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Digit Ratios and Dominance in Female Baboons (*Papio hamadryas* and *Papio ursinus*)

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Abstract A growing body of literature suggests that the ratio between the second and fourth digits of the hands (2D:4D ratio) is associated with exposure to prenatal sex hormones in a variety of animals including primates. Female baboons form dominance hierarchies composed of matrilines of related individuals, and the social mechanisms contributing to the structure of these hierarchies have been well studied. We here investigated the relationship between inferred prenatal androgen effects (PAE) and female rank in a captive troop of Hamadryas baboons (*Papio hamadryas*) with a typical social structure and three captive groups of chacma baboons (*Papio ursinus*) made up entirely of unrelated orphans. Low 2D:4D ratios (high inferred PAE) were associated with higher-ranking females and high 2D:4D ratios (low inferred PAE) with lower-ranking females in both focal species. This negative correlation between 2D:4D ratio and rank suggests prenatal androgens are linked with the maintenance of female ranks within matrilines in troops with a natural social structure and to the ranks acquired by orphan females.

Keywords 2D:4D digit ratio · Hormone · Prenatal androgens · Primate · Rank · Social hierarchy

Introduction

Sociality can have a positive influence on female fitness in many mammalian species (Hoogland *et al.* 1988; Mennella *et al.* 1990; Solomon and French 1997), including

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nonhuman primates (Silk *et al*. 2010; Sterck *et al*. 1997). The type of relationship that forms among females is dependent on the type and intensity of competition they face through group living (Sterck *et al*. 1997). If competition is indirect, or where resources are plentiful, bonds between females are weak because strong alliances are not necessary when resources are indefensible or rarely contested (Henzi *et al*. 2009; Koenig 2002; Sterck *et al*. 1997). Hierarchical relationships tend to develop when there is significant direct competition between females over essential resources (Sterck *et al*. 1997).

Dominance behavior is associated with androgen sex hormones in adults of many species, e.g., male chimpanzees (*Pan troglodytes*: Muehlenbein *et al*. 2004), Asian elephants (*Elephas maximus*: Lincoln and Ratnasooriya 1996), and domestic cattle (*Bos primigenius*: Bouissou and Gaudioso 1982). Prenatal androgens also play a key role in the development of the male phenotype during mammalian sexual differentiation (Bercovitch and Ziegler 2002; Gower 1979), being responsible for directing the otherwise female differentiation pattern along the male line (Herman *et al*. 2000; Thornton *et al*. 2009; Wallen 2005). The organizational effects that prenatal androgens have on the brain and external genitalia may cause individuals to interact and behave in a certain manner, giving them hormonally influenced predispositions (Knickmeyer *et al*. 2005; Wallen 2005).

Aggression differs from dominance in that the behavior comes with the intent to inflict injury on conspecifics whereas dominance can be asserted without intention of causing physical harm (Mazur and Booth 1998). The two behaviors are linked through the androgen hormone testosterone in primates (Higley *et al*. 1996). High cerebrospinal fluid–free testosterone is associated with aggression in competitive situations in adolescent male rhesus macaques (*Macaca mulatta*: Higley *et al*. 1996), and circulating testosterone correlates positively with male humans' self-ratings of dominance and aggression (Christiansen and Knussmann 1987). Eliminating testosterone in adult males through castration leads to a calmer and more passive animal (Tieger 1980; Worthman 1995; Wuttke and Horowski 1981), and variation in male sex hormone concentration can also significantly alter behavior in female primates. Artificially increasing the levels of prenatal androgens to which female rhesus macaques are exposed masculinizes their behavior (Tomaszycki *et al*. 2005; 2001; Zehr *et al*. 2005), and serum testosterone in adult female baboons plays a role in dominance rank, with females with the highest testosterone levels being higher in rank and more aggressive (Beehner *et al*. 2005). For many years prenatal androgen hormones have been identified as having similar effects across a wide variety of taxa in that they are capable of both masculinizing and defeminizing the behavior of individuals (Thornton *et al*. 2009).

The ratio of the lengths of the second (2D) and fourth digits (4D) of the hands (2D:4D ratio) is fixed early in development and is proposed to reflect the organizational effects of prenatal androgens in humans and other primates (Berenbaum *et al*. 2009; Malas *et al*. 2006; Manning 2002; Manning *et al*. 2003; Nelson *et al*. 2010). The 2D:4D ratio is sexually dimorphic as early as week 14 of gestation in humans, remains unchanged at puberty, and is stable during adulthood (Fink *et al*. 2003; Manning *et al*. 2002). There is some evidence that the 2D:4D ratio is not stable over growth and increases slightly with age in very young children (Trivers *et al*. 2006) but this is not unanimously supported in studies with larger sample sizes (Manning *et al*.

1998, 2004). Development of the digits and genitals is directed by the same groups of phylogenetically conserved *HOX* genes (Manning *et al*. 1998; Zákány *et al*. 1997), and low 2D:4D ratio relates to heightened activation of androgen-responsive genes involved in limb development and higher prenatal androgen effects (PAE) (Manning *et al*. 2003). Developing digit primordia have an abundance of androgen and estrogen receptors, and the activity of these is higher in the fourth digit relative to the second digit. Using the mouse (*Mus musculus*), Zheng and Cohn (2011) found that androgen receptors increase chondrocyte proliferation and oestrogen receptors reduce chondrocyte proliferation in the fourth digit. Thus individuals experiencing higher prenatal androgen levels tend to have longer fourth digits and lower 2D:4D ratios than those experiencing lower prenatal androgen levels (Manning 2011; Zheng and Cohn 2011). Correlations have been found between the 2D:4D ratio and serum testosterone levels in adult male Guinea baboons (*Papio papio*: Roney *et al*. 2004), and the 2D:4D ratio and dominance rank in free-living adult female rhesus macaques (Nelson *et al*. 2010). Low 2D:4D ratio has also been found to associate with traits such as strength (Fink *et al*. 2006), sperm count and testosterone concentration (Manning *et al*. 1998), perceived dominance (Neave *et al*. 2003), endurance running ability (Manning *et al*. 2007), sporting ability (Manning and Taylor 2001), and spatial ability in humans (van Anders and Hampson 2005). High PAE may potentially, therefore, have important positive effects on the survival and fitness of animal species.

As in many Old World monkeys, baboons live in strongly female-bonded societies (Silk *et al*. 1999; 2006; 2010). They live in extended matrilines in which close kin groom and provide social support for each another (Altmann 2001; Engh *et al*. 2006; Silk *et al*. 2010). With the sole exception of Hamadryas baboons (*Papio hamadryas*: Kummer 1968), females reside in their natal troops all their lives and so the need to negotiate complex social relationships with other group members, especially kin, is vital (Chadwick-Jones 1998; De Waal and Tyack 2003; Silk *et al*. 1999). A stable linear dominance hierarchy exists between the various matrilines in a troop and also between female kin within each matriline. Close kin often occupy adjacent ranks and kinship is important in the formation and maintenance of female bonds (Barrett 2009; Dunbar 1988; Parr *et al*. 1997). A female's position within the social hierarchy is obtained from her mother through matrilineal rank inheritance (Chalmers 1979; Chance and Jolly 1970). The status of each female within a matriline drops a position with every successive daughter that is born to the matriarch, with younger daughters displacing their older sisters (Altmann 2001; Engh *et al*. 2009). Attempts by subordinates to rise in rank are resisted aggressively by higher ranked females because this would reduce their own fitness. As a result, rank reversals rarely occur and the social hierarchy in female baboons is extremely conservative, often persisting for decades (Cheney and Seyfarth 2007; De Waal and Tyack 2003; Engh *et al*. 2006; Strier 2003). One of the fundamental mechanisms maintaining this system of rank inheritance is the capacity of mothers to come to the aid of their offspring in conflicts with other females (Chadwick-Jones 1998; Cheney and Seyfarth 2007). In a population of chacma baboons (*Papio ursinus*), orphaned females were more likely to attain unexpected ranks than females whose mothers were still living (Engh *et al*. 2009). Individuals with older sisters tended to achieve lower ranks within their matriline. Those with no sisters but with older brothers could rise in rank outside their matriline due to fraternal support in dominance conflicts, while those without siblings were likely to fall below their former matrilineal rank due to a lack of social support (Engh *et al*. 2009).

Among primates, more masculine (lower) 2D:4D ratios have been associated with species exhibiting more competitive social systems (Nelson and Shultz 2010). For example, higher (less masculine) digit ratios in bonobos (*Pan paniscus*) relative to the more socially competitive chimpanzees (*Pan troglydytes*) have been linked to their more cooperative social system and reduced masculinization among male and female bonobos (McIntyre *et al*. 2009). Although evidence exists for associations between the 2D:4D ratio and dominance rank in female rhesus macaques (Nelson *et al*. 2010), the relationship between the 2D:4D ratio and dominance has not been investigated in females of *Papio* (baboon) species. Here we aim to investigate the relationship between the 2D:4D ratio, and thus inferred PAE, and hierarchy position in captive groups of baboons. The focal species, Hamadryas and chacma baboons, differ markedly in their social behavior. Hamadryas baboons are unique among baboons in that they have a multilevel social system consisting of one male–multifemale units (OMUs), several of which come together to form clans in which the males in the OMUs are typically related. A number of clans join up to form a band, and these bands merge to form a troop of up to 200 individuals (Chadwick-Jones 1998; Colmenares 1992; Kummer 1995). Females normally remain in their natal clans, though they disperse out of their natal OMUs before reaching maturity (Sigg *et al.* 1982). Chacma baboons display typical baboon sociality and live in troops with multiple males, females and their offspring. Males of this species disperse and females remain within their natal troop throughout their lives (Chadwick-Jones 1998; Sithaldeen *et al*. 2009). The population of chacma baboons we studied are interesting in that they are made up of unrelated individuals of a similar age class and lack the social environment typically experienced by their nonorphan counterparts. These orphaned females are therefore free of the rank constraints that would normally be placed on them by their relatives and so are, in a sense, free to negotiate their own rank.

We hypothesize that an individual's PAE (inferred from the 2D:4D digit ratio) will show a relationship with female rank in both the nonorphaned Hamadryas and orphaned chacma baboons and predict that females of both species with lower 2D:4D ratios will have higher positions in the dominance hierarchy than those with higher 2D:4D ratios. In contrast, we expect the length of the individual second and fourth digits, used as a proxy for body size, will not be linked to position in the social hierarchy in either species, as female body mass is unrelated to dominance rank in other nonhuman primates (Cooper *et al*. 2004; Paoli *et al*. 2006).

Materials and Methods

We examined the relationships between 2D:4D ratios and dominance in one group of captive chacma baboons and one group of captive Hamadryas baboons. Wild-born chacma baboon infants that have been orphaned after the death of their mothers are brought to the Centre for Animal Rehabilitation and Education (C.A.R.E), Phalaborwa, South Africa, where they are raised by human surrogates. When they reach an appropriate age (typically 5 mo), they are introduced to other orphaned juveniles with which they interact, and these eventually form a troop of unrelated individuals once they have been weaned from human company at *ca*. 1 yr old. We collected data from 17 orphaned chacma baboon females housed in outdoor enclosures enriched with tyres, nets, swings, trees, and various other play toys over a 4-wk period between July and August 2010. Enclosures varied in size: 10 m (length) × 10 m (width) × 5 m (mean height), 8 m × 5 m × 4 m, and 12 m × 12 m × 8 m. These housed individuals aged between 18 mo and 4 yr that belonged to three different mixed-sex troops known in this study as 1 (13 individuals), 2 (14 individuals), and 3 (16 individuals).

We collected further data over a 6-wk period between September and October 2010 from 18 captive adult female Hamadryas baboons at Flamingo Land Zoo in North Yorkshire, UK. The troop consisted of 39 individuals housed on an outdoor "island" surrounded by a moat, adjoined by indoor sleeping quarters. Outdoor quarters contained climbing structures, tree perches, boulders, and other enrichment facilities. All baboons in the troop were accustomed to human observers. The troop included four adult males and the females that made up their OMUs. We excluded 20 adolescents and juveniles of both sexes and one male infant from the study because we were specifically interested in adult females. The structure of OMUs had been in place since the monkeys' arrival at the zoo *ca*. 20 yr previously, and females within these OMUs were most likely related members of a matriline because there was little opportunity for dispersal out of their family groups in their captive setting. As a consequence, the female relationships in this study may be more strongly bonded than those occurring in wild troops (Judge *et al*. 2006).

Determination of Social Rank

We obtained the dominance hierarchy for the chacma group from the center staff. Staff were involved in raising the majority of individuals from a very young age with the help of volunteers and had long-term experience of behavioral interactions between individuals after they had reached independence. The staff use the direction of displacement and submissive interactions between females within troops to determine the social rank of each female, with individuals assigned ranks dominant (highest ranked), high, medium, or low depending on their position in the social hierarchy. Rank levels were not equally distributed owing to differences in the number of females in each troop (troop 1: 1 dominant, 1 high, 2 medium, and 2 low; troop 2: 1 dominant, 2 high, 2 medium, and 3 low; troop 3: 1 dominant, 1 high, 1 medium, and 1 low).

Among the Hamadryas baboons we determined the four OMUs in the troop (OMU 1: seven females; OMU 2: six females; OMU 3: three females; OMU 4: two females) by observing grooming interactions between males and females, matings, following of male by females, female proximity to males, and male herding behavior (Kummer 1995; Sigg *et al*. 1982). We gave OMUs ranks within the troop as a whole by observing supplant and displacement interactions between entire OMUs (1 = highest-ranked and 4 = lowest-ranked), which followed the age-graded hierarchy of eldest to youngest typically seen among Hamadryas males (Kummer 1995).

To determine the ranks of females within each OMU, we followed each OMU over two 1-h focal sample periods per 8-h observation day for the duration of the study, amounting to 96 h of observation time (Altmann 1974;

Martin and Bateson 2007). We also recorded submissive interactions opportunistically on an *ad libitum* basis within OMUs, both within focal periods (for interactions involving adult female group members other than individuals in the focal OMU) and between focal periods. We recorded the direction of supplants and submissive interactions (move away, fear grimace, cower) data and used these to determine dominance/subordinance relationships between dyads (Altmann 1974; Cheney and Seyfarth 1999; Silk *et al*. 2006) and to assign females to dominant, high, medium, or low ranks within their OMUs. Again, rank levels were not evenly distributed: OMU 1: 1 dominant, 1 high, 3 medium, and 2 low; OMU 2: 1 dominant, 1 high, 3 medium, and 1 low; OMU 3: 1 dominant, 1 medium; and 1 low; OMU 4: 1 dominant, and 1 low. For the majority of individuals, the rank order was linear, with the dominant female displacing all other females in the OMU, a high-ranked female displacing all females other than the dominant, medium-ranked females displacing low-ranked females, and low-ranked females displacing no other individuals. In a few dyads, we did not observe any dominance interactions during the 6-wk period, with the females either tolerating or ignoring each other. We assigned equal rank to these individuals.

Digit Measurements

Baboons in the chacma group were accustomed to human handling. To measure their digits a staff member caught and held the baboon and extended the individual's wrist, enabling us to measure the second and fourth digits of the right hand of females from the basal crease where the finger joins the hand (palm side) to the tip of the extended digit (nearest mm) using Draper callipers (Manning *et al*. 1998; Rizwan *et al*. 2007).

It was not possible to get close to the Hamadryas baboons and so we took digit measurements using digital photographs. We took photographs when the individual's right hand was in a flat and straight position and digits were fully extended with the entire digit visible. When measuring from the dorsal surface the basal crease is not visible, so we measured from the webbing in between the digits (which is in line with the basal crease on the ventral surface) or an equivalent landmark to the tip of the digit. We took multiple photographs for each individual and used three in which the hand was in the optimum position for the measurements. We analyzed these digital images via computer-assisted image analysis software (ImageJ) using mouse-controlled callipers to measure lengths of the second and fourth digits of the right hand from the images in pixels (Allaway *et al*. 2009; Voracek *et al*. 2007). We obtained digit ratios for three photographs per individual, and used the mean of these as the overall 2D:4D ratio for that individual. We also took photographs of each subject's hand in which there was an object, e.g., stone or branch, of known length. We then measured the second and fourth digit lengths of the right hand with ImageJ image analysis software using this object for scale to investigate the effect of body size on female rank.

In both species, we took measurements of each digit three times to account for sampling error, and used the mean of these in analyses. We calculated 2D:4D ratios by dividing the length of the second digit by the length of the fourth digit (Nelson *et al*. 2010).

Statistical Analyses

The 2D:4D ratios were negatively skewed so we transformed them to the power 4 before analysis using a general linear model with species and rank as factors. In addition, we examined correlations between the transformed ratios and rank within each of the chacma troops and Hamadryas OMUs using Pearson's correlations. We used the lengths of the second and fourth digits as measures of body size to test whether body size is related to rank attained by females. We transformed the lengths before analysis with a general linear model, again with species and rank as factors.

Ethical Note

We carried out work at the two sites with the relevant permissions from C.A.R.E. and Flamingo Land Theme Park and Zoo. Stress to the C.A.R.E. baboons was minimized by familiarizing them with the observer, conducting their handling only by C.A.R.E. staff experienced with doing so, and releasing individuals immediately after digit measurements had been obtained.

Results

There was a significant relationship between the 2D:4D digit ratios and rank ($F_{3,\ 27}$= 17.9, $P<0.001$), with more highly-ranked baboons having lower 2D:4D ratios, medium-ranked individuals being intermediate and low-ranked baboons having higher 2D:4D ratios (Fig. 1). This relationship was more pronounced in the Hamadryas baboons than in the chacmas, with the Hamadryas baboons having a slightly greater range of digit ratios, but the interaction between species and rank was not significant ($F_{3,27}=1.76$, $P=0.179$), and the overall difference between species was also nonsignificant ($F_{1,27}=3.33$, $P=0.079$).

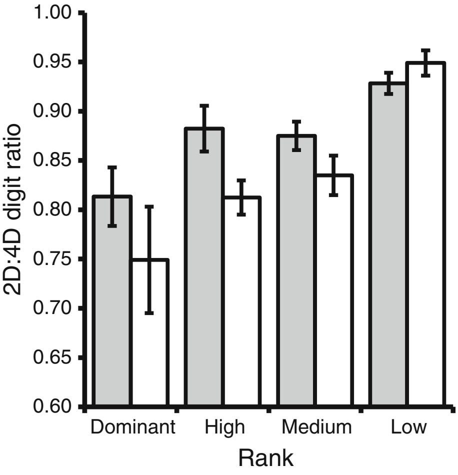

Fig. 1 Mean±SE 2D:4D digit ratios of chacma (*gray columns*) and Hamadryas (*white columns*) baboons that were dominant, high, medium, or low ranked within their troop or OMU. A lower 2D:4D ratio is indicative of higher levels of PAE.

The relationship between 2D:4D digit ratios and rank was remarkably consistent across troops or OMUs in both species (Fig. 2). In each troop or OMU, individuals with the highest 2D:4D ratios tended to be low-ranked while those with the lowest 2D:4D ratios tended to be the dominant. Only chacma troop 2 was a partial exception to this (gray squares in Fig. 2a), with the dominant-, high-, and medium-ranked individuals all having similar 2D:4D ratios. The correlation between rank and digit ratio was not significant for chacma troops 1 and 2, but was significant for chacma troop 3 (respectively: $r=0.688$, df=5, $P=0.199$; $r=0.541$, df=8, $P=0.166$; $r=0.982$, df=4, $P=0.018$). In the Hamadryas baboon OMUs, the correlation was significant for OMUs 1 and 2, but not 3 (respectively: $r=0.88$, df=7, $P=0.009$; $r=0.852$, df=6, $P=0.031$; $r=0.97$, df=3, $P=0.156$; OMU 4 had only two individuals).

Hamadryas OMUs did not differ overall in the 2D:4D ratios of their members ($F_{3,14}=0.407$, $P=0.75$). Interestingly, however, the rank of the OMU did appear to correlate with the 2D:4D ratios of the dominant female in the OMU. The dominant female in OMU 1 (which was highest ranked) had a lower 2D:4D ratio than the dominant female in OMU 2 (the next highest ranked), which in turn had a lower ratio than the dominant females in the two lowest ranked OMUs (Fig. 2b).

In contrast to the relationship between 2D:4D digit ratio and rank, there was no significant relationship between rank and body size, as measured by digit lengths (2nd digit: $F_{3,27}=0.689$, $P=0.566$; 4th digit: $F_{3,27}=0.577$, $P=0.635$). This was the

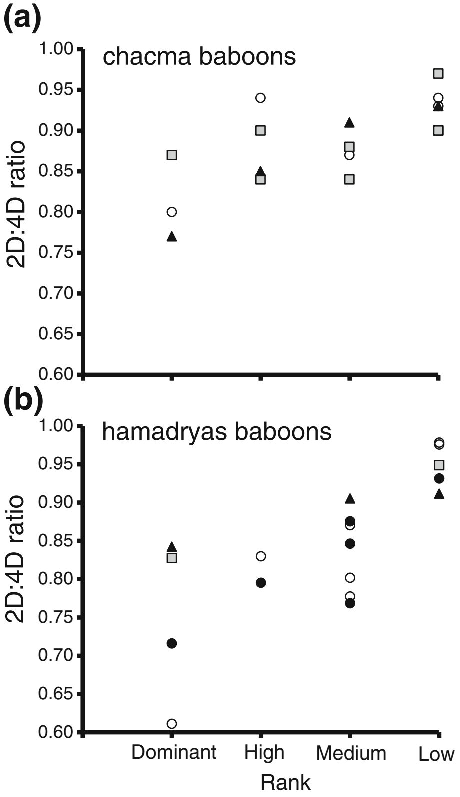

Fig. 2 The relationship between 2D:4D digit ratios and rank (dominant, high, medium, or low) in (**a**) chacma and (**b**) Hamadryas baboons. A lower 2D:4D ratio is indicative of higher levels of PAE. Different troops (in the chacma baboons) and OMUs (in the Hamadryas baboons) are indicated by different symbols. In the chacma baboons the troops were equal in rank and were: troop 1 (*white circles*), troop 2 (*gray squares*), and troop 3 (black triangles). In the Hamadryas baboons, OMUs were also ranked in the following order of dominance: OMU 1 (*white circles*), OMU 2 (*black circles*), OMU 3 (*black triangles*), and OMU 4 (*gray squares*).

case in both species, with no species by rank interaction (nd digit: $F_{3,27}=0.393$, $P=0.759$; 4th digit: $F_{3,27}=0.161$, $P=0.922$). Overall the Hamadryas baboons were slightly larger than the chacma baboons (2nd digit: $F_{1,27}=2.03$, $P=0.166$; 4th digit: $F_{3,27}=4.99$, $P=0.034$), in keeping with the Hamadryas OMUs including older individuals than the chacma troops (Fig. 3).

Discussion

This study demonstrates that PAE, as inferred by 2D:4D ratios, correlate with the dominance hierarchy of female baboons. High-ranked females have relatively shorter second digits and longer fourth digits than medium- and low-ranked females. The lengths of individual digits did not, however, show any relationship with female rank and this reinforces the suggestion that it is the ratio, reflecting prenatal hormones, which has the important link with female rank. Consistent with other studies involving female primates, we found no relationship between body size and female rank in either study species (Cooper *et al*. 2004; Paoli *et al*. 2006).

Although the chacma and Hamadryas baboons were different species, with differences in upbringing, social environment, and diet and despite differences in measurement method, we found the same relationship between 2D:4D ratio and dominance rank. The negative correlation between 2D:4D ratio and rank suggests that, as predicted, PAE may have an effect on the rank a female baboon is likely to achieve in the dominance hierarchy. Higher PAE, which is associated with low 2D:4D ratios, may cause female behavior to become more masculinized or dominant (Thornton *et al*. 2009; Wallen 2005). Animals exposed to higher PAE, as indexed by masculine (low) 2D:4D ratios, display higher reactive aggression under provocation (human females: Zeynep and Nelson 2004) are more physically aggressive (human males: Bailey and Hurd 2004), are more vigilant (humans: Coates *et al*. 2009), and may react more quickly to threats to rank (rhesus macaques: Nelson *et al*. 2010). All of these dominance-related traits may contribute to an individual attaining and

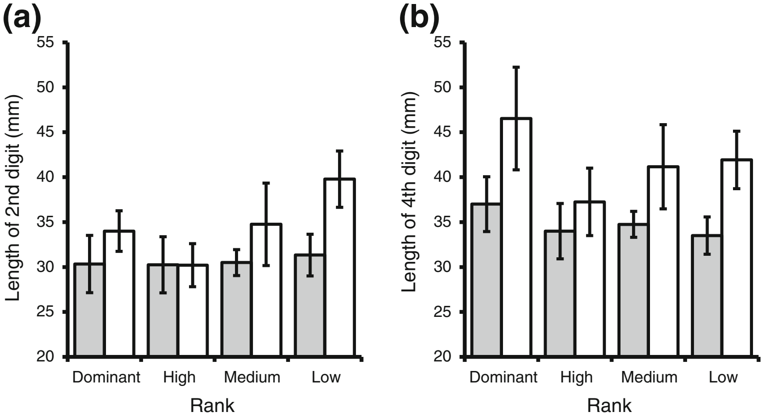

Fig. 3 Mean±SE lengths of (**a**) the second digit and (**b**) the fourth digit for chacma (*gray columns*) and Hamadryas (*white columns*) baboons that were dominant, high, medium, or low ranked within their troop or OMU. The lengths of the digits serve as indicators of body size.

maintaining high rank. Prenatal androgens are therefore capable of predisposing certain individuals to become more dominant through their masculinizing effects on the individual's adult behavior and aggressive tendencies (Nelson *et al.* 2010).

The strong negative relationship between 2D:4D ratio and rank in orphan females suggests that PAE can have a significant influence on the development of the dominance hierarchy in troops composed of unrelated individuals. The only exception to this was chacma troop 2, which had an unusual history with the dominant and second highest ranked females having been raised in close association. They may thus have regarded each other as kin and supported each other in social conflicts, resulting in both individuals rising to a higher rank than their 2D:4D ratios would predict. This suggests that PAE may therefore not act independently of social factors in wild social groups with more typical social structures.

In most cases the dominant females in a group had lower 2D:4D ratios than high-ranked females. PAE may therefore also play a role in determining who becomes dominant and who high-ranked within a troop. Nelson *et al.* (2010) found that the relationship between 2D:4D ratio and dominance in rhesus macaques was significant within, but not between, matrilines in a social group. Our sample size was not large enough to test this, but the data were suggestive of a relationship between the 2D:4D ratio of the dominant female and her OMU's rank. OMU rank in Hamadryas baboons is most likely influenced by their leader males, which follow an age-graded hierarchy of eldest to youngest (Kummer 1995). Despite their confined setting, the females in the captive population do have some dispersal opportunities through the maturation of young males. The observed negative correlation between the 2D:4D ratio of the OMU's dominant female and the OMU's rank within the troop as a whole was most likely due to preferential dispersal of low-ranked females from the larger OMUs once adolescent males came of age. These females could benefit from dispersing by becoming the dominant female in the OMU of a lower-ranking male and having fewer females to compete with for the attention of the male.

The 2D:4D ratio (and so PAE) is moderately to highly heritable in humans (Paul *et al.* 2006; Saino *et al.* 2006) and likely to be so in other nonhuman primates. Maternal testosterone during pregnancy shows substantial correlation with fetal testosterone levels, and testosterone production is highly heritable in humans (Hines 2006). Mother/offspring pairs show similar 2D:4D ratios in rhesus macaques, suggesting a substantial genetic contribution to the expression of the 2D:4D ratio (Nelson and Voracek 2010). Inheritance of dominant behavioral traits associated with high PAE may link to matrilineal rank inheritance, and may, in part, provide answers as to what processes, other than ecological and social factors (kin selection), influenced the evolution of this form of social organization.

Debates as to whether baboons have a "social concept" or simply "learn" the social hierarchy through associative conditioning have been ongoing for years (Barrett 2009; Cheney and Seyfarth 2007; Dunbar 1988). Many nonhuman primate species, including baboons, are innately predisposed to assign themselves and other group members into hierarchical categories (Bergman *et al.* 2003; Cheney and Seyfarth 2007; De Waal and Tyack 2003). The relationship between rank and 2D:4D ratio was similar in the Hamadryas and chacma baboons, suggesting that rank acquisition in orphaned baboons is achieved in a similar way to that of a troop with an intact matriline. This suggests that the behaviors affecting rank acquisition are somewhat innate, and a hierarchical understanding is not entirely a result of learning in young baboons (Barrett 2009; Bergman *et al*. 2003; Chadwick-Jones 1998; De Waal and Tyack 2003; Nelson *et al*. 2010).

The negative correlation between rank and 2D:4D ratio across both focal groups was highly significant reinforcing the suggestion that PAE are linked to the dominance hierarchy in female baboons both within matrilines and in troops without a matriline. We conclude that PAE have a significant involvement in the dominance hierarchy that arises among female baboons and the maintenance of social rank through its effects on the behaviors of female primates. Our findings suggest that developmental, as well as ecological and social, processes may have played a key role in shaping the evolution of hierarchical social systems seen in female baboons.

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