.

The specificity of the hand positions which 2D:4D ratios can be accurately measured from means that it can be more difficult to use the ‘free photo’ method on certain primate species which have natural curvatures in or do not straighten their digits during regular locomotion e.g. knuckle-walking species, highly arboreal species and some callitrichids due to their claws (Figure 6.2.2). In captive animals, hand images of these species can be obtained using the Perspex® sheet when animals are being handled for other reasons and the digits can be manipulated into the desired position. However, the necessity for the digits to be in a flat, straight and fully extended position limits the use of the ‘free photo’ data collection method on certain species in the wild. While it is not impossible to get the necessary hand images in these species, it is more difficult than in species which engage in palm-walking with their digits extended e.g. baboons, macaques, guenons, cebines, lion tamarins, saki monkeys.

Figure 6.2.2: Examples of problems encountered obtaining suitable hand photographs using the ‘free photo’ method in certain species: a) Silvery marmoset (*Mico argentatus*), the claws of marmosets and *Saguinus* tamarins cause the digits to be in a curved position during natural movements, b) ring-tailed lemur, the digits of many arboreal and semi-terrestrial species can remain in a curved position even when walking on flat surfaces.

6.3.3: Chapter 2 - PAE and intrasexual competition in male non-human primates

This is the first comprehensive cross-species examination of variation in 2D:4D ratio in male non-human primates relative to the expected strength of selection for PAE incurred by specific mating system categories and subcategories. It is the first study to investigate the relationship between 2D:4D ratios and quantitative measures of male pre-copulatory (mating skew) and post-copulatory (reproductive skew) intrasexual competition. The use of more accurate and representative mating system categories and distinguishing between forms of polygyny and polygynandry is an improvement on previous work (Nelson & Shultz 2010). These mating system categories and subcategories were able to encompass the fine-grained variation in male intrasexual competition and the subsequent variation in the strength of selection for PAE. They also highlighted the importance of considering selection for behaviours associated with POE and how these contribute to variation in male mating and social behaviour.

6.3.4: Chapter 3 – PAE and variation in human marriage systems

In spite of the fact that a great deal of the variation in behaviour between human populations can be attributed to phylogeny, much of the previous cross-cultural comparative research in human populations has failed to consider the importance of controlling for phylogenetic non-independence of traits due to common ancestry (Minocher *et al*. 2018). The analysis in this study was strengthened by employing phylogenetically controlled methods to account for relatedness between human populations and this method reduces the likelihood of obtaining false positive and false negative results which can arise when non-independence is ignored (Minocher *et al*. 2018). Additionally, using the supertree approach provides a highly comprehensive and robust phylogenetic tree (Minocher *et al*. 2018; Duda & Zrzavý 2016) and, being based on both genomic and linguistic data, it is likely more representative of relatedness between populations when compared to phylogenies based on language alone as the evolutionary processes which shape genetic diversity are not necessarily directly analogous to those which shape linguistic diversity (Duda & Zrzavý 2016).

6.3.5: Chapter 4 – PAE and social behaviour in female non-human primates

This is the first study to investigate PAE and intrasexual competition in female non-human primates using: 1) quantitative measures of female social structure (rate of female-female agonism and an index of the directional consistency of agonistic interactions among females [DCI]); 2) a quantitative ecological variable proposed to be associated with the intensity of contest competition among females (degree of frugivory); 3) a dimension of social organisation argued to result in increased within-group contest competition (group size); and 4) intersexual dominance patterns and measures of female sexual competition (mating system categories and subcategories). Further, this is the first study to explore the possibility that PAE may contribute to the documented variation in female social structure across species of the genus *Macaca.*

Variation in ecology alone is not able to fully explain the observed differences in agonism and dominance relationships among female primates (Klass & Cords 2015). There is considerable variation in how these relationships manifest themselves and species do not necessarily conform to the predictions of any socioecological model (Klass & Cords 2015; Wickberg *et al.* 2013; Robbins *et al*. 2005). Therefore, I moved away from the broad-scale descriptive classifications of female dominance relationships which are based on the effects of ecological factors (Sterck *et al.* 1997) and may or may not be accurate reflections of female primate behaviour, and instead attempted to use quantitative measures of female dominance behaviour, specifically rate of female-female agonism and DCI, the latter of which is argued to be the best measure of female despotism (Koenig *et al.* 2013; van Hooff & Wensing 1987). However, due to small sample sizes for both variables it was not possible to fully explore the relationship between 2D:4D ratios and quantitative female dominance behaviours. These small sample sizes result from these variables not often being reported in the literature, different methods being used to calculate female dominance relationships (focal, scan, time sampling, *ad libitum*) and the definitions of agonism and dominance behaviours varying from study to study (Wheeler *et al*. 2013), meaning that the pool of studies from which data can be used is reduced.

6.3.6: Chapter 5 – PAE and personality in humans and non-human primates

The use of quantifiable behavioural variables measured under experimental conditions in the personality experiments enabled the creation of standardised Z-scores which allowed the relative differences among individuals to be identified. Although this method of data collection is more time consuming and affords lower sample sizes than many questionnaire and other lexical-based methods, it appears to be a better way to measure biologically (as opposed to socially) based personality traits in humans and non-human primates as evidenced by stronger correlations between personality traits and 2D:4D ratios in comparison to those gained through lexical-based methodology (Trofimova *et al.* 2018). This makes sense as behaviour can only be measured in real-time and personality data generated from ratings or questionnaire answers concerning an individual's behaviour are more likely to reflect the rater's ideas of the trait under study and/or their experiences with the individual, rather than the individual behaviour of the animal/person (Uher 2018; Uher 2015; Uher *et al*. 2013). Additionally, methods typically used to create personality constructs from raw data such as principal components analysis and factor analysis have been adapted for use in other animals from human psychology research and are only really useful for questionnaire/rating data as lexical behaviours can be created *ad libitum*, but this is not possible for animal behaviours (Trofimova *et al.* 2018). Conversely, the stepwise method I used to formulate personality trait constructs from raw behavioural data meant that the personality trait scores are individual-specific and reflect the behavioural repertoire of the study subjects themselves within specific contexts and not the perceptions/ideas of others (Uher *et al.* 2013; Highfill *et al.* 2010). Through lexical-based methodologies large sample sizes and large amounts of data can be collected in a short space of time, but this is at the expense of essential information on individual behavioural differences which can only be gained through direct observation of subjects in specific situations.

6.4: Directions for future research

6.4.1: Improving sample sizes

Similar to the Nelson & Shultz (2010) study, constraints on animal and species numbers were brought about by the management of captive primate collections by institutions (species and sex ratio biases). Sample sizes were greater for species which can be kept in larger numbers in captivity as this replicates the group sizes of their wild counterparts e.g. baboons, macaques, mandrills and squirrel monkeys. Sample sizes were smaller for gibbons, great apes, callitrichids and the majority of lemurs, which live in smaller groups in the wild or exist in lower numbers in captivity (Tables 2.2.1 and 4.2.1). Increasing the number of primate species and the number of individuals in the 2D:4D ratio dataset (using the digital photographic data collection and computer-assisted image analysis measurement method described in this thesis) would be highly advantageous in terms of further enhancing our understanding of the expression of this trait and how PAE may act as a proximate mechanism underlying aspects of sociality across the Order Primates.

Sample sizes were small for female dominance variables and so the lack of relationship between 2D:4D ratios and these variables may have resulted from a lack of statistical power. Quantitative measures of female dominance are better able to represent the fine-grained variation we see in female social relationships than the broad classifications of traditional socioecological models and so repeating these analyses with larger sample sizes are promising avenues for future research, particularly as a trend was discernible in the predicted direction between DCI and R2D:4D.

Similarly, increasing sample sizes for male reproductive skew and mating skew could be instrumental in determining whether the insignificant results were due to the absence of a biological effect or a consequence of low statistical power. The lack of available data for these variables is likely a product of difficulties observing mating in many wild primates (particularly small arboreal species) and the fact that reliable paternity data based on molecular analysis has only become possible relatively recently and still is not often established in wild primates as obtaining and analysing genetic samples can be problematic and costly (Di Fiore 2003). Mating skew and paternity data provide information on male reproductive fitness and are therefore valuable for determining whether particular males have an advantage at both the pre-copulatory and sperm competition levels and, if so, the possibility that the competitive edge results from higher PAE (inferred from 2D:4D ratios).

6.4.2: Extending the research

Captivity has been known to influence development in primates (Smith & Jungers 1997) and the majority of the individuals in the non-human primate 2D:4D ratio dataset were captive. It would be of benefit to supplement this dataset with 2D:4D ratio data from wild primates and, as the digital photographic and computer-assisted image analysis software method can be implemented to noninvasively measure 2D:4D ratios in wild primate species (Howlett *et al.* 2015), making this improvement is a possibility.

One potential direction for extending the research would be to explore the association between the form that paternal investment and care takes and male 2D:4D ratios. The intensity and form that paternal care takes has profound effects on male physiology (Zeigler *et al*. 2004) and this is likely to be particularly significant for monogamous and polyandrous male primates. This investigation would illuminate the degree to which selection for reduced PAE could be occurring in higher investing males (e.g. infant carriers, infant provisioners) compared with males who live in close contact with their offspring and whose presence may increase infant survival (e.g. defending a territory, infanticide protection) but do not provide direct paternal care.

Although no significant associations were found between 2D:4D ratios and MCCH or CCH dimorphism, this does not rule out the possibility that PAE may influence the development of other anatomical traits associated with male intrasexual competition. It would be interesting to explore whether an association exists between 2D:4D ratio and testis size as this trait has been implicated in sperm competition and male reproductive success in non-human primates (Harcourt *et al*. 1981). Such analysis, alongside paternity data, could further elucidate the effect that prenatal sex steroids may have on post-copulatory intrasexual competition in male primates.

In addition to increasing the species sample sizes for mating skew and reproductive skew in order to conduct further cross-species comparative analysis, it would be beneficial to examine the relationships within species. The relationship between PAE and these variables is likely to be more apparent between individual males at the species level via the positive impact that PAE have on an individual's competitive ability (Schwarz *et al*. 2011; Manning & Fink 2008; Hönekopp *et al*. 2006). Studies have found links between dominance rank and male reproductive success in a number of primate species (Di Fiore 2003; Engelhardt *et al*. 2006; Setchell *et al.* 2005; Dixson *et al*. 1993) implying that this positive impact of PAE on male reproductive success could indeed be the case.

In polyandrous species, the intensity of reproductive competition between individuals of the same sex is very different. Polyandrous males tend to be tolerant of each other whereas polyandrous females are intolerant of and aggressive towards same sex competitors (Garber 1994; van Hoof & van Schaik 1994; French & Inglett 1989). Sample sizes were too small to formally test the hypothesis, but preliminary data suggest that there may be selection for higher PAE in polyandrous females (possibly to facilitate behaviours conducive to the defence of territory/mates) and reduced PAE/increased POE in polyandrous males (likely to facilitate cooperative/tolerant behaviours and infant care). An in-depth investigation into differences in male and female 2D:4D ratios in polyandrous species could provide interesting insights into how variation in PAE may underpin the observed behavioural differences between the sexes associated with this mating system.

General ecological factors are not able to explain the diversity in macaque social structure (Thierry & Aureli 2006; Thierry *et al*. 2000). However, variation in PAE/POE on brain patterning could be the mechanism underpinning differences in affiliative and competitive behaviours observed in macaque species. As the analysis in this thesis consisted of only eight species in the genus, the results can only be considered as preliminary evidence. Further investigation into the association between PAE and macaque social style grades with 2D:4D ratio data representative of every species in the genus would be enlightening.

The bias in the geographic regions in which human 2D:4D ratio data were available meant that the sample was heavily skewed in favour of monogamous populations. Additionally, although all methods can be considered sufficiently reliable (ICCs = <0.8), having a dataset based on 2D:4D ratios measured using different methods was not ideal, and both of these factors may have influenced the results. Before the possibility of a relationship between PAE and marriage systems in humans can be completely ruled out, further research with a more balanced dataset and more reliable 2D:4D ratio data needs to be carried out. Improved methodology would involve identifying specific human populations from around the world which are characterised by each marriage system and collecting 2D:4D ratio data from these populations *in situ* using the Perspex® sheet and digital photographic data collection method and computer-assisted image analysis software to measure 2D:4D ratios.

The behaviour of individuals exposed to higher PAE are reported to be more impulsive (Hanoch *et al*. 2012), less inhibited (Resnick *et al*. 1993), less risk-averse (Kim *et al*. 2014), more aggressive (Benderlioglu & Nelson 2007; 2004), more dominant (Manning & Fink 2008; Neave *et al*. 2003) than those exposed to lower PAE. The majority of studies investigating such associations in humans and non-human primates have employed lexical-based data collection methods and are therefore vulnerable to these methods' shortcomings. Further investigations into traits which are likely to be influenced by PAE and which have adaptive value (such as those described above) should use quantifiable behavioural variables measured under experimental conditions. This would help to shed light on the influence that PAE may have on the expression of personality traits in ways which are adaptive to the individual.

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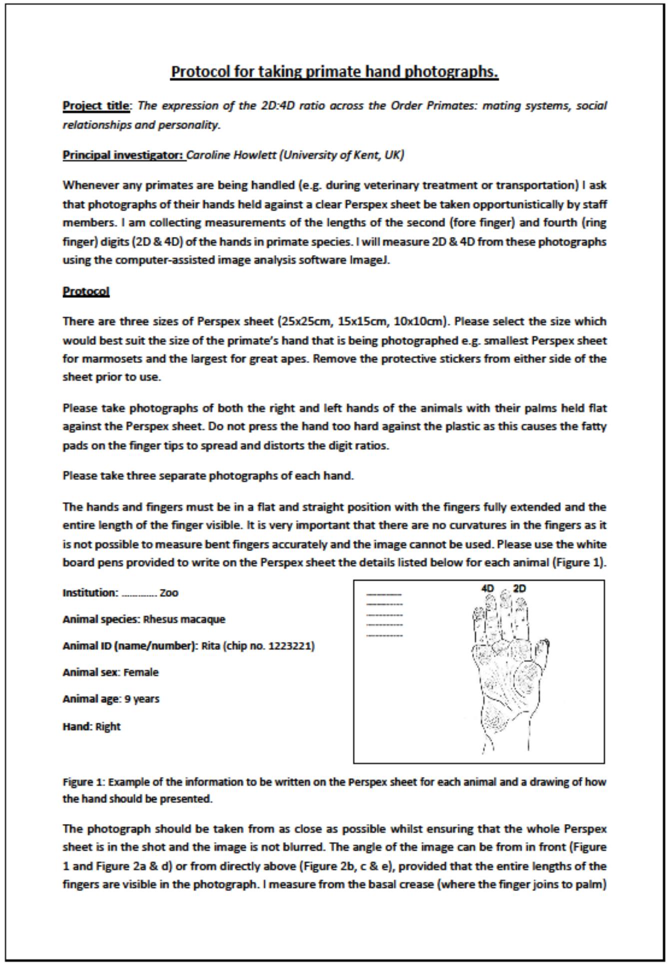
Appendix 2

Appendix 2.1: Names (in alphabetical order) and locations (by country) of participating institutions housing the 920 captive non-human primates used in this study.

Location	**Name of participating institution**
United Kingdom	Africa Alive!, Banham Zoo, Blair Drummond Safari Park, Chessington World of Adventures Resort, Chester Zoo, Colchester Zoo, Cotswolds Wildlife Park, Drusillas Zoo Park, Edinburgh Zoo, Hamerton Zoo, Highland Wildlife Park, Howlett's Wild Animal Park, Knowsley Safari Park, London Zoo, Longleat Safari Park, Marwell Wildlife Park, Newquay Zoo, Paignton Zoo, Port Lympne Reserve, Shepreth Wildlife Park, South Lakes Safari Zoo, Twycross Zoo, Whipsnade Wildlife Park, Yorkshire Wildlife Park.
Germany	Deutsches Primatenzentrum, Landau Zoo.
Italy	Fondazione Bioparco di Roma.
Netherlands	Apenheul Primate Park.
Spain	Oasis Park Fuerteventura.
South Africa	Centre for Animal Rehabilitation and Education (C.A.R.E).

Appendix 2.2: Protocol for taking hand photographs distributed to participating institutions along with the Perspex® sheet apparatus.



Protocol for taking primate hand photographs.

Project title: *The expression of the 2D:4D ratio across the Order Primates: mating systems, social relationships and personality.*

Principal investigator: *Caroline Howlett (University of Kent, UK)*

Whenever any primates are being handled (e.g. during veterinary treatment or transportation) I ask that photographs of their hands held against a clear Perspex sheet be taken opportunistically by staff members. I am collecting measurements of the lengths of the second (fore finger) and fourth (ring finger) digits (2D & 4D) of the hands in primate species. I will measure 2D & 4D from these photographs using the computer-assisted image analysis software ImageJ.

Protocol

There are three sizes of Perspex sheet (25x25cm, 15x15cm, 10x10cm). Please select the size which would best suit the size of the primate's hand that is being photographed e.g. smallest Perspex sheet for marmosets and the largest for great apes. Remove the protective stickers from either side of the sheet prior to use.

Please take photographs of both the right and left hands of the animals with their palms held flat against the Perspex sheet. Do not press the hand too hard against the plastic as this causes the fatty pads on the finger tips to spread and distorts the digit ratios.

Please take three separate photographs of each hand.

The hands and fingers must be in a flat and straight position with the fingers fully extended and the entire length of the finger visible. It is very important that there are no curvatures in the fingers as it is not possible to measure bent fingers accurately and the image cannot be used. Please use the white board pens provided to write on the Perspex sheet the details listed below for each animal (Figure 1).

Institution: ………… Zoo

Animal species: Rhesus macaque

Animal ID (name/number): Rita (chip no. 1223221)

Animal sex: Female

Animal age: 9 years

Hand: Right

Figure 1: Example of the information to be written on the Perspex sheet for each animal and a drawing of how the hand should be presented.

The photograph should be taken from as close as possible whilst ensuring that the whole Perspex sheet is in the shot and the image is not blurred. The angle of the image can be from in front (Figure 1 and Figure 2a & d) or from directly above (Figure 2b, c & e), provided that the entire lengths of the fingers are visible in the photograph. I measure from the basal crease (where the finger joins to palm)

to the tip of the extended finger, so it is important that I can see both of these landmarks clearly in the images (Figure 2b & c).

Background reflection on the Perspex sheet can be an issue. Avoid glare to minimise this light interference and that ensure the images are of a good quality. Holding the hand up and photographing from the front helps to reduce reflection on the Perspex sheet in brightly lit areas (Figure 2d).

Figure 2: Example photographs of human and primate hands with the landmarks for measuring indicated (b & c).

I will be collecting hand images until the end of November 2017. Please send all hand photographs to the email address below or share the files via Dropbox to the same email.

My contact details can be found below, please contact me with any questions about the protocol.

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Appendix 2.3: List of 80 non-human primate species represented in this thesis with sources for taxonomy and substrate use data.

Species	Source	Substrate use	Source
Eulemur collaris	Groves 2001	A	Donati *et al.* 2007, 2011
Eulemur coronatus	Groves 2001	A	Freed 1999 in Dolhinow & Fuentes 1999
Eulemur flavifrons	Mittermeier *et al.* 2008, 2009	A	Volampeno *et al*. 2011
Eulemur fulvus fulvus	Johnson 2006	A	Wheeler *et al.* 2013
Eulemur macaco	Groves 2001	A	Freed 1999 in Dolhinow & Fuentes 1999
Eulemur mongoz	Groves 2001	A	Curtis *et al*. 1999
Eulemur rubriventer	Groves 2001	A	Overdorff 1996
Hapalemur alaotrensis	Groves 2001	A	Gould & Sauther 2006
Lemur catta	Groves 2001	A/T	Franz *et al*. 2005; Milliken 1989; Sauther 1989
Prolemur simus	Groves 2001	A	Mutschler & Tan 2003
Varecia rubra	Groves 2001	A	Patel *et al*. 2015
Varecia variegata variegata	Groves 2001	A	Wheeler *et al.* 2013
Propithecus coronatus	Thalmann *et al*. 2002; Groves & Helgen 2007	A	Andriaholinirina *et al*. 2014 IUCN Redlist (retrieved Nov 2016)
Microcebus murinus	Groves 2001	A	Dodson *et al*. 1992
Galago moholi	Groves 2001	A	Dodson *et al*. 1992
Galago senegalensis	Groves 2001	A	Huq *et al.* 2015
Alouatta caraya	Groves 2001	A	Nelson & Schultz 2010
Ateles fusciceps rufiventris	Groves 2001	A	Isler 2004
Ateles paniscus	Groves 2001	A	Plavcan & van Schaik 1992
Callicebus cupreus	Groves 2001	A	Nadjafazdeh & Heymann 2008
Pithecia pithecia	Groves 2001	A	Nelson & Schultz 2010
Cebus capucinus	Groves 2001	A	Wheeler *et al*. 2013
Sapajus apella	Lynch Alfaro *et al.* 2012	A	Plavcan & van Schaik 1992
Sapajus xanthosternos	Lynch Alfaro *et al.* 2012	A	Canale *et al.* 2016
Saimiri boliviensis	Groves 2001	A	Nowak 1999; Napier & Napier 1967
Saimiri sciureus	Groves 2001	A	Nelson & Schultz 2010
Callimico goeldii	Groves 2001	A	Garber & Leigh 2001
Callithrix geoffroyi	Groves 2001	A	Nelson & Schultz 2010
Callithrix jacchus	Groves 2001	A	Nelson & Shultz 2010
Cebuella pygmaea	Groves 2001	A	Plavcan & van Schaik 1992
Leontopithecus chrysomelas	Groves 2001	A	Nelson & Schultz 2010
Leontopithecus rosalia	Groves 2001	A	Nelson & Schultz 2010
Mico argentatus	Linnaeus 1766	A	Ford *et al.* 2009
Mico melanurus	É. Geoffroy 1812	A	Ford *et al.* 2009
Saguinus bicolor	Groves 2001	A	Rowe 1996
Saguinus imperator	Groves 2001	A	Nelson & Schultz 2010
Saguinus labiatus	Groves 2001	A	Garber & Leigh 2001

Appendix 2.3 ***continued*****.**

Species	**Source**	**Substrate use**	**Source**
Saguinus midas	Groves 2001	A	Nelson & Shultz 2010
Saguinus oedipus	Groves 2001	A	Nelson & Schultz 2010
Allenopithecus nigroviridis	Groves 2001	A/T	Kingdon 2015
Cercocebus chrysogaster	Groves 2001	A/T	McGraw & Fleagle 2006
Cercocebus lunulatus	Mittermeier *et al.* 2013	A/T	McGraw & Fleagle 2006
Cercocebus torquatus	Groves 2001	A/T	Plavcan & van Schaik 1992; Gust *et al.* 1990
Cercopithecus diana	Groves 2001	A	Nelson & Schultz 2010
Cercopithecus lhoesti	Groves 2001	A/T	Nelson & Schultz 2010
Cercopithecus lowei	Groves 2001	A/T	Kingdon 2015; Wiafe 2015
Cercopithecus neglectus	Groves 2001	A/T	Nelson & Schultz 2010
Cercopithecus petaurista	Groves 2001	A	McGraw 2000
Cercopithecus pogonias	Groves 2001	A	Plavcan & van Schaik 1992
Chlorocebus pygerythrus	Groves 2001	A/T	Nelson & Schultz 2010
Colobus guereza	Groves 2001	A	Nelson & Schultz 2010
Colobus polykomos	Groves 2001	A	Plavcan & van Schaik 1992
Erythrocebus patas	Groves 2001	T	Plavcan & van Schiak 1992
Macaca fascicularis	Groves 2001	A/T	Nelson & Schultz 2010
Macaca fuscata	Groves 2001	A/T	Nelson & Schultz 2010
Macaca hecki	Groves 2001	A/T	Plavcan & van Schaik 1992
Macaca mulatta	Groves 2001	A/T	Nelson & Schultz 2010
Macaca nemestrina	Groves 2001	A/T	Plavcan & van Schaik 1992
Macaca nigra	Groves 2001	A/T	Nelson & Schultz 2010
Macaca silenus	Groves 2001	A	Singh *et al*. 2001; Hohmann & Herzog 1985
Macaca sylvanus	Groves 2001	T	Fooden 2007
Mandrillus leucophaeus	Groves 2001	A/T	Nelson & Schultz 2010
Mandrillus sphinx	Groves 2001	A/T	Nelson & Schultz 2010
Papio hamadryas	Groves 2001	T	Nelson & Schultz 2010
Papio papio	Groves 2001	T	Barrett & Henzi 2008
Papio ursinus	Groves 2001	T	Wheeler *et al.* 2013
Presbytis melalophus	Groves 2001	A	Nelson & Shultz 2010
Theropithecus gelada	Groves 2001	T	Plavcan & van Schaik 1992
Trachypithecus auratus	Groves 2001	A	Kool 1989
Trachypithecus francoisi	Groves 2001	A	Nelson & Shultz 2010
Trachypithecus obscurus	Groves 2001	A	Nelson & Schultz 2010
Hylobates agilis	Groves 2001	A	Cannon & Leighton 1994
Hylobates lar	Groves 2001	A	Nelson & Schultz 2010
Hylobates muelleri	Groves 2001	A	Leighton 1987
Hylobates pileatus	Groves 2001	A	Nelson & Schultz 2010
Nomascus leucogenys	Groves 2001	A	Nelson & Schultz 2010
Symphalangus syndactylus	Groves 2001	A	Nelson & Schultz 2010
Gorilla gorilla gorilla	Groves 2001	A/T	Nelson & Schultz 2010
Pan paniscus	Groves 2001	A/T	Nelson & Schultz 2010
Pan troglodytes	Groves 2001	A/T	Nelson & Schultz 2010

Substrate use: A = arboreal, A/T = arboreal/terrestrial, T = terrestrial.

Appendix 2.4: Average male body mass (grams) for each species and sources of data. Data from wild animals unless otherwise stated.

Species	Average adult male body mass (g)	Source
Eulemur collaris	2375	Fleagle 2013
Eulemur coronatus	1280	Smith & Jungers 1997
Eulemur flavifrons	1880	Smith & Jungers 1997
Eulemur fulvus fulvus	2250	Fleagle 2013
Eulemur macaco	2350	Fleagle 2013
Eulemur mongoz	1410	Smith & Jungers 1997
Eulemur rubriventer	1980	Smith & Jungers 1997
Hapalemur alaotrensis	1400	Garbutt 1999
Lemur catta	2213	Sussman 1991
Prolemur simus	2150	Smith & Jungers 1997
Varecia rubra	3630	Fleagle 2013
Varecia variegata variegata	3630	Smith & Jungers 1997
Propithecus coronatus	3206	Taylor & Schwitzer 2012
Microcebus murinus	59	Schmid & Kappeler 1998
Galago senegalensis	227	Smith & Jungers 1997
Alouatta caraya	6420	Smith & Jungers 1997
Ateles fusciceps rufiventris	8890	Ford & Davis 1992
Ateles paniscus	9110	Smith & Jungers 1997
Callicebus cupreus	1020	Smith & Jungers 1997
Pithecia pithecia	1940	Smith & Jungers 1997
Cebus capucinus	3680	Smith & Jungers 1997
Sapajus apella	3650	Smith & Jungers 1997
Sapajus xanthosternos	2714	Fleagle 2013
Saimiri boliviensis	1015	Ford & Davis 1992
Saimiri sciureus	852	Ford & Davis 1992
Callimico goeldii	278	Ford & Davis 1992
Callithrix geoffroyi	290	Ford & Davis 1992
Callithrix jacchus	362	Smith & Jungers 1997
Cebuella pygmaea	110	Smith & Jungers 1997
Leontopithecus chrysomelas	620	Smith & Jungers 1997
Leontopithecus rosalia	620	Smith & Jungers 1997
Mico argentatus	333	Fleagle 2013
Mico melanurus	370	Fleagle 2013
Saguinus imperator	474	Smith & Jungers 1997
Saguinus labiatus	490	Smith & Jungers 1997
Saguinus midas	515	Smith & Jungers 1997
Saguinus oedipus	418	Smith & Jungers 1997
Cercocebus chrysogaster	12000	Kingdon 2015
Cercocebus lunulatus	9900	Fleagle 2013
Cercocebus torquatus	9740	Smith & Jungers 1997

Appendix 2.4 ***continued***.

Species	**Average adult male body mass (g)**	**Source**
Cercopithecus diana	5200	Smith & Jungers 1997
Cercopithecus lhoesti	5970	Smith & Jungers 1997
Cercopithecus loweii	5800	Kingdon 2015
Cercopithecus neglectus	7350	Smith & Jungers 1997
Chlorocebus pygerythrus	4260	Smith & Jungers 1997
Colobus guereza	13500	Smith & Jungers 1997
Colobus polykomos	9900	Smith & Jungers 1997
Erythrocebus patas	12400	Smith & Jungers 1997
Macaca fascicularis	5360	Smith & Jungers 1997
Macaca fuscata	11000	Smith & Jungers 1997
Macaca hecki	11200**	Smith & Jungers 1997
Macaca mulatta	7710	Smith & Jungers 1997
Macaca nemestrina	11200	Smith & Jungers 1997
Macaca nigra	9890	Smith & Jungers 1997
Macaca silenus	8900	Smith & Jungers 1997
Macaca sylvanus	11100	Smith & Jungers 1997
Mandrillus leucophaeus	20000	Smith & Jungers 1997
Mandrillus sphinx	24500	Kingdon 2015
Papio hamadryas	16900	Smith & Jungers 1997
Papio papio	19000	Kingdon 2015
Papio ursinus	29800	Smith & Jungers 1997
Presbytis melalophos	6590	Smith & Jungers 1997
Theropithecus gelada	19000	Smith & Jungers 1997
Trachypithecus auratus	6656	Fleagle 2013
Trachypithecus francoisi	7700	Smith & Jungers 1997
Trachypithecus obscurus	7900	Smith & Jungers 1997
Hylobates agilis	5880	Smith & Jungers 1997
Hylobates lar	5900	Smith & Jungers 1997
Hylobates pileatus	5500	Smith & Jungers 1997
Nomascus leucogenys	7410	Smith & Jungers 1997
Symphalangus syndactylus	11900	Smith & Jungers 1997
Gorilla gorilla	170400	Smith & Jungers 1997
Pan troglodytes	59700	Smith & Jungers 1997

**Data from captive animals.

Appendix 2.5: The 80 non-human primate species represented in this thesis with corresponding mating system, mating system subcategory and the sources of these data.

Species	**Mating system**	**Subcategory**	**Source**
Eulemur collaris	Polygynandry	Contest competition polygynandry	Johnson 2006; Johnson *et al*. 2005
Eulemur coronatus	Polygynandry	Contest competition polygynandry	DeCasien *et al.* 2017
Eulemur flavifrons	Polygynandry	Contest competition polygynandry	C. Eschmann (pers.comm)
Eulemur fulvus fulvus	Polygynandry	Contest competition polygynandry	DeCasien *et al*. 2017; Johnson 2006; Johnson *et al*. 2005
Eulemur macaco	Polygynandry	Contest competition polygynandry	C. Eschmann (pers.comm); Bayart & Simmen 2005; Colquhoun 1997
Eulemur mongoz	Monogamy	Monogamy	Freed 1999 in Dolhinow & Fuentes 1999
Eulemur rubriventer	Monogamy	Monogamy	Freed 1999 in Dolhinow & Fuentes 1999
Hapalemur alaotrensis	Monogamy	Monogamy	Nievergelt *et al*. 2002
Lemur catta	Polygynandry	Contest competition polygynandry	Pereira & Weiss 1991
Prolemur simus	Polygyny	Harem polygyny	Mutschler & Tan 2003; Tan 1999
Varecia rubra	Polygynandry	Contest competition polygynandry	Vasey 2007
Varecia variegata variegata	Polygynandry	Contest competition polygynandry	Morland 1993
Propithecus coronatus	Polyandry	Polyandry	Roullet 2014; Rakotonirina *et al.* 2014; Pichon 2012
Microcebus murinus	Polygynandry	Scramble competition polygynandry	Fietz 1999; Eberle & Kappeler 2002
Galago moholi	Polygynandry	Scramble competition polygynandry	Pullen *et al*. 2000
Galago senegalensis	Polygyny	Spatial polygyny	DeCasien *et al.* 2017
Alouatta caraya	Polygynandry	Cooperative defence polygynandry	Oklander *et al*. 2014
Ateles fusciceps rufiventris	Polygynandry	Contest competition polygynandry	Campbell *et al*. 2011
Ateles paniscus	Polygynandry	Contest competition polygynandry	Campbell *et al*. 2011
Callicebus cupreus	Monogamy	Monogamy	Carp *et al*. 2015
Pithecia pithecia	Polygynandry	Contest competition polygynandry	DeCasien *et al*. 2017; Thompson 2016; Thompson 2011; Poyas 2008

Appendix 2.5 ***continued*****.**

Species	**Mating system**	**Subcategory**	**Source**
Cebus capucinus	Polygyny	Harem polygyny	DeCasien *et al*. 2017
Sapajus apella	Polygynandry	Contest competition polygynandry	Campbell *et al*. 2011; Carosi *et al*. 2005; Escobar-Paramo 2000; Janson 1984
Sapajus xanthosternos	Polygynandry	Contest competition polygynandry	Campbell *et al*. 2011
Saimiri boliviensis	Polygynandry	Contest competition polygynandry	Zimbler-DeLorenzo & Stone 2011
Saimiri sciureus	Polygynandry	Contest competition polygynandry	Stone 2014; Izar *et al*. 2008
Callimico goeldii	Monogamy	Monogamy	Poyas 2008
Callithrix geoffroyi	Monogamy	Monogamy	DeCasien *et al*. 2017
Callithrix jacchus	Polyandry	Polyandry	DeCasien *et al.* 2017
Cebuella pygmaea	Monogamy	Monogamy	Fuentes 1998; Converse *et al.* 1995; Garber 1994
Leontopithecus chrysomelas	Monogamy	Monogamy	DeCasien *et al*. 2017
Leontopithecus rosalia	Monogamy	Monogamy	Harcourt *et al*. 1995
Mico argentatus	Monogamy	Monogamy	DeCasien *et al.* 2017
Mico melanurus	Monogamy	Monogamy	Garber 1994
Saguinus bicolor	Polyandry	Polyandry	Kinzey 1997
Saguinus imperator	Polyandry	Polyandry	Kinzey 1997
Saguinus labiatus	Monogamy	Monogamy	Suarez 2007
Saguinus midas	Polyandry	Polyandry	DeCasien *et al.* 2017
Saguinus oedipus	Monogamy	Monogamy	Harcourt *et al.* 1981
Allenopithecus nigroviridis	Polygyny	Harem polygyny	Sillen-Tullberg & Moller 1993
Cercocebus chrysogaster	Polygynandry	Contest competition polygynandry	Walker *et al*. 2004
Cercocebus lunulatus	Polygynandry	Contest competition polygynandry	McGraw *et al.* 2007; Range 2005
Cercocebus torquatus	Polygynandry	×××	DeCasien *et al*. 2017
Cercopithecus diana	Polygyny	Harem polygyny	DeCasien *et al.* 2017

Appendix 2.5 *continued*.

Species	**Mating system**	**Subcategory**	**Source**
Cercopithecus lhoesti	Polygyny	Harem polygyny	DeCasien *et al.* 2017
Cercopithecus lowei	Polygyny	Harem polygyny	Kingdon 2015
Cercopithecus neglectus	Polygyny	Harem polygyny	DeCasien *et al*. 2017
Cercopithecus petaurista	Polygyny	Harem polygyny	Fleagle 2013; Anderson *et al*. 2004; Zuberbühler & Jenny 2002
Cercopithecus pogonias	Polygyny	Harem polygyny	Fleagle 2013
Chlorocebus pygerythrus	Polygynandry	Contest competition polygynandry	DeCasien *et al.* 2017
Colobus guereza	Polygyny	Harem polygyny	Harris & Monfort 2006
Colobus polykomos	Polygyny	Harem polygyny	Short 1997; Harcourt *et al.* 1981
Erythrocebus patas	Polygyny	Harem polygyny	Ohsawa *et al.* 1993
Macaca fascicularis	Polygynandry	Contest competition polygynandry	DeCasien *et al.* 2017; Short 1997
Macaca fuscata	Polygynandry	Contest competition polygynandry	DeCasien *et al.* 2017
Macaca hecki	Polygynandry	Contest competition polygynandry	Campbell *et al*. 2011; Maestripieri 1997
Macaca mulatta	Polygynandry	Contest competition polygynandry	Dubuc *et al*. 2014; Short 1997
Macaca nemestrina	Polygynandry	Contest competition polygynandry	DeCasien *et al.* 2017; Short 1997
Macaca nigra	Polygynandry	Contest competition polygynandry	Engelhardt *et al*. 2017; Marty *et al.* 2015
Macaca silenus	Polygynandry	Contest competition polygynandry	DeCasien *et al.* 2017
Macaca sylvanus	Polygynandry	Contest competition polygynandry	DeCasien *et al.* 2017
Mandrillus leucophaeus	Polygynandry	Contest competition polygynandry	DeCasien *et al*. 2017; Marty *et al.* 2009
Mandrillus sphinx	Polygynandry	Contest competition polygynandry	Wickings *et al.* 1993
Papio hamadryas	Polygyny	Harem polygyny	Jolly & Phillips-Conroy 2003; Short 1997; Stammbach 1987
Papio papio	Polygyny	Harem polygyny	Goffe *et al.* 2016; Maestripieri *et al.* 2005, 2007

Appendix 2.5 *continued*.

Species	**Mating system**	**Subcategory**	**Source**
Papio ursinus	Polygynandry	Contest competition polygynandry	DeCasien *et al.* 2017; Short 1997
Presbytis melalophos	Polygyny	Harem polygyny	Newton & Dunbar 1994
Theropithecus gelada	Polygyny	Harem polygyny	Short 1997; Stammbach 1987 in Smuts *et al.* 1987
Trachypithecus auratus	Polygyny	Harem polygyny	Campbell *et al*. 2011; Yeager & Kool 2000
Trachypithecus francoisi	Polygyny	Harem polygyny	Yeager & Kool 2000
Trachypithecus obscurus	Polygyny	Harem polygyny	Short 1997; Harcourt *et al*. 1981
Hylobates agilis	Monogamy	Monogamy	DeCasien *et al*. 2017
Hylobates lar	Monogamy	Monogamy	Barrelli *et al.* 2013
Hylobates muelleri	Monogamy	Monogamy	Mitani 1984
Hylobates pileatus	Monogamy	Monogamy	DeCasien *et al*. 2017
Nomascus leucogenys	Monogamy	Monogamy	Poyas 2008
Symphalangus syndactylus	Monogamy	Monogamy	DeCasien *et al*. 2017
Gorilla gorilla gorilla	Polygyny	Harem polygyny	DeCasien *et al*. 2017
Pan paniscus	Polygynandry	Contest competition polygynandry	Furuichi & Hashimoto 2004; Reichert *et al.* 2002
Pan troglodytes	Polygynandry	Cooperative defence polygynandry	Watts 1998

^{xxx}Data not available.

Appendix 2.6: Species with reproductive skew (percentage of alpha/resident male paternity across species) and source of data. All data from wild populations unless otherwise stated.

Species	**Reproductive skew**	**Source**
Eulemur fulvus fulvus	80**	Gogarten & Koenig 2013
Eulemur rubriventer	100	Merenlender 1993
Hapalemur alaotrensis	91.53	Nievergelt *et al*. 2002
Microcebus murinus	54.5**	Radespiel *et al*. 2002
Alouatta caraya	100	Oklander *et al*. 2014
Cebus capucinus	74.50	Gogarten & Koenig 2013; Muniz *et al*. 2010; Ostner *et al*. 2008; Jack & Fedigan 2006
Sapajus apella	77.03	Escobar-Paramo 2000
Callithrix jacchus	77.78	Nievergelt *et al*. 2000
Saguinus labiatus	100	Suarez 2007
Colobus guereza	90	Dr Tara Harris (pers.comm)
Erythrocebus patas	50	Ohsawa *et al*. 1993
Macaca fascicularis	71	Gogarten & Koenig 2013; Ostner *et al*. 2008
Macaca fuscata	50	Gogarten & Koenig 2013; Soltis *et al*. 2001
Macaca mulatta	24*	Gogarten & Koenig 2013; Widdig *et al*. 2004; Berard *et al.* 1993
Macaca nigra	64.63	Engelhardt *et al.* 2017
Macaca sylvanus	24	Taub 1980
Mandrillus sphinx	72.35	Gogarten & Koenig 2013; Ostner *et al*. 2008
Papio ursinus	68.75	Huchard *et al.* 2013
Theropithecus gelada	100	Snyder-Mackler *et al*. 2012
Hylobates lar	90.5	Barreli *et al*. 2013
Gorilla gorilla gorilla	100	Inoue *et al.* 2013
Pan troglodytes	48.5	Vigilant *et al*. 2001; Constable *et al.* 2001

*Data from free-ranging populations.

**Data from captive populations.

Appendix 2.7: Species with mating skew (percentage of alpha/resident male mating success) and source of data. All data from wild populations unless otherwise stated.

Species	**Mating skew**	**Source**
Lemur catta	28.1	Parga 2006
Alouatta caraya	68.5	Oklander *et al*. 2014
Sapajus apella	38.18	Kutsukake & Nunn 2006
Callithrix jacchus	76.2	Digby 1999
Colobus guereza	100	Harris & Monfort 2006
Erythrocebus patas	100	Ohsawa *et al*. 1993
Macaca fascicularis	26	Kutsukake & Nunn 2006
Macaca fuscata	43.9	Soltis *et al*. 2001
Macaca mulatta	27.6*	Georgiev *et al*. 2015
Macaca nemestrina	56.35	Kutsukake & Nunn 2006
Macaca nigra	23.1	Reed *et al.* 1997
Macaca sylvanus	28	Young *et al.* 2013
Mandrillus leucophaeus	61	Marty *et al*. 2009
Mandrillus sphinx	80*	Kutsukake & Nunn 2006; Dixson *et al.* 1993
Papio ursinus	43	Kutsukake & Nunn 2006
Hylobates lar	91.7	Savini *et al*. 2009
Symphalangus syndactylus	100	Morino 2016
Pan troglodytes	21.5	Newton-Fisher 2004

*Data from free-ranging populations.

Appendix 2.8: The 80 non-human primate species with male (MCCH) and female (FCCH) maxillary canine tooth crown height (millimetres) and maxillary canine crown height (CCH) dimorphism data with corresponding data source.

Species	MCCH (mm)	FCCH (mm)	Source	CCH dimorphism
Eulemur collaris	×××	×××	×××	×××
Eulemur coronatus	9.43	8.48	Plavcan & Ruff 2008	1.11
Eulemur flavifrons	×××	×××	×××	×××
Eulemur fulvus fulvus	11.87	10.09	Plavcan & Ruff 2008	1.18
Eulemur macaco	10.58	10.34	Plavcan & Ruff 2008	1.02
Eulemur mongoz	9.63	8.06	Plavcan & Ruff 2008	1.19
Eulemur rubriventer	10.49	9.98	Plavcan & Ruff 2008	1.05
Hapalemur alaotrensis	×××	×××	×××	×××
Lemur catta	10.86	9.16	Plavcan & Ruff 2008	1.19
Prolemur simus	×××	×××	×××	×××
Varecia rubra	×××	×××	×××	×××
Varecia variegata variegata	13.08	12.6	Plavcan & Ruff 2008	1.04
Propithecus coronatus	×××	×××	×××	×××
Microcebus murinus	2.07	2.08	Plavcan & Ruff 2008	1.00
Galago moholi	3.67	3.45	Plavcan & Ruff 2008	1.06
Galago senegalensis	4.01	3.61	Plavcan & Ruff 2008	1.11
Alouatta caraya	14.74	9.56	Plavcan & Ruff 2008	1.54
Ateles fusciceps rufiventris	×××	×××	×××	×××
Ateles paniscus	12.11	7.73	Plavcan & Ruff 2008	1.57
Callicebus cupreus	×××	×××	×××	×××
Pithecia pithecia	8.90	7.58	Plavcan & Ruff 2008	1.17
Cebus capucinus	14.25	9.01	Plavcan & Ruff 2008	1.58
Sapajus apella	14.10	9.69	Plavcan & Ruff 2008	1.46
Sapajus xanthosternos	×××	×××	×××	×××
Saimiri boliviensis	6.65	4.12	Plavcan & Ruff 2008	1.61
Saimiri sciureus	×××	×××	×××	×××
Callimico goeldii	×××	×××	×××	×××
Callithrix geoffroyi	×××	×××	×××	×××
Callithrix jacchus	5.08	4.81	Plavcan & Ruff 2008	1.06
Cebuella pygmaea	3.08	2.98	Plavcan & Ruff 2008	1.03
Leontopithecus chrysomelas	×××	×××	×××	×××
Leontopithecus rosalia	×××	×××	×××	×××
Mico argentatus	×××	×××	×××	×××
Mico melanurus	×××	×××	×××	×××
Sagunius bicolor	×××	×××	×××	×××
Saguinus imperator	×××	×××	×××	×××
Saguinus labiatus	×××	×××	×××	×××
Saguinus midas	5.37	5.42	Plavcan & Ruff 2008	0.99
Saguinus oedipus	×××	×××	×××	×××

Appendix 2.8 *continued*.

Species	**MCCH (mm)**	**FCCH (mm)**	**Source**	**CCH dimorphism**
Allenopithecus nigroviridis	18.41	8.33	Plavcan & Ruff 2008	2.21
Cercocebus chrysogaster	xxx	xxx	xxx	xxx
Cercocebus lunulatus	xxx	xxx	xxx	xxx
Cercocebus torquatus	xxx	xxx	xxx	xxx
Cercopithecus diana	19.94	12.32	Plavcan & Ruff 2008	1.62
Cercopithecus lhoesti	19.93	10.82	Plavcan & Ruff 2008	1.84
Cercopithecus lowei	xxx	xxx	xxx	xxx
Cercopithecus neglectus	20.68	11.64	Plavcan & Ruff 2008	1.78
Cercopithecus petaurista	16.16	9.09	Plavcan & Ruff 2008	1.78
Cercopithecus pogonias	16.22	9.28	Plavcan & Ruff 2008	1.75
Chlorocebus pygerythrus	xxx	xxx	xxx	xxx
Colobus guereza	20.31	13.49	Plavcan & Ruff 2008	1.51
Colobus polykomos	19.13	10.81	Plavcan & Ruff 2008	1.77
Erythrocebus patas	26.50	12.43	Plavcan & Ruff 2008	2.13
Macaca fascicularis	24.09	10.67	Plavcan & Ruff 2008	2.26
Macaca fuscata	19.56	9.59	Plavcan & Ruff 2008	2.04
Macaca hecki	24.36	11.85	Plavcan & Ruff 2008	2.06
Macaca mulatta	16.97	8.19	Plavcan & Ruff 2008	2.07
Macaca nemestrina	28.89	12.24	Plavcan & Ruff 2008	2.36
Macaca nigra	29.73	11.38	Plavcan & Ruff 2008	2.61
Macaca silenus	24.66	10.12	Plavcan & Ruff 2008	2.44
Macaca sylvanus	22.81	11.29	Plavcan & Ruff 2008	2.02
Mandrillus leucophaeus	47.97	11.7	Plavcan & Ruff 2008	4.10
Mandrillus sphinx	49.58	9.42	Plavcan & Ruff 2008	5.26
Papio hamadryas	30.64	11.17	Plavcan & Ruff 2008	2.74
Papio papio	xxx	xxx	xxx	xxx
Papio ursinus	46.53	12.12	Plavcan & Ruff 2008	3.84
Presbytis melalophos	13.95	8.15	Plavcan & Ruff 2008	1.71
Theropithecus gelada	39.62	12.27	Plavcan & Ruff 2008	3.23
Trachypithecus auratus	xxx	xxx	xxx	xxx
Trachypithecus francoisi	17.91	10.42	Plavcan & Ruff 2008	1.72
Trachypithecus obscurus	15.44	8.51	Plavcan & Ruff 2008	1.81
Hylobates agilis	xxx	xxx	xxx	xxx
Hylobates lar	18.32	15.79	Plavcan & Ruff 2008	1.16
Hylobates muelleri	xxx	xxx	xxx	xxx
Hylobates pileatus	16.75	16.87	Plavcan & Ruff 2008	0.99
Nomascus leucogenys	xxx	xxx	xxx	xxx
Symphalangus syndactylus	21.45	18.04	Plavcan & Ruff 2008	1.19
Gorilla gorilla gorilla	30.26	17.4	Plavcan & Ruff 2008	1.74
Pan paniscus	15.56	11.24	Plavcan & Ruff 2008	1.38
Pan troglodytes	21.72	11.24	Plavcan & Ruff 2008	1.42

xxxData not available.

Appendix 2.9: Results of ICC for all species in the sample as a whole and each primate family tested separately (both sexes). All values reported are 'single measures' ICC results.

Sample	Right hand 2D:4D ratio	Left hand 2D:4D ratio
All species	ICC = 0.992, $F_{885,12390}$ = 1901.088, P = <0.001***	ICC = 0.992, $F_{885,12390}$ = 1856.180, P = <0.001***
Lemuridae	ICC = 0.990, $F_{84,1176}$ = 1569.927, P = <0.001***	ICC = 0.989, $F_{84,1176}$ = 1297.485, P = <0.001***
Indriidae	ICC = 0.997, $F_{1,14}$ = 6278.195, P = <0.001***	ICC = 0.994, $F_{1,14}$ = 3300.120, P = <0.001***
Cheirogaleidae	ICC = 0.884, $F_{7,98}$ = 114.953, P = <0.001***	ICC = 0.903, $F_{7,98}$ = 133.974, P = <0.001***
Galagidae	ICC = 0.958, $F_{2,28}$ = 369.398, P = <0.001***	ICC = 0.986, $F_{2,28}$ = 992.404, P = <0.001***
Atelidae	ICC = 0.975, $F_{33,462}$ = 575.941, P = <0.001***	ICC = 0.971, $F_{33,462}$ = 499.092, P = <0.001***
Cebidae	ICC = 0.974, $F_{119,1666}$ = 568.775, P = <0.001***	ICC = 0.978, $F_{119,1666}$ = 670.140, P = <0.001***
Pitheciidae	ICC = 0.988, $F_{20,280}$ = 1207.213, P = <0.001***	ICC = 0.988, $F_{20,280}$ = 1165.757, P = <0.001***
Callitrichidae	ICC = 0.978, $F_{68,952}$ = 662.514, P = <0.001***	ICC = 0.977, $F_{68,952}$ = 651.626, P = <0.001***
Cercopithecidae	ICC = 0.981, $F_{495,6930}$ = 783.707, P = <0.001***	ICC = 0.979, $F_{495,6930}$ = 715.552, P = <0.001***
Hylobatidae	ICC = 0.992, $F_{21,294}$ = 2127.426, P = <0.001***	ICC = 0.989, $F_{21,294}$ = 1331.760, P = <0.001***
Hominidae	ICC = 0.974, $F_{25,350}$ = 561.507, P = <0.001***	ICC = 0.977, $F_{25,350}$ = 615.033, P = <0.001***

Appendix 2.10: Phylogenetic signal results using Pagel's λ for each variable in the male non-human primates analyses. Significant results are indicated in bold.

Variable	λ	LogL[a]	*p*	*n*[b]
Male R2D:4D	**0.967**	**111.123**	**<0.001*****	**73**
Male L2D:4D	**0.992**	**123.870**	**<0.001*****	**73**
Male M2D:4D	**1.000**	**127.500**	**<0.001*****	**73**
Male body mass	**1.000**	**-61.353**	**<0.001*****	**73**
Substrate use	**1.000**	**-32.096**	**<0.001*****	**73**
MCCH	**1.000**	**-15.776**	**<0.001*****	**45**
CCH dimorphism	**0.962**	**-42.832**	**<0.001*****	**45**
Mating system	**1.000**	**-95.276**	**<0.001*****	**73**
Mating system subcategory	**1.000**	**-140.281**	**<0.001*****	**72**
Reproductive skew	0.121	-100.143	0.797	22
Mating skew	0.000	-14.344	1.000	18

[a] Log-likelihood ratio statistic.

[b] Number of species.

Appendix 3

Appendix 3.1: Countries of origin and ethnicity of the 52 populations in the sample, number (*n*) of males and females in each sample alongside the latitude (°North or °South of the equator) where these populations are found (Lat. °N/°S). The age range (in years) of the sample is provided where participants were not all adult. Data are provided on population averages for the 2D:4D ratio of the right (R2D:4D) and left (L2D:4D) hands and the mean (M2D:4D) in both sexes. Information on the 2D:4D ratio measurement methods used (PC = photocopies, DS = digital scans, CIAS = computer-assisted image analysis software) are listed and the sources of these data are given.

Country	Population ethnicity	Lat. °N	*n* Male	*n* Female	Age range (years)	Male R2D:4D	Male L2D:4D	Male M2D:4D	Female R2D:4D	Female L2D:4D	Female M2D:4D	2D:4D measurement method	Source of 2D:4D data
Finland	Finnish	60.16	24	17	4-7	xxx	xxx	0.940	xxx	xxx	0.960	Indirect (PC)	[1]
Sweden	Swedish	60.13[b]	24	24	Adult	xxx	xxx	0.950	xxx	xxx	1.010	Direct	[2]
Lithuania	Lithuanian	55.17[b]	23	86	Adult	0.950	0.953	0.952	0.971	0.973	0.972	Indirect (PC)[d]	[3]
Russia	Russian	57.45	221	161	8-17	0.982	0.970	0.976	0.988	0.984	0.986	Direct	[4]
Russia	Russian	55.75	150	156	8-17	0.966	0.975	0.971	0.983	0.989	0.986	Direct	[4]
Russia	Russian	54.43	58	48	16-23	xxx	xxx	0.969	xxx	xxx	0.993	Direct	[4]
Russia	Russian	54.31	128	168	8-17	0.962	0.976	0.969	0.979	0.987	0.983	Direct	[4]
Russia	Russian	43.19	146	158	8-17	0.967	0.969	0.968	0.990	0.984	0.987	Direct	[4]
Russia	Mordvin	54.24	65	92	8-17	0.966	0.965	0.966	0.984	0.986	0.985	Direct	[5]
UK	British	53.39	117	183	Adult	0.980	0.980	0.980	0.990	0.990	0.990	Direct	[1]
UK	British	51.50	106	105	Adult	0.970	0.975	0.973	0.980	0.983	0.982	Direct	[6]
Germany	German	52.37[a]	109	96	Adult	xxx	xxx	0.960	xxx	xxx	0.970	Indirect (PC)	[1]
Austria	Austrian	48.21	80	0	Adult	0.969	0.965	0.967	xxx	xxx	xxx	Indirect (PC)[e]	[7]
Poland	Polish	52.41	144	180	Adult	0.992	0.991	0.992	0.997	0.998	0.998	Direct	[8]

Appendix 3.1 *continued.*

Country	Population ethnicity	Lat. °N/°S	*n* Male	*n* Female	Age range (years)	Male R2D:4D	Male L2D:4D	Male M2D:4D	Female R2D:4D	Female L2D:4D	Female M2D:4D	2D:4D measurement method	Source of 2D:4D data
Poland	Polish	49.66	238	0	Adult	0.970	0.970	0.970	xxx	xxx	xxx	Direct	[9]
Hungary	Hungarian gypsy	46.07	12	39	Adult	xxx	xxx	0.960	xxx	xxx	0.960	Direct	[1]
Hungary	Hungarian	46.07	15	30	Adult	xxx	xxx	0.970	xxx	xxx	0.980	Direct	[1]
Greece	Greek	39.07[b]	60	60	Adult	0.974	0.973	0.974	1.002	1.001	1.002	Direct	[10]
Spain	Spanish	37.18	260	363	Adult	0.965	0.959	0.962	0.975	0.972	0.973	Indirect (CIAS)	[11]
Spain	Spanish	37.18	40	45	Adult	0.990	0.980	0.985	0.990	0.980	0.985	Direct	[12]
Spain	Spanish	28.29	63	101	Adult	0.954	0.954	0.954	0.963	0.963	0.963	Direct	[13]
Morocco	Berber	34.00[b]	54	36	6-14	0.945	xxx	xxx	0.957	xxx	xxx	Indirect (PC)	[14]
Nigeria	Yoruba	7.59	210	210	13-19	0.960	0.940	0.950	0.970	0.950	0.960	Direct	[15]
Nigeria	Igbo	4.85	210	210	13-20	0.960	0.940	0.950	0.970	0.950	0.960	Direct	[15]
Nigeria	Ijaw	4.50	350	352	15-60	xxx	xxx	0.950	xxx	xxx	0.960	Direct	[16]
Tanzania	Hadza	3.90	142	171	16-70	0.972	0.979	0.976	0.980	0.990	0.985	Direct	[17], [18]
Tanzania	Datooga	3.63	240	146	Adult	0.960	0.960	0.960	0.970	0.980	0.975	Direct	[18]
Namibia	Himba	22.96[b]	39	58	Adult	0.939	xxx	xxx	0.996	xxx	xxx	Indirect (CIAS)	[19]
South Africa	Zulu	29.86	60	60	Adult	xxx	xxx	0.940	xxx	xxx	0.950	Direct	[20]
India	Rajput	31.82	70	70	14-18	0.960	0.960	0.960	0.970	0.970	0.970	Direct	[21]
India	Indian	29.06	100	0	Adult	0.945	0.955	0.950	xxx	xxx	xxx	Direct [c]	[22]
India	Rajbanshi	22.99	250	250	Adult	0.970	0.960	0.965	0.970	0.960	0.965	Direct	[23]
India	Indian	22.97[a]	500	464	Adult	0.967	0.963	0.965	0.982	0.974	0.978	Direct	[24]
India	Indian	17.93	100	95	Adult	0.960	0.957	0.959	0.982	0.980	0.981	Direct	[25]
India	Indian (Telugu)	16.45	96	104	Adult	0.981	0.973	0.977	0.989	1.038	1.014	Direct	[26]

Appendix 3.1 ***continued.***

Country	Population ethnicity	Lat. °N/°S	*n* Male	*n* Female	Age range (years)	Male R2D:4D	Male L2D:4D	Male M2D:4D	Female R2D:4D	Female L2D:4D	Female M2D:4D	2D:4D measurement method	Source of 2D:4D data
India	Sugali & Yanadi	16.45	80	80	Adult	xxx	xxx	0.960	xxx	xxx	0.970	Direct	[20]
India	Indian	12.91	80	80	Adult	1.010	0.970	0.990	0.980	0.970	0.975	Direct	[27]
China	Hui	37.19	119	227	15-22	0.934	0.932	0.933	0.952	0.952	0.952	Indirect (CIAS)	[28]
China	Uyghur	42.52	209	229	6-14	0.940	xxx	xxx	0.950	xxx	xxx	Indirect (PC)	[14]
China	Maonan	24.83	275	159	Adult	0.938	0.940	0.939	0.944	0.943	0.944	Direct	[29]
China	Bouyei	26.84	153	159	Adult	0.966	0.954	0.960	0.984	0.985	0.985	Direct	[30]
China	Hani	24.48	80	60	Adult	0.932	0.942	0.937	0.952	0.955	0.954	Indirect (CIAS)	[31]
China	Han	41.94	128	122	Adult	0.960	0.950	0.955	0.970	0.960	0.965	Direct	[32]
China	Han	28.31	150	150	Adult	0.958	0.957	0.958	0.972	0.969	0.971	Direct	[33]
China	Han	27.32	132	412	Adult	0.948	0.937	0.943	0.958	0.952	0.955	Direct	[34]
South Korea	Korean	36.81	95	88	Adult	0.952	0.950	0.951	0.971	0.973	0.972	Indirect (PC)[c]	[35]
Japan	Japanese	36.20[b]	96	202	14-30	0.950	0.940	0.945	0.960	0.960	0.960	Indirect (PC)	[36]
Malaysia	Malaysian	3.07	150	150	Adult	0.982	0.987	0.985	0.977	0.984	0.981	Direct	[37]
Papua, Indonesia	Yali	4.27	47	32	Adult	0.950	0.970	0.960	0.940	0.950	0.945	Direct & Indirect (CIAS)[f]	[38]
Australia	Australian*	27.47	233	280	Adult	0.965	0.972	0.969	0.982	0.982	0.982	Indirect (PC)	[39]
USA	American	30.27	57	56	Adult	0.957	0.951	0.954	0.975	0.966	0.971	Indirect (DS)	[39], [40]
Brazil	Brazilian	18.51	60	60	Adult	0.955	0.962	0.959	0.953	0.963	0.958	Direct[c]	[41]

[xxx] Data not available.

*British ancestry

[a] where participants originated from more than one area within a country then the latitude for the midway point between the areas was used.

[b] where the area of origin of participants within a country was not provided then the latitude of the central region of the country was used.

[c] data from control group only.

[d] data from contemporary sample only.

[e] data from heterosexual sample only.

[f] Authors found both measurement methods to be comparable and so reported the mean of the measurements gained from the two methods.

[1] Manning *et al.* 2000; [2] Sanders *et al*. 2005; [3] Voracek *et al.* 2007b; [4] Butovskaya *et al.* 2013; [5] Bakholdina *et al.* 2018; [6] Richards *et al.* 2018; [7] Voracek *et al*. 2005; [8] Szwed *et al.* 2017; [9] Klimek *et al*. 2014; [10] Kyriakidis & Papaioannidou 2008; [11] Bosh-Domenech *et al*. 2014; [12] Manning *et al.* 2002; [13] Hernandez *et al.* 2018; [14] Manning *et al.* 2004a; [15] Gabriel *et al*. 2009; [16] Gwunireama *et al.* 2010; [17] Butovskaya *et al*. 2012; [18] Butovskaya *et al*. 2015; [19] Sorokowski *et al.* 2012; [20] Manning *et al.* 2003; [21] Krishnan *et al*. 2013; [22] Yadav *et al.* 2016; [23] Sen *et al*. 2015; [24] Maitra *et al*. 2016; [25] Mohammed *et al*. 2013; [26] Gayathri & Vallabhajosyula 2016; [27] Jacob *et al*. 2015; [28] Lu *et al.* 2017; [29] Chen *et al*. 2012; [30] Li *et al*. 2011; [31] Zhoa *et al*. 2013; [32] Xi *et al.* 2014; [33] Li 2010; [34] Zhang *et al.* 2012; [35] Kim *et al.* 2011; [36] Hiraishi *et al*. 2012; [37] Nadankutty *et al.* 2014; [38] Marczak *et al.* 2018; [39] Loehlin *et al*. 2006; [40] McFadden *et al.* 2005; [41] Goncalves *et al.* 2017.

Appendix 3.2: Table showing the marriage system practised by each society and the sources of these data. Marriage system data are given for each country's population and only repeated within countries where the ethnicities of the populations differ. The marriage system categories are; monogamy (MO), limited polygyny (LP) and general polygyny (GP).

Country	Population Ethnicity	Marriage system	Source
Finland	Finnish	MO	Brown *et al*. 2009; Levinson 1991
Sweden	Swedish	MO	Brown *et al*. 2009; Levinson 1991
Lithuania	Lithuanian	MO	Manning 2008; Kanazawa & Still 1999; Levinson 1991
Russia	Russian	MO	Murdock 1967
Russia	Mordvin	MO	Kirby *et al.* 2016
UK	British	MO	Levinson 1991
Germany	German	MO	Manning 2008; Kanazawa & Still 1999; Levison 1991
Austria	Austrian	MO	McDermott 2016
Poland	Polish	MO	Manning 2008; Kanazawa, & Still 1999; Levinson 1991
Hungary	Hungarian gypsy	MO	Manning 2008; Levinson 1991
Hungary	Hungarian	MO	Manning 2008; Levinson 1991
Greece	Greek	MO	Scheidel 2009; Levinson 1991
Spain	Spanish	MO	Manning 2008; Levinson 1991
Morocco	Berber	LP	Hart 2011
Nigeria	Yoruba	GP	Holden & Mace 1999; Murdock 1967
Nigeria	Igbo	GP	Holden & Mace 1999; Murdock 1967
Nigeria	Ijaw	GP	Brisibe & Ordinioha 2011; Brabin 1984
Tanzania	Hadza	LP	Holden & Mace 1999; Murdock 1967
Tanzania	Datooga	GP	Butovskaya *et al*. 2015, 2013, 2012
Namibia	Himba	GP	Sorokowski *et al.* 2012; Bollig 2005

Appendix 3.2 ***continued.***

Country	**Population Ethnicity**	**Marriage system**	**Source**
South Africa	Zulu	GP	Holden & Mace 1999; Murdock 1967
India	Rajput	MO	Singh *et al*. 1999; Singhji 1994
India	Indian	MO	Kirby *et al.* 2016; Holden & Mace 1999; Murdock 1967
India	Rajbanshi	MO	Sengupta 1993
India	Telugu	MO	Kirby *et al.* 2016
India	Sugali & Yanadi	MO	Kirby *et al.* 2016
China	Hui	MO	Li & Luckert 1994
China	Uyghur	MO	Freeberne 1966
China	Maonan	MO	Ogata *et al*. 2007; Guo & Dong 2000
China	Bouyei	MO	Chang 2003
China	Hani	MO	Hu *et al*. 2017
China	Han	MO	Murdock 1967; Watson & Ebrey 1991
South Korea	Korean	MO	Holden & Mace 1999; Levinson 1991; Murdock 1967
Japan	Japanese	MO	Kanazawa & Still 1999; Murdock 1967
Malaysia	Malaysian	MO	Peletz 1996; Peletz 1988
Papua, Indonesia	Yali	GP	Marczak *et al*. 2017; Sorokowski *et al.* 2013
Australia	Australian*	MO	McDermott 2016
USA	American	MO	Brown *et al*. 2009
Brazil	Brazilian	MO	Levinson 1991

*British ancestry

Appendix 3.3: Phylogenetic signal results for each variable in the human analyses using Pagel's λ. Significant results are indicated in bold.

Variable	λ	LogL[a]	*p*	*n*[b]
Male R2D:4D	0.322	83.949	0.197	31
Male L2D:4D	0.375	79.461	0.140	28
Male M2D:4D	0.344	97.333	0.088	34
Female R2D:4D	0.231	79.898	0.186	29
Female L2D:4D	0.299	69.323	0.160	26
Female M2D:4D	0.242	89.270	0.065	33
Marriage system	**1**	**5.367**	**<0.001*****	**37**

[a] Log-likelihood ratio statistic.

[b] Sample number.

Appendix 4

Appendix 4.1: Average female body mass (grams) for each species and the sources of these data. Data from wild animals unless otherwise stated.

Species	**Average adult female body mass (g)**	**Source**
Eulemur collaris	2375	Fleagle 2013
Eulemur coronatus	1080	Smith & Jungers 1997
Eulemur flavifrons	2510	Smith & Jungers 1997
Eulemur macaco	2430	Fleagle 2013
Eulemur mongoz	1560	Smith & Jungers 1997
Eulemur rubriventer	1940	Smith & Jungers 1997
Hapalemur alaotrensis	1600	Garbutt 1999
Lemur catta	2207	Sussman 1991
Prolemur simus	1300	Smith & Jungers 1997
Varecia rubra	3520	Fleagle 2013
Varecia variegata variegata	3520	Smith & Jungers 1997
Propithecus coronatus	3738	Taylor & Schwittzer 2012
Microcebus murinus	62.83	Schmid & Kappeler 1998
Galago moholi	173	Smith & Jungers 1997
Alouatta caraya	4330	Smith & Jungers 1997
Ateles fusciceps rufiventris	9163	Ford & Davis 1992
Ateles paniscus	8440	Smith & Jungers 1997
Callicebus cupreus	1120	Smith & Jungers 1997
Pithecia pithecia	1589	Smith & Jungers 1997
Cebus capucinus	2540	Smith & Jungers 1997
Sapajus apella	2520	Smith & Jungers 1997
Sapajus xanthosternos	2167	Fleagle 2013
Saimiri boliviensis	700	Ford & Davis 1992
Saimiri sciureus	675	Ford & Davis 1992
Callimico goeldii	468**	Fleagle 2013
Callithrix geoffroyi	190	Ford & Davis 1992
Cebuella pygmaea	122	Smith & Jungers 1997
Leontopithecus chrysomelas	535	Smith & Jungers 1997
Leontopithecus rosalia	598	Smith & Jungers 1997
Mico argentatus	360	Fleagle 2013
Mico melanurus	390	Fleagle 2013
Saguinus bicolor	430	Smith & Jungers 1997
Saguinus imperator	475	Smith & Jungers 1997
Sanuinus oedipus	404	Smith & Jungers 1997
Allenopithecus nigroviridis	3180	Smith & Jungers 1997

Appendix 4.1 ***continued.***

Species	**Average adult female body mass (g)**	**Source**
Cercocebus chrysogaster	7000	Kingdon 2015
Cercocebus lunulatus	5300	Fleagle 2013
Cercocebus torquatus	5500	Smith & Jungers 1997
Cercopithecus diana	3900	Smith & Jungers 1997
Cercopithecus lhoesti	3450	Smith & Jungers 1997
Cercopithecus lowei	3000	Kingdon 2015
Cercopithecus neglectus	4130	Smith & Jungers 1997
Cercopithecus petaurista	2900	Smith & Jungers 1997
Cercopithecus pogonias	2900	Smith & Jungers 1997
Chlorocebus pygerythrus	2980	Smith & Jungers 1997
Colobus guereza	9200	Smith & Jungers 1997
Colobus polykomos	8300	Smith & Jungers 1997
Macaca fascicularis	3590	Smith & Jungers 1997
Macaca fuscata	8030	Smith & Jungers 1997
Macaca hecki	6800**	Smith & Jungers 1997
Macaca mulatta	5370	Smith & Jungers 1997
Macaca nemestrina	6500	Smith & Jungers 1997
Macaca nigra	5470	Smith & Jungers 1997
Macaca silenus	6100	Smith & Jungers 1997
Macaca sylvanus	5500	Kindgon 2015
Mandrillus leucophaeus	12500	Smith & Jungers 1997
Mandrillus sphinx	12500	Kingdon 2015
Papio hamadryas	9900	Smith & Jungers 1997
Papio papio	12100	Smith & Jungers 1997
Papio ursinus	14800	Smith & Jungers 1997
Theropithecus gelada	11700	Smith & Jungers 1997
Trachypithecus auratus	5841	Fleagle 2013
Trachypithecus obscurus	6260	Smith & Jungers 1997
Hylobates agilis	5820	Smith & Jungers 1997
Hylobates lar	5340	Smith & Jungers 1997
Hylobates muelleri	5350	Smith & Jungers 1997
Hylobates pileatus	5440	Smith & Jungers 1997
Nomascus leucogenys	7320	Smith & Jungers 1997
Symphalangus syndactylus	10700	Smith & Jungers 1997
Gorilla gorilla gorilla	71500	Smith & Jungers 1997
Pan paniscus	33200	Smith & Jungers 1997
Pan troglodytes	45800	Smith & Jungers 1997

** Data from captive animals.

Appendix 4.2: Average percentage of fruit in diet (including nuts, seeds and seed pods) for each species and the sources of these data.

Species	Percentage fruit^{a,b}	Source
Eulemur collaris	78.05	Sato *et al*. 2015
Eulemur coronatus	70	Godfrey *et al*. 2004; Freed 1999 in Dolhinow & Fuentes 1999
Eulemur flavifrons	79	Van den Abbeele 2014
Eulemur macaco	73.5	Sato *et al*. 2015
Eulemur mongoz	65	Sato *et al*. 2015
Eulemur rubriventer	80.6	Sato *et al*. 2015
Hapalemur alaotrensis	0	Randrianarisoa 1999 in Godfrey *et al*. 2004
Lemur catta	62	Gould & Gabriel 2015
Prolemur simus	0.5	Tan 1999
Varecia rubra	61	Martinez & Razafindratsima 2014
Varecia variegata variegata	67.3	Wheeler *et al.* 2013
Propithecus coronatus	7.5	Pichon *et al*. 2010
Microcebus murinus	31.33	Dammhahn & Kappeler 2008; Lahann 2007; Radespiel *et al*. 2006
Alouatta caraya	19.0	Bravo & Sallenave 2003
Ateles paniscus	82.9	Van Roosalen 1985
Callicebus cupreus	90.35	Kulp & Heymann 2015
Pithecia pithecia	86.35	Homburg 1997; Norconk 1996; Kinzey & Norconk 1993
Cebus capucinus	60	Wheeler *et al.* 2013
Sapajus apella	17.6	Smuts *et al*. 1987
Sapajus xanthosternos	42.7	Canale *et al*. 2016
Saimiri boliviensis	93	Rosenberger 1992
Saimiri sciureus	67.9	Pinheiro *et al*. 2013
Callimico goeldii	29	Porter 2001a
Callithrix geoffroyi	15	Passamani & Rylands 2000
Cebuella pygmaea	0	Ramirez *et al*. 1977
Leontopithecus chrysomelas	35.1	Catenacci *et al.* 2016
Leontopithecus rosalia	77	Smith & Smith 2013
Mico argentatus	36	Smith & Smith 2013; Campbell *et al*. 2011
Saguinus bicolor	39	Smith & Smith 2013
Saguinus oedipus	38	Smith & Smith 2013
Cercocebus torquatus	80	Mitani 1989
Cercopithecus diana	59.7	Buzzard 2006; Curtin 2002
Cercopithecus petaurista	55.5	Buzzard 2006
Chlorocebus pygerythrus	19.6	Wrangham & Waterman 1981; Whitten 1983

Appendix 4.2 ***continued.***

Species	**Percentage fruit**[a,b]	**Source**
Colobus guereza	20.8	Campbell *et al*. 2011; Wasserman & Chapman 2003; Fashing 2001a
Colobus polykomos	36.0	Davies *et al.* 1999
Macaca fascicularis	76.85	Yeager 1996; Wheatley 1980
Macaca fuscata	51.4	Agetsuma & Nakagawa 1998; Hill 1997; Agetsuma 1995
Macaca mulatta	8.5	Goldstein & Richard 1989
Macaca nemestrina	74.2	Caldecott 1986
Macaca nigra	65.4	Wheeler *et al*. 2013
Macaca silenus	78.1	Roy *et al*. 2011
Macaca sylvanus	32.0	Ménard & Vallet 1996
Mandrillus leucophaeus	58	Gonzalez-Kirchner & Sainz de la Maza 1996
Mandrillus sphinx	81	Tutin *et al*. 1997
Papio hamadryas	54.1	Schreier 2009; Swedell *et al*. 2008
Papio papio	77	Sharman 1981
Papio ursinus	43.3	Hill 1997; Gaynor 1994; Whiten *et al*. 1987, 1991; Davidge 1978
Theropithecus gelada	3.5	Hunter 2001; Dunbar & Dunbar 1975
Trachypithecus auratus	32	Kool 1992, 1993
Trachypithecus obscurus	35	Curtin 1976, 1980
Hylobates agilis	58	Smuts *et al*. 1987
Hylobates lar	62.7	Palombit 1997; Smuts *et al*. 1987
Hylobates muelleri	62	Smuts *et al*. 1987
Hylobates pileatus	71	Srikosamatara 1980; Srikosamatara 1984
Symphalangus syndactylus	46.7	Palombit 1997; Chivers 1974
Gorilla gorilla gorilla	48	Conkliin-Brittain *et al*. 1998
Pan paniscus	55	Campbell *et al.* 2011
Pan troglodytes	62.5	Campbell *et al*. 2011; Smuts *et al*. 1987

[a] Includes fruit, nuts, seeds and seed pods.

[b] Data presented as percentage of time spent feeding on food items or calculated from equivalent methods (see Methods section 4.2.3.3: Ecological Variables).

Appendix 4.3: Mean group size for each species (all age and sex classes) and the sources of these data.

Species	**Mean group size**[a]	**Source**
Eulemur collaris	5.0	Donati & Borgogini-Tarli 2002; Feistner & Schmid 1999; Mittermeier *et al.* 1994
Eulemur coronatus	7.0	Freed 1996; Wilson et al. 1989
Eulemur flavifrons	8.0	Volampeno *et al*. 2010
Eulemur macaco	10.0	Andrews & Birkinshaw 1998; Colquhoun 1993
Eulemur mongoz	5.5	Curtis & Zaramody 1997; Harrington 1978; Tattersall 1977
Eulemur rubriventer	3.0	Overdorff 1993
Hapalemur alaotrensis	6.0	Mutschler 2002; Nievergelt *et al*. 1998
Lemur catta	14.4	Gould *et al*. 2003; Jolly *et al*. 2002; Koyama *et al*. 2002; Sussman 1977, 1991; Budnitz & Dainis 1975
Prolemur simus	8.0	Tan 1999; Meier & Rumpler 1987; Wright *et al.* 1987
Varecia rubra	14.3	Vasey 2002, 2006; Rigamonti 1993
Varecia variegata variegata	8.0	Ratsimbazafy 2002; Britt *et al.* 2001; Balko 1998; Morland 1991; White 1989
Propithecus coronatus	5.0	Müller *et al*. 2002; Curtis *et al*. 1998; Mittermeier *et al*. 1994; Petter *et al*. 1977
Microcebus murinus	8.0	Ramananjato & Ganzhorn 2001; Radespiel *et al*. 1998; Pages-Feuillade 1989; Martin 1972, 1973
Galago moholi	4.0	Campbell *et al*. 2011
Alouatta caraya	10.1	Bravo & Sallenave 2003; Agoramoorthy & Lohmann 1999; Rumiz 1990
Ateles fusciceps rufiventris	25.0	Symington 1990; Van Roosmalen & Klein 1988
Ateles paniscus	15.0	Norconk & Kinzey 1994; van Roosmalen 1985
Callicebus cupreus	3.4	Bennett *et al*. 2001
Pithecia pithecia	4.6	Cunningham & Janson 2007; Norconk 2006; Cunninhgam 2003; Norconk *et al*. 2003; Lehman *et al*. 2001; Vié *et al*. 2001; Kessler 1998; Homburg 1997; Mittermeier 1977; Muckenhirn *et al*. 1975
Cebus capucinus	16.4	Fragaszy *et al*. 2004
Sapajus apella	15.5	Fragaszy *et al*. 2004; Barton 1996
Sapajus xanthosternos	30.0	Suscke *et al.* 2017
Saimiri boliviensis	54.0	Bionski *et al*. 2003
Saimiri sciureus	23.0	Bionski *et al*. 2003
Callimico goeldii	8.0	Campbell *et al.* 2011; Porter 2001b
Callithrix geoffroyi	5.0	Price *et al*. 2002; Chiarello & de Melo 2001; Passamani 1998
Cebuella pygmaea	5.5	Yépez *et al*. 2005; de la Torre *et al*. 2000; Heymann & Soini 1999; Soini 1982, 1988
Leontopithecus chrysomelas	6.5	Raboy & Dietz 2004; Baker *et al*. 2002; Dietz *et al*. 1994
Leontopithecus rosalia	6.5	Baker *et al*. 1993; Dietz & Baker 1993
Mico argentatus	8.0	Tavares & Ferrari 2002; Albernaz & Magnusson 1999
Mico melanurus	6.2	Stallings 1985; Stallings & Mittermeier 1983

Appendix 4.3 *continued*.

Species	**Mean group size**[a]	**Source**
Saguinus bicolor	4.8	Vidal & Cintra 2006
Saguinus imperator	5.6	Buchanan-Smith 1999
Saguinus oedipus	6.0	Savage *et al*. 1996
Allenopithecus nigroviridis	22.0	McGraw 1994; Gautier 1985
Cercocebus chrysogaster	15.0	Gautier-Hion *et al*. 1999
Cercocebus lunulatus	30.5	Kingdon *et al.* 2013
Cercocebus torquatus	27.2	Kingdon *et al.* 2013; Mitani 1989; Jones & Pi 1968
Cercopithecus diana	23.9	Buzzard & Eckhardt 2007; Shultz *et al*. 2004; McGraw *et al*. 2002; Shultz & Noe 2002; Whitesides 1989
Cercopithecus lhoesti	23.5	Kaplin 2001; Mitani *et al.* 2001
Cercopithecus lowei	10.0	Kingdon 2015
Cercopithecus neglectus	7.8	Wahome *et al*. 1993; Gautier-Hion & Gautier 1978
Cercopithecus petaurista	10.7	Buzzard & Eckhardt 2007; Shultz *et al*. 2004; Shultz & Noe 2002
Cercopithecus pogonias	18.0	Gautier-Hion *et al*. 1983
Chlorocebus pygerythrus	21.0	Campbell *et al.* 2011
Colobus guereza	9.0	Harris 2006; Fashing 2001b; Fashing & Cords 2000; Grimes 2000; Onderdonk & Chapman 2000; Krüger *et al*. 1998; Bocian 1997; Struhsaker 1997; Oates 1994; Dunbar 1987; Suzuki 1979; Rose 1978; Oates 1977, 1974; Schenkel & Schenkel-Hulliger 1967
Colobus polykomos	13.6	Korstjens 2001; Dasilva 1989, 1994; Whitesides *et al*. 1988
Macaca fascicularis	27.7	Wheatley 1980; Kurland 1973; Bernstein 1967; Furuya 1965
Macaca fuscata	45.5	Takasaki 1984
Macaca hecki	15	Supriatna & Hendras 2000
Macaca mulatta	40.8	Melnick 1981; Makwana 1978; Neville 1968; Southwick *et al*. 1965
Macaca nemestrina	18.3	Crockett & Wilson 1980
Macaca nigra	50.0	Marty 2015
Macaca silenus	21.0	Green & Minkowski 1977
Macaca sylvanus	18.3	Deag & Crook 1971
Mandrillus leucophaeus	58.0	Astaras *et al.* 2008; Wild *et al*. 2005; Gonzalez-Kirchner & Sainz de la Maza 1996; Gartlan 1970; Struhsaker 1969
Mandrillus sphinx	52.0	Hoshino *et al*. 1984
Papio hamadryas	77.4[1]	Swedell 2002, 2006; Zinner *et al*. 2001; Al-Safadi 1994; Boug *et al.* 1994; Biquand *et al.* 1992; Abegglen 1984; Sigg *et al*. 1982; Kummer *et al*. 1981; Sigg & Stolba 1981; Nagel 1973; Kummer 1968
Papio papio	62.0[2]	Galat-Luong *et al*. 2006

Appendix 4.3 ***continued*.**

Species	**Mean group size**[a]	**Source**
Papio ursinus	48.7	Gwenzi *et al*. 2007; Cheney *et al.* 2004, 2006; Weingrill *et al*. 2003; Weingrill 2000; Henzi *et al*. 1999; Cowlishaw 1997a,b; Ron *et al*. 1996; Henzi & Lycett 1995; Henzi *et al*. 1990; Bulger & Hamilton 1987; Anderson 1981a,b; Davidge 1978; Hamilton *et al*. 1976; Seyfarth 1976; Saayman 1970; Stoltz & Saayman 1970; Hall 1962
Theropithecus gelada	113.0[1]	Hunter 2001; Iwamoto 1979; Dunbar & Dunbar 1974
Trachypithecus auratus	14.0	Kool 1993
Trachypithecus obscurus	17.0	Curtin 1980
Hylobates agilis	4.4	Smuts *et al*. 1987
Hylobates lar	4.0	Asensio *et al.* 2017
Hylobates muelleri	3.4	Smuts *et al*. 1987
Hylobates pileatus	4.1	Asensio *et al*. 2017
Nomascus leucogenys	3.6	Bach & Rawson 2011; Hu *et al*. 1989
Symphalangus syndactylus	4.0	Smuts *et al*. 1987
Gorilla gorilla gorilla	10.0	Barton 1996
Pan paniscus	9.5[3]	Myers Thompson 2002; Kano 1992; Thompson-Handler 1990; Badrian & Malenky 1984
Pan troglodytes	8.3[3]	Mitani *et al*. 2002; Boesch 1996

[a] Includes all animals of the same species in a group e.g. both sexes and all age-sex classes.

[1] Group size here refers to average band size.

[2] Group size here refers to average 3rd level grouping size (analogous to bands).

[3] Group size here refers to average party size.

Appendix 4.4: Female directional consistency index (DCI) for each species and the sources of these data.

Species	**DCI**	**Source**
Varecia variegata variegata	*X*	Koenig *et al*. in prep
Cebus capucinus	*X*	Koenig *et al*. in prep
Sapajus apella	*X*	Koenig *et al.* in prep
Chlorocebus pygerythrus	*X*	Koenig *et al*. in prep
Colobus polykomos	0.746	Koenig *et al*. 2013; Korstjens *et al*. 2002
Macaca fascicularis	1.000	Koenig *et al*. 2013
Macaca fuscata	*X*	Koenig *et al.* in prep
Macaca nigra	*X*	Koenig *et al*. in prep
Macaca sylvanus	*X*	Koenig *et al*. in prep
Papio ursinus	*X*	Koenig *et al.* in prep
Theropithecus gelada	*X*	Koenig *et al*. in prep
Pan paniscus	*X*	Koenig *et al*. in prep
Pan troglodytes	*X*	Koenig *et al*. in prep

X Data are from Koenig *et al*. in prep and are withheld at the request of the providing author.

Appendix 4.5: Female rates of agonism (per hour of observation time) and the sources of these data.

Species	**Rate of agonism**	**Source**
Varecia variegata variegata	0.160	Morland 1991
Cebus capucinus	1.107	Bergstrom & Fedigan 2010; Bergstrom 2009; Rose 1998
Colobus polykomos	0.600	Korstjens *et al.* 2002
Macaca fascicularis	1.520	van Noordwijk & van Schaik 1987
Macaca fuscata	1.020	Hill & Okasayu 1995; Saito 1996
Macaca nigra	*X*	Koenig *et al*. in prep
Papio ursinus	1.558	Wheeler *et al* 2013; Huchard & Cowlishaw 2011; Henzi and Barrett 2003; Barrett *et al.* 2002; Hill 1999; Ron *et al*. 1996; Gaynor 1994; Hamilton *et al*. 1978
Pan troglodytes	0.150	Wheeler *et al.* 2013

X Data are from Koenig *et al*. in prep and are withheld at the request of the providing author.

Appendix 4.6: Dominance relationship between the sexes for each species and the sources of these data. M = Males are the dominant sex, F = Females are the dominant sex, CO = Sexes are codominant/there is no clear dominance relationship between the sexes.

Species	**Intersexual dominance pattern**	**Source**
Eulemur collaris	CO	Balestri *et al*. 2014
Eulemur coronatus	F	Marlof *et al.* 2007; Eichmueller *et al.* 2013
Eulemur flavifrons	F	Digby & Kahlenberg 2002; Eichmueller *et al*. 2013
Eulemur macaco	F	Fornasieri & Roeder 1993; Eichmueller *et al*. 2013
Eulemur mongoz	F	Curtis & Zaramody 1999; Eichmueller *et al*. 2013
Eulemur rubriventer	F	Marlof *et al.* 2007; Eichmueller *et al*. 2013
Hapalemur alaotrensis	F	Mutschler 1999; Waeber & Hemelrijk 2003; Eichmueller *et al*. 2013
Lemur catta	F	Kappeler 1990; Eichmueller *et al*. 2013
Prolemur simus	M	Andriaholinirina *et al*. 2003; Tan 2006; Tan 1999.
Varecia rubra	F	Meyer *et al.* 1999; Eichmueller *et al.* 2013
Varecia variegata variegata	F	Kaufmann 1991; Eichmueller *et al*. 2013
Propithecus coronatus	F	Ramanamisata *et al*. 2014
Microcebus murinus	F	Hohenbrink *et al*. 2016; Génin 2013; Radespiel & Zimmerman 2001
Galago moholi	M	Bearder 1999
Alouatta caraya	M	Neville *et al*. 1988
Ateles fusciceps rufiventris	M	Smuts *et al*. 1987
Ateles paniscus	M	Smuts *et al.* 1987
Callicebus cupreus	CO	Kinzey 1981; Kinzey 1997
Pithecia pithecia	M	Thompson 2011; Harrison & Norconk 1999
Cebus capucinus	M	Perry 1997
Sapajus apella	M	Izawa 1980
Sapajus xanthosternos	M	Fragaszy *et al*. 2004
Saimiri boliviensis	F	Mitchell 1994
Saimiri sciureus	F	Hrdy 1981
Callimico goeldii	CO	Smuts *et al*. 1987
Callithrix geoffroyi	CO	Koba *et al*. 2012; Smuts *et al.* 1987
Cebuella pygmaea	CO	Koba *et al*. 2012; Smuts *et al*. 1987
Mico argentatus	CO	Koba *et al*. 2012; Smuts *et al*. 1987
Mico melanurus	CO	Koba *et al*. 2012; Smuts *et al.* 1987
Leontopithecus chrysomelas	CO	Smuts *et al*. 1987
Leontopithecus rosalia	CO	Smuts *et al*. 1987
Saguinus bicolor	CO	Smuts *et al*. 1987
Saguinus imperator	CO	Smuts *et al*. 1987
Saguinus oedipus	CO	Savage *et al*. 1988; Smuts *et al*. 1987
Allenopithecus nigroviridis	M	Mitani *et al*. 2012
Cercocebus chrysogaster	M	Mitani *et al*. 2012
Cercocebus lunulatus	M	Mitani *et al*. 2012

Appendix 4.6 ***continued***.

Species	**Intersexual dominance pattern**	**Source**
Cercocebus torquatus	M	Mitani *et al*. 2012
Cercopithecus diana	M	Mitani *et al*. 2012
Cercopithecus lhoesti	M	Mitani *et al*. 2012
Cercopithecus lowei	M	Mitani *et al*. 2012
Cercopithecus neglectus	M	Mitani *et al*. 2012
Cercopithecus petaurista	M	Mitani *et al*. 2012
Cercopithecus pogonias	M	Mitani *et al*. 2012
Chlorocebus pygerythrus	M	Hemelrijk *et al.* 2008
Colobus guereza	M	Newton & Dunbar 1994
Colobus polykomos	M	Newton & Dunbar 1994
Macaca fascicularis	M	Mitani *et al*. 2012
Macaca fuscata	M	Mitani *et al*. 2012
Macaca hecki	M	Mitani *et al.* 2012
Macaca mulatta	M	Mitani *et al*. 2012
Macaca nemestrina	M	Hemelrijk *et al*. 2008
Macaca nigra	M	Mitani *et al*. 2012
Macaca silenus	M	Mitani *et al*. 2012
Macaca sylvanus	M	Mitani *et al*. 2012
Mandrillus leucophaeus	M	Mitani *et al*. 2012
Mandrillus sphinx	M	Hemelrijk *et al*. 2008
Papio hamadryas	M	Swedell 2006; Kummer 1995
Papio papio	M	Maestripieri *et al*. 2007
Papio ursinus	M	Engh *et al*. 2009
Theropithecus gelada	M	Mitani *et al*. 2012
Trachypithecus auratus	M	Mitani *et al*. 2012
Trachypithecus obscurus	M	Mitani *et al.* 2012; Arnold 1997
Hylobates agilis	CO	Carpenter 1940; Leighton 1987; Reichard & Barelli 2008; Barelli *et al*. 2011
Hylobates lar	CO	Carpenter 1940; Leighton 1987; Reichard & Barelli 2008; Barelli *et al*. 2011
Hylobates muelleri	CO	Carpenter 1940; Leighton 1987; Reichard & Barelli 2008; Barelli *et al*. 2011
Hylobates pileatus	CO	Carpenter 1940; Leighton 1987; Reichard & Barelli 2008; Barelli *et al*. 2011
Nomascus leucogenys	CO	Carpenter 1940; Leighton 1987; Reichard & Barelli 2008; Barelli *et al*. 2011
Symphalangus syndactylus	CO	Carpenter 1940; Leighton 1987; Reichard & Barelli 2008; Barelli *et al*. 2011
Gorilla gorilla gorilla	M	Breuer *et al*. 2016
Pan paniscus	F	Parish 1994
Pan troglodytes	M	Parish 1994

Appendix 4.7: Phylogenetic signal results using Pagel's λ for each variable in the female non-human primates analyses. Significant results are indicated in bold.

Variable	λ	LogL[a]	*p*	*n*[b]
Female R2D:4D	**1.000**	**108.455**	**<0.001*****	**71**
Female L2D:4D	**0.988**	**109.936**	**<0.001*****	**71**
Female M2D:4D	**0.997**	**114.575**	**<0.001*****	**71**
Female body mass	**1.000**	**-58.003**	**<0.001*****	**71**
Substrate use	**1.000**	**-32.096**	**<0.001*****	**71**
Mating system	**1.000**	**-99.634**	**<0.001*****	**71**
Mating system subcategory	**1.000**	**-128.191**	**<0.001*****	**71**
Intersexual dominance	**0.890**	**-56.050**	**<0.001*****	**71**
Macaque social style	**1.000**	**-12.286**	**<0.001*****	**8**
Group size	**0.964**	**-59.644**	**<0.001*****	**71**
Percentage fruit	0.000	-274.837	1.000	71
DCI	0.000	1.775	1.000	13
Rate of agonism	0.000	-5.995	1.000	8

[a] Log-likelihood ratio statistic.

[b] Number of species.

Appendix 5

Appendix 5.1: Results of ICC in each study group for both sexes and each sex separately. All values reported are 'single measures' ICC results.

Sample	Right hand 2D:4D ratio	Left hand 2D:4D ratio
Ring-tailed lemurs (both sexes)	ICC = 0.935, $F_{10,140}$ = 220.960, P = <0.001***	ICC = 0.986, $F_{10,140}$ = 1030.294, P = <0.001***
Ring-tailed lemurs (males only)	ICC = 0.941, $F_{6,84}$ = 252.985, P = <0.001***	ICC = 0.986, $F_{5,70}$ = 946.108, P = <0.001***
Ring-tailed lemurs (females only)	ICC = 0.940, $F_{3,42}$ = 199.952, P = <0.001***	ICC = 0.976, $F_{3,42}$= 667.813, P = <0.001***
Robust capuchins (both sexes)	ICC = 0.986, $F_{9,126}$ = 973.072, P = <0.001***	ICC = 0.993, $F_{6,84}$ = 2068.595, P = <0.001***
Robust capuchins (males only)	ICC = 0.963, $F_{4,56}$ = 388.020, P = <0.001***	ICC = 0.982, $F_{2,28}$ = 648.589, P = <0.001***
Robust capuchins (females only)	ICC = 0.991, $F_{4,56}$ = 1615.312, P = <0.001***	ICC = 0.996, $F_{3,42}$ = 3522.059, P = <0.001***
Human children (both sexes)	ICC = 0.986, $F_{34,476}$ = 1043.200, P = <0.001***	ICC = 0.990, $F_{34,476}$ = 1425.912, P = <0.001***
Human children (boys only)	ICC = 0.983, $F_{16,224}$ = 837.813, P = <0.001***	ICC = 0.993, $F_{16,224}$ = 2147.327, P = <0.001***
Human children (girls only)	ICC = 0.979, $F_{17,238}$ = 684.118, P = <0.001***	ICC = 0.985, $F_{17,238}$ = 998.849, P = <0.001***

Appendix 5.2: Test-retest reliability *(r* and p values) and sample size (*n*) for contextualised behavioural measurements listed by personality trait and test in ring-tailed lemurs. Significant test-retest correlations are indicated in bold.

Personality Trait	Test	Behavioural variable	Correlation	*r*	*p*	*n*
Boldness	Novel object 1, Novel object 2, Exploration cubes, Banana bottle	Latency to approach*	SR	**0.529**	**<0.001**	44
		Number of approaches	SR	**0.537**	**<0.001**	44
		Time spent in proximity	P	**0.647**	**<0.001**	44
		Frequency of moderate arousal 'clicks'	SR	**0.405**	**0.006**	44
Exploration tendency	Novel object 1, Novel object 2, Exploration cubes, Banana bottle	Latency to touch*	SR	**0.576**	**<0.001**	44
	Novel object 1, Novel object 2, Exploration cubes	Time spent manipulating	SR	**0.648**	**<0.001**	33
	Exploration cubes	Number of cubes visually explored	SR	**0.760**	**0.007**	11
		Number of cubes tactilely explored	P	0.023	0.946	11
	Banana bottle	Latency to detect reward*	SR	**0.774**	**0.005**	11
Persistency	Banana bottle	Time spent trying to reach reward	P	**0.714**	**0.014**	11
		Number of attempts on the bottle	P	**0.704**	**0.016**	11
		Average time spent trying per attempt	SR	0.352	0.289	11

*scores reversed due to the variable’s meaning for the trait.

SR = Spearman Rank correlation, P = Pearson correlation.

Appendix 5.3: Test-retest reliability *(r* and p values) and sample size (*n*) for contextualised behavioural measurements listed by personality trait and test in boys. Significant test-retest correlations are indicated in bold.

Personality Trait	Test	Behavioural variable	Correlation	*r*	*p*	*n*
Boldness	Novel objects A-D, Exploration cubes, Puzzle ball	Latency to approach*	P	**0.311**	**0.010**	68
		Number of approaches	SP	**0.323**	**0.007**	68
		Time spent in proximity	SP	**0.385**	**0.001**	68
Exploration tendency	Novel objects A-D, Exploration cubes, Puzzle ball	Latency to touch*	P	**0.371**	**0.002**	68
	Novel objects A-D, Exploration cubes	Time spent manipulating	SP	**0.426**	**0.002**	51
	Exploration cubes	Number of cubes visually explored	P	0.372	0.141	17
		Number of cubes tactilely explored	P	**0.514**	**0.035**	17
Persistency	Puzzle ball	Time spent trying to reach reward	SP	0.252	0.329	17
		Number of attempts on the bottle	P	**0.523**	**0.031**	17
		Average time spent trying per attempt	P	0.243	0.348	17

*scores reversed due to the variable's meaning for the trait.

SR = Spearman Rank correlation, P = Pearson correlation.

Appendix 5.4: Test-retest reliability *(r* and p values) and sample size (*n*) for contextualised behavioural measurements listed by personality trait and test in girls. Significant test-retest correlations are indicated in bold.

Personality Trait	**Test**	**Behavioural variable**	**Correlation**	***r***	***p***	***n***
Boldness	Novel objects A-D, Exploration cubes, Puzzle ball	Latency to approach*	SR	**0.257**	**0.029**	72
		Number of approaches	SR	**0.287**	**0.014**	72
		Time spent in proximity	SR	0.139	0.243	72
Exploration tendency	Novel objects A-D, Exploration cubes, Puzzle ball	Latency to touch*	P	**0.344**	**0.004**	72
	Novel objects A-D, Exploration cubes	Time spent manipulating	SR	0.265	0.053	54
	Exploration cubes	Number of cubes visually explored	P	0.263	0.292	18
		Number of cubes tactilely explored	P	0.234	0.350	18
Persistency	Puzzle ball	Time spent trying to reach reward	SR	**0.494**	**0.037**	18
		Number of attempts on the bottle	SR	**0.766**	**<0.001**	18
		Average time spent trying per attempt	SR	**0.654**	**0.003**	18

*scores reversed due to the variable's meaning for the trait.

SR = Spearman Rank correlation, P = Pearson correlation.