The 2D:4D digit ratio and social behaviour in wild female chacma baboons (*Papio ursinus*) in relation to dominance, aggression, interest in infants, affiliation, and heritability.

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Abstract Prenatal androgens are responsible for sex differences in behaviour and morphology in many species, causing changes in neural structure and function that persist throughout life. Some variation in the expression of behaviour between individuals of the same sex can also be attributed to differences in exposure to prenatal sex hormones. The ratio of the second and fourth digits (2D:4D ratio) is a proposed biomarker for prenatal androgen effects (PAE). Through assessment of 2D:4D ratios, this study aimed to investigate the relationship between inferred PAE and social behaviours in female chacma baboons (*Papio ursinus*). We validated a new method to measure 2D:4D indirectly using digital photographs and computer-assisted image analysis software. There was strong correlation between 2D:4D ratio and dominance rank among female baboons. Low 2D:4D ratios were associated with high rank, lower submission rates and higher rates of non-contact and contact aggression. This is consistent with the hypothesis that prenatal androgens are linked to the expression of these behaviours in female baboons, although it was not possible to separate the effects of PAE and dominance rank on some rank-related behaviours. The 2D:4D ratio did not correlate with interest in infants or with the rate of affiliative behaviours, possibly because these behaviours are more affected by ovarian hormones in adult life than by PAE. Finally, mean 2D:4D ratios were positively correlated in six mother/infant pairs, consistent with a heritable basis for the 2D:4D ratio in primates. We suggest that PAE contribute significantly to the patterning of social relationships in female primates.

Key Words: hormone, primate, human, development, ImageJ.

Introduction

Behavioural differences between the sexes reflect, in part, the organisational effects of prenatal sex hormones on brain development. Behavioural predispositions that arise from these processes are then transformed into behaviour by the social environment in which the animal finds itself (Wallen 2005). Numerous studies have examined sex differences in behaviour (Eaton et al. 1985; Johnston and File 1991; Balthazart and Ball 1995; Moore et al. 2005; Adkins-Regan 2009; Hines 2010), but there is also marked variation in the expression of behaviour between individuals of the same sex. In some cases, this has also been attributed to differences in exposure to prenatal sex hormones, such as androgens (Forstmeier et al. 2008; Nelson et al. 2010; Clipperton-Allen et al. 2011; Coleman et al. 2011). Prenatal androgens have masculinising and defeminising effects on morphology, brain structure and behaviour in mammals (Bailey and Hurd 2005; Bodo and Rissman 2008; Thornton et al. 2009), while oestrogens play important roles in the regulation of sociality and affiliative behaviour both pre- and postnatally (Ross and Young 2009). Prenatal sex hormones may, therefore, play important roles in the expression of behaviour.

The phases in development when the sex hormones have their masculinising or feminising effects on the brain, and consequently on behaviour, are also the phases when the growth of the digits is influenced by androgen and oestrogen receptor activity (Knoll et al. 2007; Zheng and Cohn 2011). The ratio of the lengths of the second digit (2D) and fourth digit (4D) (2D:4D ratio) of the hands is thus proposed as a biomarker for prenatal androgen effects (PAE) (Manning et al. 1998, 2013). Sex hormones affect digit ratio during the early stages of foetal development in humans and the trait remains relatively stable thereafter (Knickmeyer et al. 2011). In human males the 4D is typically longer than the 2D and in females the 2D is either equal to, or longer than, the 4D (Manning et al. 1998, 2000, 2004). This dimorphism can be explained by the fact that developing digits differ in their sensitivity to androgen and oestrogen hormones, the levels of which differ between the two sexes (Zheng and Cohn 2011). Androgen receptors increase chondrocyte proliferation in the 4D, while oestrogen receptors reduce proliferation (Zheng and Cohn 2011), so the 2D:4D ratio is determined by the balance of these two hormones in the fourth digit during prenatal development (Auger et al. 2013). Males are exposed to higher prenatal androgen levels, promoting the growth of the 4D and resulting in a lower (more masculine) 2D:4D ratio. Females, on the other hand, are exposed to higher prenatal oestrogen levels, reducing the growth of the 4D and leading to a higher (more feminine) 2D:4D ratio. Consequently, lower 2D:4D ratios are indicative of higher PAE (Brown et al. 2002; McIntyre et al. 2005; Lombardo and Thorpe 2008; Manning 2011; Zheng and Cohn 2011; but see Trivers et al. 2006). Right hand 2D:4D minus left hand 2D:4D (Dr-l) is unrelated to adult sex hormone levels (Hönekopp et al. 2007) and has been associated with sensitivity to testosterone and high prenatal testosterone in humans. As such, it may also be a negative correlate of PAE in humans (Manning 2002; Manning et al. 2003).

The behaviour of individuals exposed to higher PAE is likely to be more masculinised, dominant and aggressive than individuals exposed to lower PAE. Unusually high PAE are associated with disorders in which sociality is impaired in humans (Manning et al. 2001) and animal studies implicate PAE as having some influence over the shaping of an individual’s tendency toward aggressive behaviour in adulthood (Christiansen and Knussmann 1987; Mazur and Booth 1998). Concordant with the hypothesis that it is a marker for PAE, the 2D:4D ratio correlates with several sexually dimorphic behavioural measures across a variety of species (Fisher et al. 2010; Zheng and Cohn 2011). Studies have reported correlations between the 2D:4D ratio and behaviours linked to dominance and aggression (Neave et al. 2003; Bailey and Hurd 2005; McIntyre et al. 2009; Hurd et al. 2011). Low 2D:4D ratios are correlated with higher dominance-related behaviours and higher drives for social status in both sexes in humans (Millet and Dewitte 2007, 2009). Humans with low 2D:4D ratios are also perceived as more dominant (Neave et al. 2003) and show higher reactive aggression (Benderlioglu and Nelson 2004; Zeynep and Nelson 2004). In general, nonhuman primates have more masculinised digit ratios than do humans (Manning et al. 2003; Nelson and Shultz 2010). Polygynous primates tend to have lower 2D:4D ratios (high PAE) and pair-bonded species tend to have higher 2D:4D ratios (low PAE) (Nelson and Shultz 2010).

Females may be subject to PAE as well as males. In free-ranging adult female rhesus macaques (*Macaca mulatta*) the 2D:4D ratio correlated negatively with dominance rank (Nelson et al. 2010) and right hand 2D:4D ratio also negatively correlated with dominance rank in captive adult female hamadryas baboons (*Papio hamadryas*) and in orphaned juvenile female chacma baboons (*Papio ursinus*) (Howlett et al. 2012). Other sexually dimorphic behaviours, such as interest shown in infants, are more prevalent in females (Lovejoy and Wallen 1988; Herman et al. 2003). Hence, this behaviour is hypothesised to be oestrogen-dependent, and it is reduced in androgenised female humans and rhesus macaques (Leveroni and Berenbuam 1998; Herman et al. 2003). Ovarian hormones and the hypothalamic neuropeptides oxytocin and vasopressin are involved in the regulation of social behaviour. Oestrogen is associated with the expression of social affiliative behaviours (Witt et al. 1992) and oxytocin facilitates social motivation and approach behaviour (Lim and Young 2006). Both neuropeptides are necessary for the discrimination of familiar individuals and social bonding (Bielsky and Young 2004) and many of the behavioural effects of oxcytocin are brought about by oestrogen activity (Razzoli et al. 2003; Young et al. 1998). Ovariectomized female Japanese macaques (*Macaca fuscata*) exhibit a reduction in positive social behaviours when compared to intact tube-ligated females. Successful navigation of the social environment by macaque females and other cercopithecine primates may depend on ovarian hormones in adulthood and the predisposing effects of sex hormones on brain patterning during development (Ross and Young 2009; Coleman et al. 2011). Thus, the evidence suggests that the 2D:4D ratio can act as a biomarker for PAE effects on the behaviour of both human and nonhuman primates, both between and within sexes. Moreover, heritability studies in rhesus macaques, humans and zebra finches (*Taeniopygia guttata*) point towards considerable genetic contributions to the expression of the 2D:4D ratio (Forstmeier 2005; Paul et al. 2006; Forstmeier et al. 2008; Nelson and Voracek 2010) and testosterone production is highly heritable in humans (Hines 2006).

A few studies have investigated digit ratios in nonhuman primates, most of which relied on direct measurements using callipers (Roney et al. 2004; Nelson et al. 2010) or measurements from scanned images (McIntyre et al. 2009). The problem with measuring digit ratios in non-anaesthetised nonhuman primates is their unpredictable behaviour. Further issues arise from the study of wild populations, which cannot be trained to hold their limbs in certain positions or anaesthetised to obtain direct measurements of digits. Our first objective was to develop and validate a method of measuring 2D:4D ratios indirectly in wild primates using digital photographs. We then applied this method to explore the relationship between mean 2D:4D ratio and Dr-l measures and social behaviour in wild female chacma baboons. We also aimed to investigate the heritability of the 2D:4D ratio by comparing it in mother/infant pairs. As Dr-l is postulated to be a negative correlate of PAE in humans, where low Dr-l is indicative of high PAE (Manning 2002; Manning et al. 2003), our predictions regarding Dr-l focus on those variables which may be influenced more by the masculinising effects of androgens (rate of aggression and dominance rank) rather than those which would be more influenced by oestrogens (rate of interest in infants and rate of affiliation).

We hypothesise that PAE (inferred from 2D:4D ratios) will show a relationship with female dominance rank and rate of submission. We predict that females with lower (masculine) 2D:4D ratios and lower (masculine) Dr-l will occupy higher positions in the dominance hierarchy than females with higher 2D:4D ratios (Prediction 1) and females with lower 2D:4D ratios and lower Dr-l will show lower rates of submission than females with higher 2D:4D ratios (Prediction 2).

We hypothesise that PAE will show a relationship with a female's tendency toward aggressive behaviour and predict that females with lower 2D:4D ratios and lower Dr-l will display higher rates of both non-contact and contact aggression (Prediction 3a). We predict that only highly masculinised (low 2D:4D) individuals will show physical aggression at high rates and that the correlation between 2D:4D ratio measures and rate of contact aggression will be higher than between 2D:4D ratio measures and rate of non-contact aggression (Prediction 3b). Additionally, we predict that females with lower 2D:4D ratios will receive aggression from other group members at lower rates than females with higher 2D:4D ratios (Prediction 3c).

We hypothesise that 2D:4D ratios will show a negative relationship with the rate of interest shown by females in infants (Prediction 4). Females exposed to lower PAE may show greater interest in infants than those exposed to higher PAE. Social preferences may be partly prenatally determined though the effects of sex hormones and are influenced by circulating sex steroids in human females (Buser, 2012). Female baboons exposed to lower PAE may be more motivated to form social bonds and seek social contact than females exposed to higher PAE (Lim and Young 2006). Therefore, we predict that females with lower 2D:4D ratios will show lower rates of affiliation than females with higher 2D:4D ratios (Prediction 5a), that females with lower 2D:4D ratios will have fewer grooming and social partners than those with higher 2D:4D ratios (Prediction 5b), and that females with lower 2D:4D ratios will groom others at lower rates and will receive grooming at higher rates than females with higher 2D:4D ratios (Prediction 5c).

Finally, we hypothesise that a relationship will exist between a mother's 2D:4D ratio and the 2D:4D ratio of her offspring. We predict that there will be a high positive correlation between maternal 2D:4D ratios and the corresponding 2D:4D ratios in her infant (Prediction 6a) and that maternal rank will correlate negatively with offspring 2D:4D ratio (Prediction 6b). These hypotheses are summarised in Table 1.

Methods

Validation of digit measurements

We first tested the ability of a digital photographic and computer-assisted analysis method to provide accurate 2D:4D ratio measurements in a captive group of baboons. The methods we used to test this are outlined first, followed by field work we then conducted on a wild group of baboons.

Study site

We validated our method for measuring 2D:4D ratios from photographs using a captive group of juvenile chacma baboons at the Centre for Animal Rehabilitation and Education (C.A.R.E), Phalaborwa, South Africa from 7th – 21st February 2012. Animals at C.A.R.E are housed in outdoor enclosures enriched with tyres, nets, ropes, tree branches and other toys. The study group contained 21 individuals of both sexes, 20 of whom were approximately 18 months old, and one older male juvenile of approximately three years of age who was not used in this study. Study subjects comprised 12 members of this troop (three females and nine males). These individuals had all been raised by human surrogates from a very early age and engaged in contact with several carers for up to 12 hours a day after weaning. As a result these animals were comfortable being handled and photographed at close quarters.

Data collection

We habituated the animals to observer presence over four days. We obtained digit measurements over three days in one-hour periods. Animals voluntarily approached us and we held them whilst taking measurements. We measured the 2D and 4D of each hand of each animal directly from the basal crease to the tip of the extended digit (nearest mm) using Draper callipers and calculated 2D:4D ratios (Howlett et al. 2012). We could only obtain direct measurements of the left hand for four of the male baboons as they became difficult to handle during the procedure and we released them to avoid causing unnecessary stress. We considered ratios from calliper measurements as the 'true' 2D:4D ratios and used these to compare the accuracy of 2D:4D ratios we obtained from digital photographs.

We took five photographs each of the dorsal view of the right and left hands of each baboon in using a Panasonic FZ150 digital camera in 'burst shooting' mode in which the camera was set to take 12 frames per shot. We photographed hands whilst they were in optimum positions for digit measurements: hand and digits in a flat and straight position, digits fully extended and the entire length of both digits visible (Fig. 1). We measured the 2D and 4D 10 times for each photograph using computer-assisted software (ImageJ) and mouse-controlled callipers to measure digit lengths from the photographs. We used mean digit lengths for each image to calculate the 2D:4D ratio for that image. We used the mean of the five images for each individual as the overall image 2D:4D ratio for that subject and hand.

Statistical analyses

Data were normally distributed (Kolmogorov-Smirnov tests: true ratio: $P = 0.906$; image ratio: $P = 0.966$). We used Pearson's correlations to analyse the relationship between true 2D:4D ratios and image 2D:4D ratios for method validation.

Fieldwork

Study site

We conducted research on a wild baboon group at Lajuma Research Centre in the Soutpansberg Mountain Range, South Africa. The range is a narrow ridge set in the Limpopo Province, and varies 15-60 km north to south and extends 250 km east to west (lying from 23°05' S, 29° 17' E to 22°25' S, 31° 20' E) (Berger et al.

2003). Altitude ranges 1150 - 1750 m (Willems et al. 2009; Willems and Hill 2009) with a complex mosaic of habitat types classified under the Soutpansberg mist-belt forest group (von Maltitz 2003). Local climatic conditions are mesothermal with cool dry winters (April–September) and warm wet summers (October–March) and a mean annual temperature of 17.1°C; mean annual rainfall is 724 mm (Willems et al. 2009; Willems and Hill 2009).

The wild study group comprised approximately 80 chacma baboons: 12 adult males, four adolescent males, 17 juvenile males, 20 adult females, five adolescent females, seven juvenile females, four infant females and eight infant males. Females were considered adolescent once they had had their first sexual swelling but had not yet conceived and as adult once they were reproductively mature and had achieved adult body size. The 20 adult and five adolescent females in the group were the focus of this study. We used six mother/infant pairs in the troop (two male infants and four female infants) in which mothers held a range of dominance ranks to assess heritability of the 2D:4D ratio.

Data collection

All data collection and analysis were carried out by the same author. The author was blind with regards to results of behavioural measures when calculating digit ratios, as these were measured and behavioural data collected whilst in the field and all data sorting and analyses conducted once the author had returned to the UK.

Behavioural data

Animals were fully habituated to human observers and were followed from their morning sleeping site to their evening sleeping site on an almost daily basis. Data collection commenced on the 3rd April 2012 and lasted until the 20th June 2012.

We conducted 10-minute focal samples on each adult and adolescent female group member in randomised order and recorded behavioural interactions on a continuous basis on a Psion Walkabout Pro PDA device equipped with Observer XT 10 software. We collected data over three sample periods to ensure an equal spread of samples across the day: morning (6 - 10am), midday (10am – 2pm) and afternoon (2 – 6pm) for the duration of the study. We balanced focal samples for each female across these periods, obtaining two hours per female for each observation period and a total of six hours focal observation time per female. One female disappeared during the study period so we collected only three hours and 40 minutes of focal data for this individual. Since these data were balanced across the three sample periods (with 70 minutes, 70 minutes and 80 minutes, respectively) they were retained within the analysis.

We recorded all interactions initiated by the focal individual and those directed toward the focal individual by other group members, along with the identity of the social partner for adult and adolescent females or age/sex class for other group members. We collected data on affiliative, submissive, contact aggressive and non-contact aggressive behaviours and a female’s interest in infants. We also recorded the number of grooming partners and the number of social partners a female had in total. Grooming partners were those who were observed grooming or receiving grooming from the focal female. We defined a social partner as any female seen to interact with the focal female in an affiliative manner that was not grooming.

Dominance hierarchy

We ascertained female rank in the wild group via the direction of supplant and displacement interactions between females (Altmann 1974). A supplant is where one individual's actions cause another to move away without any direct interaction occurring between the two. A displacement occurs when one individual actively causes another individual to move location where the first individual may take over the action of the other. We recorded the direction of submissive behaviours (fear grimace, fear keck, cower, flee, submissive scream) opportunistically on an *ad libitum* basis both within focal periods (for interactions involving group members other than the focal individual) and between focal periods (Martin and Bateson 2007). Based on our observations we constructed a matrix of decided dominance relationships which showed a transitive linear hierarchy. Linearity was calculated using Landau index (h'= 1.000; P = 0.001) as there were no reversals, inconsistencies or unknown dominance relationships in this group. We assigned a female dominance rank ranging from 1 (highest-ranked) to 25 (lowest-ranked).

2D:4D ratio measurements

We obtained 2D:4D ratio measurements of wild baboons using the same method described for validation above. We took multiple photographs of the dorsal view of each individual's right and left hands and identified 10 photographs per hand per individual in which hands were in optimum positions. We analysed photographs as above with ImageJ and determined an individual's mean 2D:4D ratio by taking the mean of the right and left hand 2D:4D ratios. We determined Dr-l by calculating right hand 2D:4D ratio minus the left hand 2D:4D ratio.

Statistical analyses

Female mean, right, left 2D:4D ratios and Dr-l were all normally distributed (Kolmogorov-Smirnov tests: mean: P = 0.155; right: P = 0.135; left: P = 0.126; Dr-l: P = 0.200), as were infant left (P = 0.200), right (P = 0.200) and mean (P = 0.200) 2D:4D ratios. All other variables were normally distributed except for rate of non-contact aggression and rate of contact aggression (Kolmogorov-Smirnov tests: P <0.001 and P = 0.011, respectively) and this problem was not solved by data transformation, due to the data containing several zero scores.

We used repeated measures ANOVAs to determine whether differences in 2D:4D ratio between subjects were significantly larger than measurement error. We used the intraclass correlation coefficient (ICC) set to the 'absolute agreement' definition to test intra-observer reliability and investigated differences in left and right 2D:4D ratios of females and infants using a paired *t*-test (two-tailed).

We used Pearson's correlations to assess the relationship between a female's dominance rank and her mean 2D:4D ratio and Dr-l.

We converted all behavioural data into rates per hour of observation time prior to analysis. We used Pearson's correlations to test the relationship between rate of submission, rate at which individuals received aggression, rate of interest in infants and rate of affiliation and mean 2D:4D ratio. We employed Pearson's correlations to assess the relationships between 2D:4D ratio data and rate of grooming given and rate of grooming received, number of grooming partners and number of social partners.

We used Spearman's rank correlations when investigating relationships between rate of non-contact and contact aggression and 2D:4D ratio data. We used Pearson's correlations to test the relationship between dominance rank and rank-related behaviours: rate of submission, rate of received aggression; and Spearman's rank correlations for rate of non-contact and contact aggression. We also used Partial correlation tests to investigate the relationship between 2D:4D ratio the rank-related behaviours detailed above whilst controlling for dominance rank. Additionally, as we hypothesise that PAE is a predictor of dominance rank, we also carried out Partial correlations on dominance rank and the rank-related behaviours whilst controlling for 2D:4D ratio (inferred effects of PAE).

Due to the small sample size of six mother/infant pairs we also used Spearman's rank correlations to examine the relationship between 2D:4D ratios in mother/infant pairs and to assess the relationship between infant 2D:4D ratio measures and the dominance rank of their mothers.

We conducted all data analyses using IBM SPSS statistics for Windows version 19, with significance levels set at $P<0.05$.

Results

Validation

True 2D:4D ratios and image 2D:4D ratios obtained from digital photographs of the captive group correlated strongly and positively (r = 0.999, df = 20, P = 0.01). When we analysed true and image ratios of each hand separately we also found very high, significant and positive correlations (right hand: r = 0.999, df = 8, P = 0.01; left hand: r = 0.999, df = 12, P = 0.01). The mean image 2D:4D ratio differed from the true 2D:4D ratio in only 3 of twenty cases, in each case by less than 0.008 (Table 2).

Reliability

Repeated measures of 2D:4D ratio from photographs of wild baboons showed no significant difference within females, for either hand (repeated measures ANOVA, right hand: $F_{9, 216}$ = 0.673, P = 0.733; left hand: $F_{9, 216}$ = 0.851, P = 0.570), suggesting that measurements were highly repeatable (Fig. 2a). The intra-class correlation coefficient (ICC) also showed that 2D:4D ratio measurements for females were highly repeatable for the right (ICC = 0.968, $F_{24, 216}$ = 299.062, P <0.001) and left (ICC = 0.969, $F_{24, 216}$ = 309.784, P <0.001) hands, indicating a high level of intra-observer reliability. Left and right 2D:4D ratios in females were not significantly different (t_{24} = 0.842, P = 0.408) and were tightly correlated (r = 0.919, df = 25, P <0.001). Repeated measures of 2D:4D ratio from photographs in infants showed no significant difference within individuals (repeated measures ANOVA, right hand: $F_{1, 5}$ = 3.971, P = 0.103; left hand: $F_{1, 5}$ = 0.600, P = 0.474) and ICC indicated a fair agreement in 2D:4D measurements of the right hand (ICC = 0.362, $F_{5, 45}$ = 6.662, P <0.001) and moderate agreement in the left hand (ICC = 0.559, $F_{5, 45}$ = 12.613, P <0.001). As in the females, left and right 2D:4D ratios in infants were not significantly different (t_6 = 0.650, P = 0.544) and were tightly correlated (r = 0.829, df = 6, P = 0.042) so the mean 2D:4D ratios of both hands were used for females and infants in subsequent analyses.

Prediction 1: Digit ratios and dominance rank

Mean 2D:4D ratio and dominance rank were highly negatively correlated (*r* = 0.833, df = 25, P <0.001, Fig. 2a, b). Dr-l, however, did not correlate significantly with dominance rank (Fig. 2c).

Prediction 2: Digit ratios and rate of submission

The rate of submission was positively correlated with mean 2D:4D ratio (*r* = 0.594, df = 25, P = 0.002, Fig. 3). However, Dr-l was not significantly correlated with rate of submission (*r* = 0.110, df = 25, P = 0.601).

Predictions 3a, b and c: Digit ratios and rate of aggression

Mean 2D:4D ratio correlated significantly and negatively with rate of non-contact aggression (*r* = - 0.490, df = 25, P = 0.013, Fig. 4a) and contact aggression (*r* = - 0.449, df = 25, P = 0.024, Fig. 4b). Dr-l was not significantly correlated with either rate of non-contact aggression (r = - 0.169, df = 25, P = 0.418) or contact aggression (r = - 0.372, df = 25, P = 0.067).

The rate at which a female received aggression from other group members was positively correlated with her mean 2D:4D ratio (*r* = 0.630, df = 25, P = 0.001, Fig. 4c).

Partial correlations: 2D:4D ratio, dominance rank and rank-related behaviours

Dominance rank and rate of submission correlated highly and significantly. 2D:4D ratio was not significantly correlated with rate of submission when dominance rank was controlled. When examining the relationship between dominance rank and rate of submission whilst controlling for 2D:4D ratio, the positive correlation was reduced compared to when just dominance rank and the behaviour were investigated, but still significant (Table 3).

Dominance rank and rate of non-contact aggression correlated significantly. Rate of non-contact aggression and 2D:4D ratio were not significantly correlated when controlling for dominance rank. When controlling for 2D:4D ratio, the correlation between dominance rank and rate of non-contact aggression was much reduced and non-significant. Dominance rank and rate of contact aggression showed moderate, significant correlation. There was no significant correlation between 2D:4D ratio and rate of contact aggression when controlling for dominance rank. When controlling for 2D:4D ratio, the negative correlation between dominance rank and rate of contact aggression was much lower but still significant (Table 3).

Dominance rank and rate of received aggression were highly significantly correlated. The rate at which a female received aggression from other group members was not correlated with her 2D:4D ratio when dominance rank was controlled. The correlation between rate of received aggression and dominance rank was low and non-significant when controlling for 2D:4D ratio than when just comparing the two variables alone (Table 3).

Prediction 4: Digit ratios and rate of interest in infants

There was no significant correlation between a female's interest in infants and her mean 2D:4D ratio (*r* = 0.190, df = 25, P = 0.364).

Predictions 5a, b and c: Digit ratios and rate of affiliation

We found no significant correlations between a female's rate of affiliation and her mean 2D:4D ratio (r = 0.086, df = 25, P = 0.682). A female's mean 2D:4D ratio was also not significantly correlated with her number of grooming partners (r = 0.206, df = 25, P = 0.324) or with her number of social partners (r = 0.112, df = 25, P = 0.593). We found no significant correlations between the rate at which a female groomed another female or was groomed by another female and her mean 2D:4D ratio (grooming given: r = 0.164, df = 25, P = 0.433; grooming received: r = 0.261, df = 25, P = 0.207).

Predictions 6a and b: Mother-infant correlations

The correlation between female's mean 2D:4D ratio and her infant's mean 2D:4D ratio was strong and significant (r = 0.829, df = 6, P = 0.042, Fig. 5).

Infant mean 2D:4D ratio showed a significant negative correlation with maternal dominance rank (r = 0.829, df = 6, P = 0.042).

Discussion

This study demonstrates that PAE, as inferred from 2D:4D ratios, correlates with dominance rank in wild female chacma baboons. In support of prediction 1, higher-ranked females had lower 2D:4D ratios in both hands and lower mean 2D:4D ratios than lower-ranked females. The negative correlation between 2D:4D ratio and dominance rank is consistent with PAE influencing a female's position in the dominance hierarchy in natural groups. The effects of higher PAE may predispose behaviour in low 2D:4D ratio individuals to be more masculinised and, in this case, dominant (Wallen 2005; Thornton et al. 2009). This is consistent with other research in cercopithecine primates in which female dominance rank was negatively correlated with 2D:4D ratio (Nelson et al. 2010; Howlett et al. 2012). Mean 2D:4D ratio showed a positive association with rate of submission in our study. Females with lower 2D:4D ratios showed lower rates of submission than females with higher 2D:4D ratios, suggesting that females exposed to higher PAE are less submissive than those exposed to lower levels of PAE. This notion is supported by the fact that female rhesus macaques withdrew less often from the approaches of other animals after they had been treated with testosterone propionate during prenatal development (Thornton et al. 2009). As in the macaque females, higher PAE may predispose female baboons to be less submissive.

PAE may also affect a female's dominance rank though the influence that the hormones have in shaping her future tendency towards aggressive behaviour (Higley et al. 1996). All 2D:4D ratio measures correlated negatively with rate of non-contact aggression. Females with lower 2D:4D ratios displayed non-contact aggression at higher rates than those with higher 2D:4D ratios. The same pattern was observed between 2D:4D ratio measures and contact aggression. Females with lower 2D:4D ratios displayed contact aggressive behaviours at higher rates than those with higher 2D:4D ratios. However, our prediction (3b) that the correlation between 2D:4D ratio measures would be higher for contact aggressive behaviours than non-contact aggressive behaviours was not supported. In fact, correlations were consistently higher for non-contact aggression than contact aggression. This may be due to the generally low rates of contact aggression among the females in the study group and the fact that seven of the 25 females were never observed to engage in any contact aggressive behaviours.

Females with lower 2D:4D ratios received less aggression than females with higher 2D:4D ratios. Other group members may target subordinate females (those with high 2D:4D ratios) as they are less likely to be faced with repercussions from those females or their allies. Female baboons exposed to high PAE (those with low 2D:4D ratios) may have a greater tendency to retaliate to any aggression they receive than those exposed to low PAE who may be more likely to submit to any aggression they receive. Also, as individuals with higher 2D:4D ratios in this group are also those lower in rank, it is likely to be a reflection of individuals being targeted based on their social rank. It would not be adaptive for a low-ranked female, after receiving aggression, to retaliate toward a higher-ranked female as this is likely to cause escalation of an asymmetric contest. Therefore, PAE may increase the potential for confrontational behaviour in high-ranked (low 2D:4D ratio) animals and promote submissive behaviour in low-ranked (high 2D:4D ratio) animals (Nelson et al. 2010).

As would be expected, a close relationship existed between rank-related behaviours and current dominance rank amongst females. The results of the partial correlations suggest that it is not possible to entirely separate out the effects of PAE on dominance rank and on dominance-related behaviours. PAE may promote rank-appropriate behaviours (Nelson et al. 2010) and the fact that the correlations between dominance rank and rank-related behaviours were much reduced, and in two cases became non-significant when controlling for 2D:4D ratio (inferred PAE), suggests that PAE may have an effect on the expression of these behaviours but once females have well-established ranks their behaviour is appropriate to their position in the hierarchy.

Dr-l (right hand 2D:4D ratio minus left hand 2D:4D ratio) was not related to dominance rank or submissive or aggressive behaviours in females. In this study Dr-l did not act as a negative correlate for PAE in chacma baboons, as it has been shown to do in humans (Manning 2002). The 2D:4D ratios of the right and left hands were tightly correlated in this study, which differs from data on human right and left 2D:4D ratios where the correlation is much lower (Manning et al. 2000; Manning 2002). Humans show strong, species-wide manual lateralisation or handedness which is not mirrored in non-human primates (Fitch and Braccini, 2013) and the relationship observed between low Dr-l and high PAE may be due to lateralised sex hormone effects in humans (Manning, et al. 2003). The 2D:4D ratio varies widely between human populations (Manning 2002) and this may also be the pattern among baboons. The lack of correlation between behaviour and Dr-l here may also be due to the sample consisting solely of female study subjects. In humans, sexually dimorphic traits, including the 2D:4D ratio (Hönekopp and Watson 2010), tend to be displayed in the masculine form more strongly on the right side of the body (Tanner 1990; Kimura 1994) and it is possible that the difference between right and left 2D:4D ratios may be greater among male than female baboons. Research into the developmental mechanisms which may contribute to the observed differences human and baboon 2D:4D ratios would be interesting, particularly from an evolutionary perspective.

Contrary to prediction 4, the 2D:4D ratio was not correlated with rate of interest in infants. Females with lower 2D:4D ratios did not show less interest in infants than those with higher 2D:4D ratios. The lack of association between 2D:4D ratios and interest in infants among females in this study group may be due to variation within normal levels of PAE having little influence on female-typical behaviours. However, experimental evidence suggests that abnormally high levels of PAE may influence interest in infants. Reduced interest in infants was shown in female rhesus macaques whose mothers experienced increased testosterone during pregnancy due to treatment with the anti-androgen flutamide (Wallen 2005) and in girls with congenital adrenal hyperplasia

(CAH) (Leveroni and Berenbaum 1998). Contrary to prediction 5a, the rate of affiliation and 2D:4D ratio measures were not significantly correlated, suggesting that PAE are not involved in the expression of affiliative behaviour in female baboons. Normal levels of PAE may therefore not affect the expression of female-typical behavioural patterns, such as affiliation and interest in infants, which are governed by ovarian hormones, specifically oestrogen, in adult life (Witt et al. 1992; Lim and Young 2006). Prenatal androgens may have the largest effects on behaviours that are mediated by male sex hormones such as dominance and aggression in female baboons.

Prediction 5b was not supported, as there was no association between the number of grooming partners and non-grooming social partners a female had and her mean 2D:4D ratio. The number of grooming partners a female had was positively correlated with the number of social partners she had. Contradictory to prediction 5c, we found no relationship between a female's 2D:4D ratios and the rate of grooming she gave or rate of grooming she received. In human females the 2D:4D ratio correlates positively with rates of giving whereas women with lower 2D:4D ratios have been shown to be less reciprocal in ultimatum games (Buser, 2012). However, in baboon females, grooming interactions may be related to hygienic as well as social needs (Akinyi et al. 2013) and are used as 'currency' by females, for example to obtain tolerance at feeding sights from higher-ranked females or to gain access to another female's infant (Barrett et al. 1999, 2002). Therefore, the rate of grooming a female gives and receives is unlikely to be just a simple reflection of prenatal sex hormones predisposing how reciprocal a female is or her motivation to seek/avoid social interaction with other females.

In support of prediction 6a, mean 2D:4D ratios of mothers and their infants were positively correlated, consistent with a genetic contribution to the expression of the mean 2D:4D ratio in chacma baboons. This is also consistent with the significant heritability of 2D:4D ratio in mother/son pairs of rhesus macaques, although the ratio is not heritable in mother/daughter pairs of rhesus macaques, possibly because the androgen receptor gene is maternally determined in males (Nelson and Voracek 2010). Unfortunately, our sample size precluded a comparison of mother/son and mother/daughter pairs. In support of prediction 6b, mean 2D:4D ratio was highly negatively correlated with maternal rank, suggesting that higher-ranked mothers produce infants with lower mean 2D:4D ratios. Infants in our mother/infant pairs were of mixed sex and infant age was not uniform across the group with some being close to weaning age and others being much younger. The 2D:4D ratio is known to increase over age in very young human children (McIntyre et al. 2005) but to remain stable in adulthood (Manning 2002). It is possible therefore that 2D:4D ratios may change as infants age suggesting that older offspring should be used when comparing mother/offspring 2D:4D ratios, although this could potentially increase the affects of non-shared environmental influences on 2D:4D ratios.

In conclusion, we validated the use of a digital photographic, computer-assisted method for indirectly measuring 2D:4D ratios in wild baboons. Our new methods offer significant potential for future studies to explore these relationships in a wide range of species in their natural habitats. Our results suggest that PAE, as indexed by 2D:4D ratios, may influence the development of mechanisms that play a role in dominance relationships in wild female baboons. PAE-influenced mechanisms may contribute to the maintenance of female rank through their effects on aggression or may even be linked to maternal effects. In hierarchical social systems, small differences in an individual's ability to dominate others are likely to influence an individual's fitness and so PAE could have positive effects on the fitness of primates in despotic groups. However, it is difficult to separate the effects that PAE and dominance rank may be having on some rank-related behaviours. PAE appear not to influence the expression of interest in infants and affiliation in female baboons and may have limited influence on behaviours regulated by female sex hormones in non-hormonally manipulated female primates. Although our results for heritability (inferred from mother-offspring correlations) are preliminary due to a small sample size, they are consistent with genetic and/or gestational contributions to the expression of the 2D:4D ratio in baboons. The effects that PAE have on brain patterning may be involved in shaping aspects of social behaviour in wild female primates.

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Ethical Standards

All fieldwork was approved by the Life Sciences Ethical Review Process Committee at Durham University, UK, and the Department of Anthropology Ethics Committee. All work at Lajuma was conducted with permission from the Limpopo Department of Economic Development, Environment and Tourism, South Africa

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Figure legends

Fig. 1 Examples of digital photographs used to measure digit lengths in chacma baboons

Fig. 2a Mean ± standard deviation of right (grey bars) and left (black bars) 2D:4D ratios for female chacma baboons vs. dominance rank. Rank is in descending order from highest (1) to lowest (25)

Fig. 2b The relationship between mean 2D:4D ratio and dominance rank in female chacma baboons. Dominance is shown in descending rank order from highest (1) to lowest (25)

Fig. 2c Relationship between Dr-l and dominance rank in female chacma baboons

Fig. 3 The relationship between mean 2D:4D ratio (white triangles, black solid line), right 2D:4D (grey diamonds, grey solid line) and left 2D:4D (black circles, black dotted line) and rate of submission in female chacma baboons.

Fig. 4a Relationship between mean 2D:4D ratio (white triangles, black solid line), right 2D:4D (grey diamonds, grey solid line) and left 2D:4D (black circles, black dotted line) and rate of non-contact aggression in female chacma baboons

Fig. 4b Relationship between mean 2D:4D ratio (white triangles, black solid line), right 2D:4D (grey diamonds, grey solid line) and left 2D:4D (black circles, black dotted line) and rate of contact aggression in female chacma baboons

Fig. 4c Relationship between mean 2D:4D ratio (white triangles, black solid line), right 2D:4D (grey diamonds, grey solid line) and left 2D:4D (black circles, black dotted line) and rate at which a female received aggression from another group member in female chacma baboons

Fig. 5 Relationship between mother’s mean 2D:4D ratio (grey circles) and her infant’s mean 2D:4D ratio (black diamonds) in female chacma baboons

Figure 1

Figure 2a

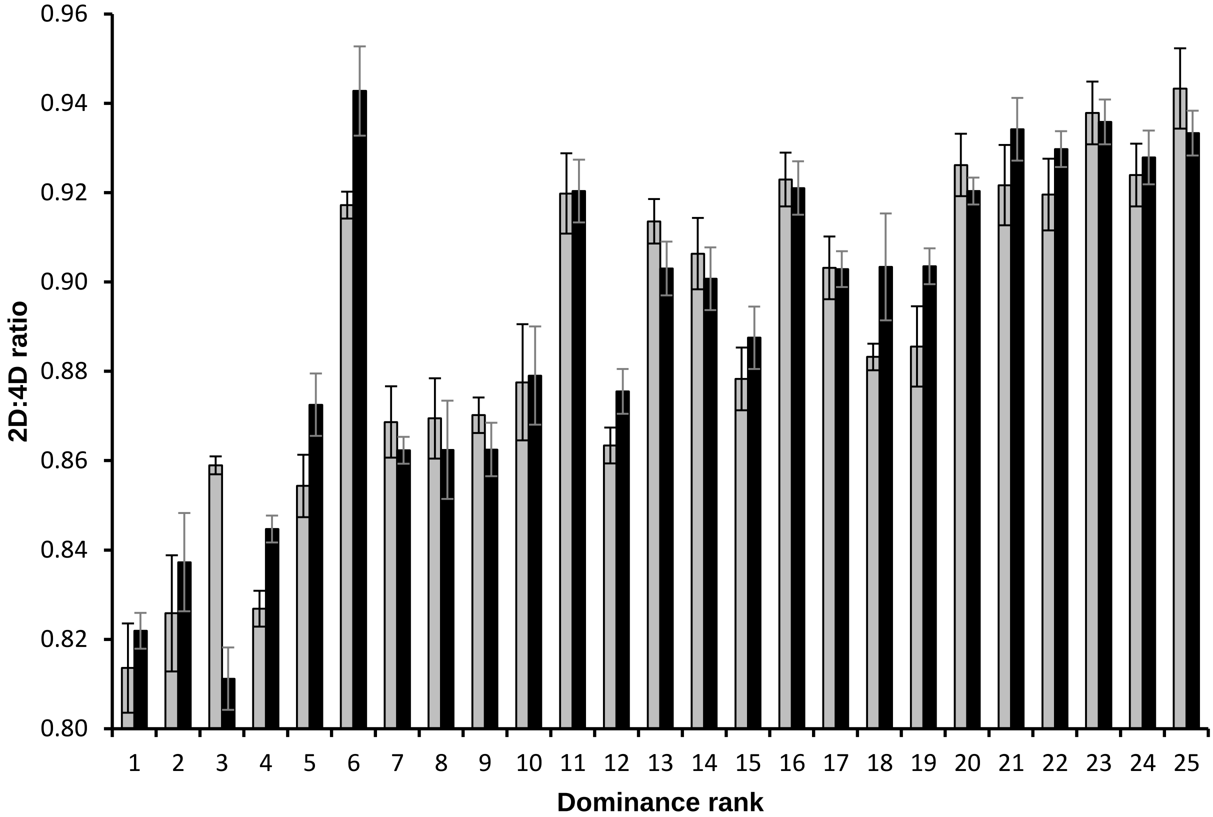
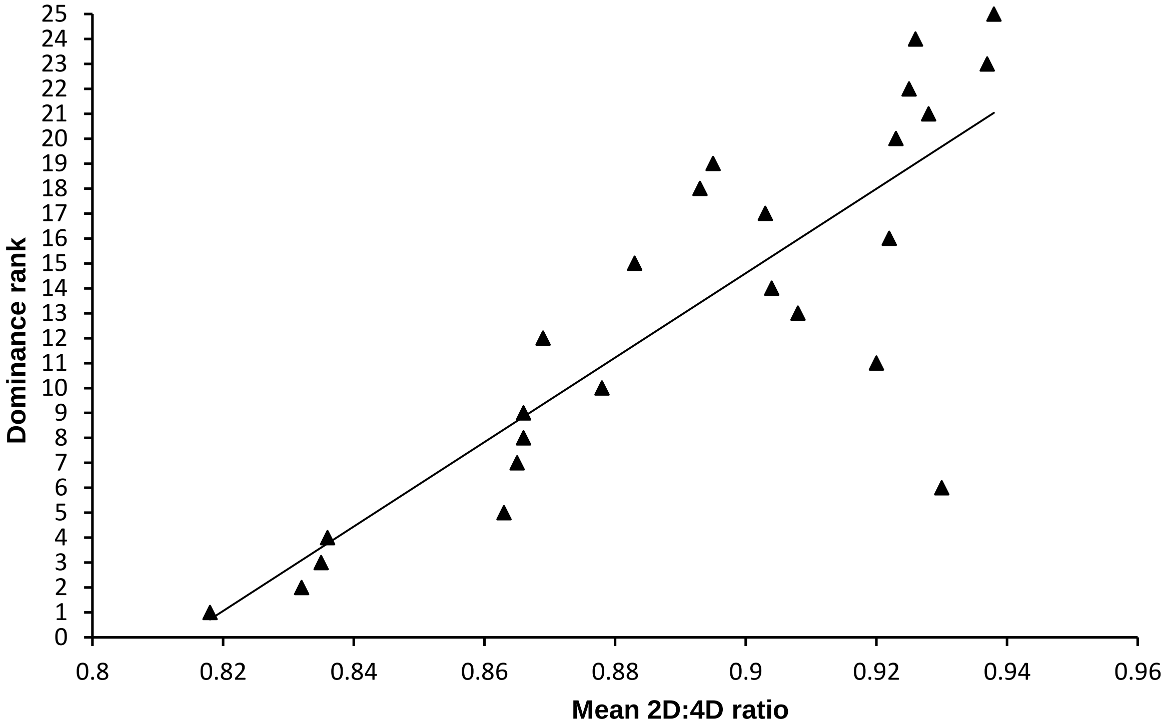

2D:4D ratio
0.96
0.94
0.92
0.90
0.88
0.86
0.84
0.82
0.80
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
Dominance rank

Figure 2b



Dominance rank
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
0.8
0.82
0.84
0.86
0.88
0.9
0.92
0.94
0.96
Mean 2D:4D ratio

Figure 2c

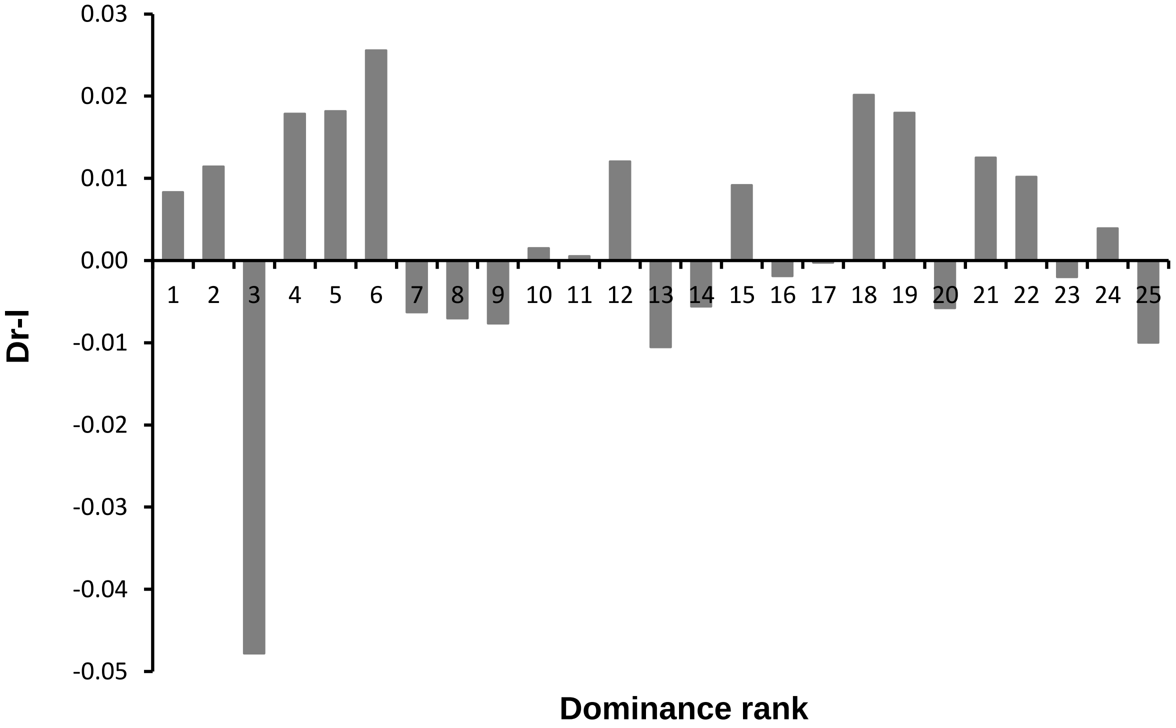
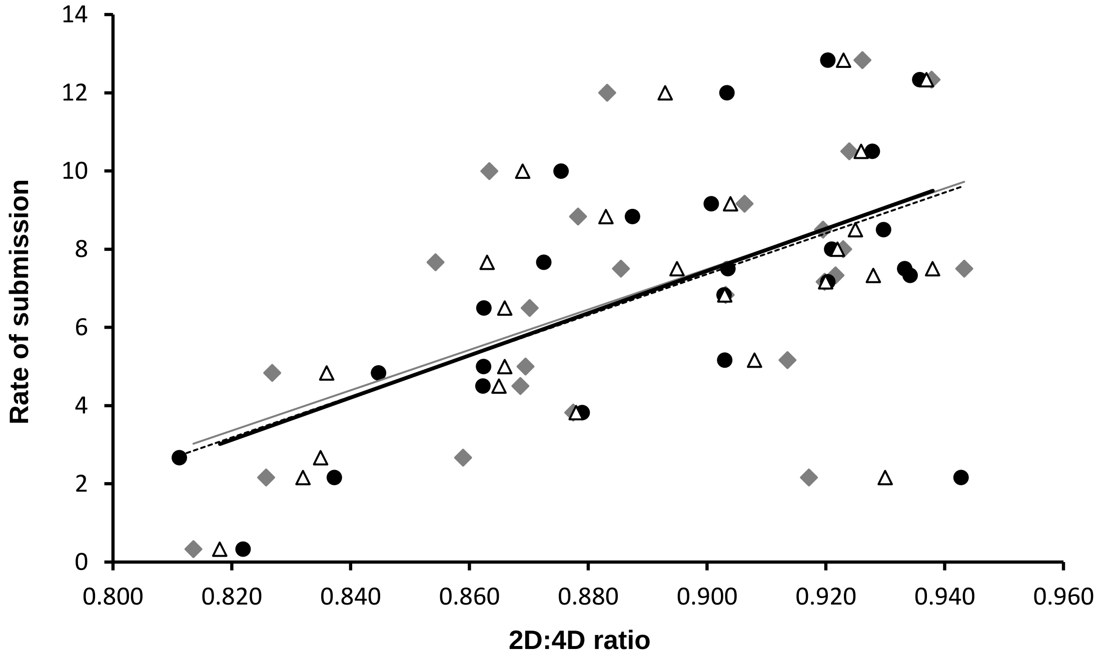

0.03
0.02
0.01
0.00
-0.01
-0.02
-0.03
-0.04
-0.05
Dr-I
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
Dominance rank

Figure 3



14
12
10
8
6
4
2
0
Rate of submission
0.800
0.820
0.840
0.860
0.880
0.900
0.920
0.940
0.960
2D:4D ratio

Figure 4a

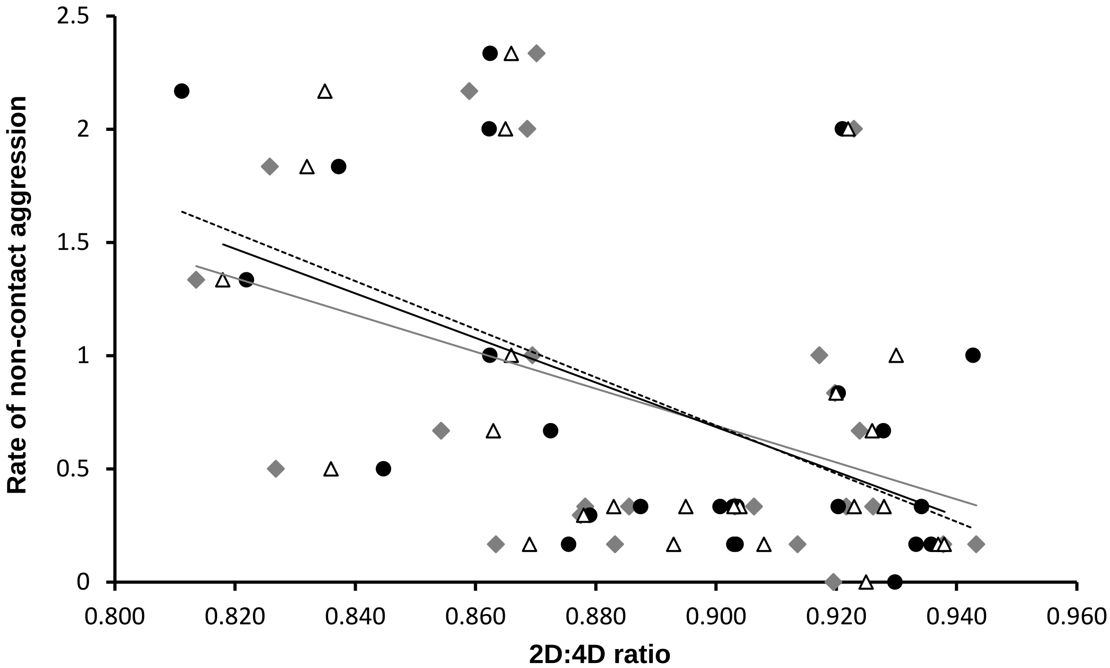

Rate of non-contact aggression
2.5
2
1.5
1
0.5
0
0.800
0.820
0.840
0.860
0.880
0.900
0.920
0.940
0.960
2D:4D ratio

Figure 4b

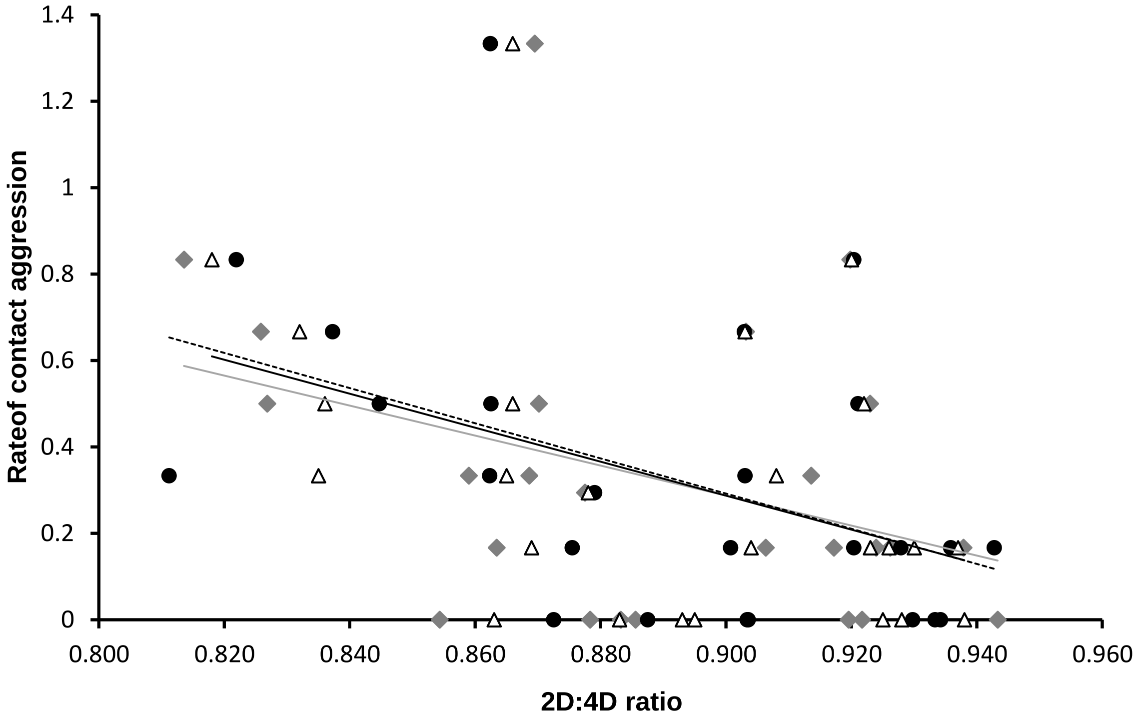
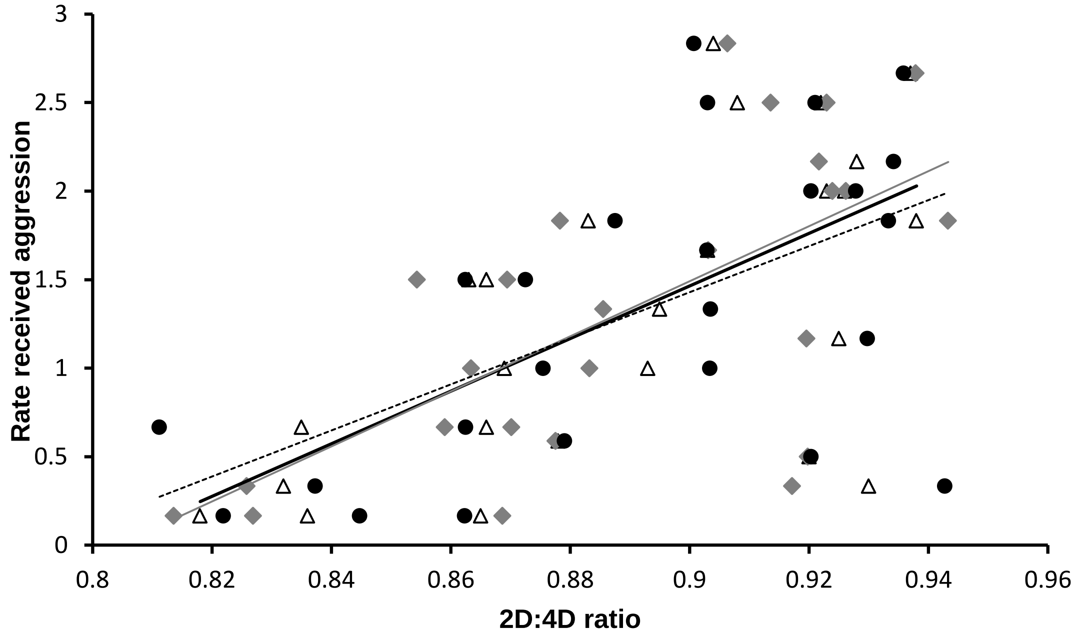

Rateof contact aggression
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0.800
0.820
0.840
0.860
0.880
0.900
0.920
0.940
0.960
2D:4D ratio

Figure 4c



Rate received aggression
0
0.5
1
1.5
2
2.5
3
0.8
0.82
0.84
0.86
0.88
0.9
0.92
0.94
0.96
2D:4D ratio

Figure 5

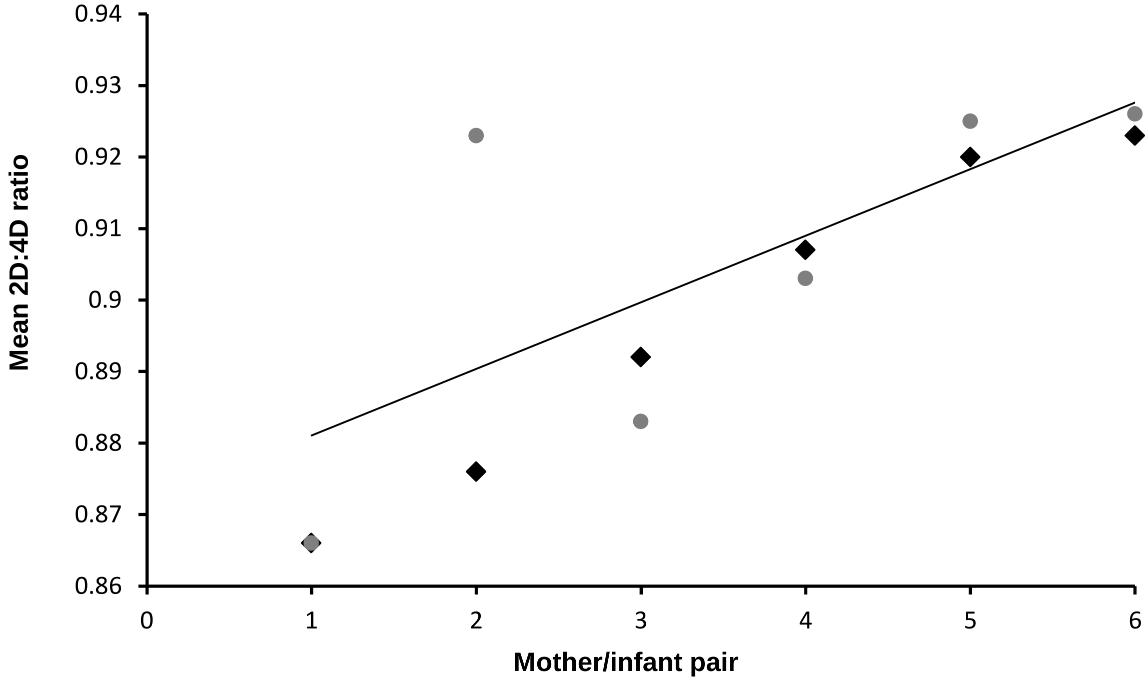

Mean 2D:4D ratio
0.94
0.93
0.92
0.91
0.9
0.89
0.88
0.87
0.86
0
1
2
3
4
5
6
Mother/infant pair

Table 1 Summary of predictions

	Summary of predictions
1	2D:4D ratios and Dr-l will correlate negatively with dominance rank
2	2D:4D ratios and Dr-l will correlate positively with rate of submission
3a	2D:4D ratios and Dr-l will correlate negatively with rate of contact and non-contact aggression
3b	The negative correlation between 2D:4D ratios and rate of contact aggression will be higher than between 2D:4D ratios and rate of non-contact aggression
3c	2D:4D ratios will correlate positively with rate of received aggression
4	2D:4D ratios will correlate positively with rate of interest in infants
5a	2D:4D ratios will correlate positively with rate of affiliation
5b	2D:4D ratios will correlate positively with number of social partners and number of grooming partners
5c	2D:4D ratios will correlate positively with the rate of grooming given by a female but will correlate negatively with the rate of grooming received by a female
6a	There will be a positive correlation between a mother's 2D:4D ratios and the 2D:4D ratios of her infant
6b	Maternal dominance rank will correlate negatively with offspring 2D:4D ratio

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

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

Table 3 Bivariate correlations between behavioural variables and dominance rank and partial correlations between behavioural variables and 2D:4D ratio when controlling for dominance rank (*) and behavioural variables and dominance rank when controlling for 2D:4D ratio (●)

Behavioural variable	**Dominance rank**	**2D:4D ratio**	**Dominance rank**
Rate of submission	*r* = 0.772, df = 25, P > 0.001	*r* = - 0.138, df = 22, P 0.520*	*r* = 0.623, df = 22, P 0.001●
Rate of non-contact aggression	*r* = - 0.644, df = 25 P 0.001	*r* = 0.053, df = 22, P 0.807*	*r* = - 0.387, df = 22, P 0.062●
Rate of contact aggression	*r* = - 0.577, df = 25, P 0.003	*r* = - 0.577, df = 25, P 0.003*	*r* = - 0.326, df = 22, P 0.001 ●
Rate of received aggression	*r* = 0.684, df = 25, P > 0.001	*r* = 0.269, df = 22, P 0.204*	*r* = 0.370, df = 22, P 0.075●