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Prenatal Androgen Effects as a Proximate Mechanism Underpinning Variation in Social Behavior Among Female Nonhuman Primates



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Abstract

While the role of ecological factors in shaping primate social systems has been a central focus for decades, less attention has been given to 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 (PAEs), and aspects of social behavior in female nonhuman primates using the 2D:4D ratio as a proxy for PAEs and phylogenetically controlled methods. In general, female 2D:4D ratios were highest in monogamous species (low inferred PAEs) and lowest in polygynandrous and polygynous species (high inferred PAEs). 2D:4D ratios also varied with the form of polygyny/polygynandry, potentially with regard to the need for competitive over cooperative behaviors and the intensity of female reproductive competition. Species characterized by female dominance had lower 2D:4D ratios than species characterized by male dominance or codominance. There were no significant relationships between 2D:4D ratio and either degree of frugivory or group size. Relationships between 2D:4D ratios and the directional consistency index and 2D:4D ratios and rates of female–female agonism were also nonsignificant although sample sizes for both of these variables were small. Female social relationships are a manifestation of complex competitive and cooperative behaviors and the results suggest that PAEs may act as a proximate mechanism underlying the expression of certain aspects of behavior in female primates in ways that are adaptive to their social system.

Keywords 2D:4D ratio · Phylogenetics · Sex hormones · Socioecology

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Introduction

A basic assumption of socioecological theory is that females compete for access to nutritional resources and males compete for access to females (Kappeler and 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 and van Hooff 1983). Predation risk is argued to lead diurnal female primates to form groups for safety (van Schaik 1983), which in turn leads to intragroup competition for essential resources (Terborgh and Janson 1986; van Schaik 1989). Relationships among females are thought to be influenced by the type and strength of the feeding competition they face within and between their social groups, and this is affected by the distribution of resources (Chapman *et al.* 1995; Isbell 1991; Koenig 2002; Sterck *et al.* 1997).

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 and van Schaik 2002). Display of aggressive behavior 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 1985; Janson and van Schaik 1988), and hierarchies (if detectable) are expected to be indistinct and non-linear (Sterck *et al.* 1997). However, when resources are clumped and monopolizable then direct (contest) competition is expected to occur (Janson and 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 unmonopolizable (Isbell 1991; *cf.* Koenig *et al.* 1998). Frugivory is typically thought to favour despotic relationships because ripe fruits tend to be high-quality, monopolizable and, therefore, contestable. Some studies have shown that agonism occurs disproportionately during feeding in primates, particularly when feeding on fruits (Cords 2000; Klass and Cords 2015). 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 (McKenna 1979; Snaith and Chapman 2007). However, in a cross-taxa analysis, the expected association between high rates of agonism and frugivory in female primates was not generally supported (Wheeler *et al.* 2013) and some folivorous female primates show relatively low rates of agonism but still form decided dominance relationships (*Gorilla beringei*: Robbins *et al.* 2005; *Trachypithecus phayrei*: Koenig *et al.* 2004).

In addition to the distribution and quality of food, ecology can also indirectly affect female social structure by its effect on group size (Terborgh and Janson 1986) and there is notable variation in group size across the primate Order (Campbell *et al.* 2011; Kappeler and van Schaik 2002). The intensity of intragroup competition levels may increase with group size (Klass and Cords 2015; Koenig and Borries 2006; Terborgh

and Janson 1986) and studies have found that primates living in larger groups are characterized by higher rates of agonism (Cowl and Shultz 2017; Wheeler *et al.* 2013). Furthermore, the demographic factor, female philopatry, is thought to be involved in the formation of female relationships (Isbell 2004; Kappeler and van Schaik 2002; Sterck *et al.* 1997). In species in which females disperse, female relationships are predicted to be egalitarian. In species in which females remain in their natal group, relationships vary depending on the levels of intra- and intergroup contest competition (Sterck *et al.* 1997).

Although the broad-scale descriptive classifications of female dominance relationships used by Sterck *et al.* (1997) are useful, there is considerable variation in how these relationships manifest themselves between (and sometimes even within) species (Klass and Cords 2015; Wikberg *et al.* 2013). This observed variation is beyond the descriptive scope proposed by Sterck *et al.* (1997) and species often do not conform to some predictions of the socioecological models described above (Klass and Cords 2015; Robbins *et al.* 2005; Wheeler *et al.* 2013; Wikberg *et al.* 2013), leading researchers to position species into the categories which they most closely match. For example, in a study on a population of predominantly folivorous *Colobus vellerosus* (a species with facultative female dispersal: Wikberg *et al.* 2014), occasional foraging on temporally available, clumped foods lead females to form individualistic dominance hierarchies of intermediate strength and high directional consistency (Wikberg *et al.* 2013).

The shortcomings of current socioecological models highlight the importance of considering quantitative measures of female dominance behavior (e.g., hierarchical steepness and linearity, directional consistency in dominance interactions and rates of agonism), as these may better represent the variation we see across primate species (Klass and Cords 2015). Unlike hierarchical linearity and steepness (Klass and 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 and 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 behavior (Klass and Cords 2015; Thierry 2008).

Reproductive competition can be a strong selective force in females (Rosvall 2011) but most studies investigating sexual competition focus on males (Clutton-Brock 2009). Studies in primates have revealed associations between the development of female ornamentation and weaponry and the form of reproductive competition between females (Clutton-Brock and Harvey 1976; Clutton-Brock and Huchard 2013). A study in wild female chacma baboons revealed that aggression between females was associated with access to mates (Huchard and Cowlishaw 2011). Females received aggression from other female group members at higher rates when they were reproductively active (displaying a sexual swelling 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 (Huchard and Cowlishaw 2011). When investigating aspects of intrasexual competition between females, it is thus important to consider the impacts of a species' mating system, alongside ecological factors relating to social

structure and dominance relationships (e.g., Huchard and Cowlshaw 2011). Indeed, sexual competition, in addition to competition for access to food resources, may shape female social relationships, even in large polygynandrous primate groups in which females are the high investing sex and males are the principal competitors (Huchard and Cowlshaw 2011).

Aggression between females is typically less frequent and intense than between males (Clutton-Brock and Huchard 2013) but this general pattern is often not the case for cooperatively breeding primate species where a single dominant female is able to monopolize reproduction (Garber 1994; Saltzman *et al.* 2009). Among primates, cooperative breeding is largely limited to the small-bodied callitrichine monkeys characterized by monogamous or polyandrous mating systems. Variance in reproductive success may be higher among females than males in cooperative breeders and so reproductive competition is likely to be a major selective factor for monogamous and polyandrous females (Garber 1994). Indeed, in monogamous species both sexes often play a role in territory and mate defense and are therefore mostly intolerant of same-sex intruders (Garber 1994), whereas in polyandrous species, it is typically the breeding female that is intolerant of same-sex competitors and males have a more relaxed approach to each other (Garber 1994; van Hoof and van Schaik 1994). 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).

Another social factor possibly influenced by a species' ecology is the relationships between males and females. In mammalian species, male dominance over females is the norm, and this is true of most primates (Dunham 2008; Kappeler 1993; Pereira *et al.* 1990). In some primate species, however, 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 (e.g., callitrichines and gibbons; Carpenter 1940; Koba *et al.* 2012; Reichard and Barelli 2008; Savage *et al.* 1988). Such dominance appears to correlate with monogamous and polyandrous mating systems, with some exceptions (*Eulemur collaris*: Balestri *et al.* 2014; *Brachyteles arachnoides*: Strier 1990). Female dominance, while rare, is most prevalent among Lemuriformes (Eichmueller *et al.* 2013; Kappeler 1993; Pereira *et al.* 1990) and occurs in some haplorhines such as *Pan paniscus* (Parish 1994) and some species of *Saimiri* (Mitchell 1994), and this pattern does not appear to be associated with particular mating systems (Kappeler 1991, 1993; Petty and Drea 2015).

While the hypothesized ecological factors contributing to aspects of social relationships among females and between females and males in primates have been discussed extensively, the role that underlying proximate mechanisms may play in regulating behaviors 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 behavior plays an integral part (Klass and Cords 2015; Sterck *et al.* 1997). Animal studies implicate prenatal androgen effects (PAEs) as having some influence over the shaping of an individual's tendency towards future aggressive behavior (Mazur and Booth 1998), and higher PAEs have been known to increase offspring competitive abilities (Burley and Foster 2004). In species in which competition for resources is high, the ability to out-compete challengers is highly advantageous. Therefore, high PAEs may enhance competitive behaviors in female primates that 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 PAEs in females of highly frugivorous species.

It is not yet known whether PAEs play a role in intersexual dominance patterns in primates. In the female dominant *Hapalemur alaotrensis*, females are more aggressive than males (Waeber and Hemelrijk 2003) and a study on six captive *Eulemur* species found that in female dominant species, females directed more dominance and aggressive behavior toward their male partner than they received whereas codominant females showed less dominance behavior than and equal rates of aggression as their male counterparts (Petty and Drea 2015). Species characterized by female dominance also had more masculine androgen profiles than females of codominant species and the authors suggest a hormonal mechanism may underlie the evolution of female dominance (Petty and 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 behaviorally masculinized, as selection should favor increased expression of aggressive and competitive behavior.

The ratio between the lengths of the second and fourth digits of the hands (2D:4D ratio) is a proposed negative correlate of PAEs and positive correlate of prenatal estrogen effects (POEs) (Zheng and Cohn 2011). Artificially increasing PAEs in female *Macaca mulatta* resulted in masculinized (lower) right hand 2D:4D ratios, and the degree of this masculinization correlated strongly with prenatal androgen-dependent trait anogenital distance (Abbott *et al.* 2012; Thankamony *et al.* 2016), although males have been observed with higher 2D:4D ratios than females in this species (Baxter *et al.* 2018). In 37 species of anthropoid primate, greater sexual dimorphism in 2D:4D ratio was observed in non-pair-bonded species in comparison with pair-bonded species and all species displayed significant sex differences in 2D:4D ratio (Nelson and Shultz 2010). This pattern was not mirrored in a study investigating sexual dimorphism in the second and fourth metacarpal ratio in six species of nonhuman primate, but it is likely that the growth of the metacarpals and phalanges respond differently to PAEs (Hart 2018). Low 2D:4D ratios (inferred high PAEs) are associated with higher social rank and behaviors linked to dominance and aggression in cercopithecine female nonhuman primates (Howlett *et al.* 2012, 2015; Hurd *et al.* 2011; Nelson *et al.* 2010) and humans (Benderlioglu and Nelson 2004). Using classifications of female social relationships (Sterck *et al.* 1997), female 2D:4D ratio was found to decrease with increasing intrasexual competition levels (Nelson and Shultz 2010) and these findings are concurrent with higher PAEs being of adaptive value for female primates experiencing high levels of contest competition (Nelson and Shultz 2010).

Studies suggest there is a link between high 2D:4D ratios (low inferred PAEs) and the increased postnatal expression of behaviors linked with oestrogen and its associated neuropeptides oxytocin (OT) and vasopressin (VA) (Fink *et al.* 2007; Fisher *et al.* 2010; Williams *et al.* 2003). Many of the behaviors characteristic of a monogamous mating system such as pair bonding, partner preference, and parental care are all facilitated through the actions of estrogen, OT, and VA (French *et al.* 2018; Lee *et al.* 2009; Neumann 2008), potentially resulting in increased selection for reduced PAEs and/or increased POEs in monogamous and polyandrous female primates. Consistent with this, pair-bonded anthropoid primates have generally higher 2D:4D ratios (indicate lower PAEs) than non-pair-bonded species (Nelson and Shultz 2010). However, in describing

species only in terms of pair-bonded or non-pair-bonded, much of the variation in mating systems is lost. Primates display a diverse array of mating systems and distinguishing between these (and the different forms they take) may elucidate how variation in female sexual competition levels affects the strength of selection for PAEs. Because the classifications of female social relationships used by Sterck *et al.* (1997) have been criticized due to inconsistencies between model predictions and observed behavior (Klass and Cords 2015; Thierry 2008; Wikberg *et al.* 2013) and the 2D:4D ratio measurement methods used by Nelson and Shultz (2010) could be improved upon in terms of accuracy and reliability (Allaway *et al.* 2009; Kemper and Schwerdtfeger 2009; Ranson *et al.* 2013; Voracek *et al.* 2007), a reexamination of the relationship between female social structure and PAEs, preferably using quantitative measures of female dominance behavior and more reliable 2D:4D ratio data, is desirable.

This study investigates variation in 2D:4D ratio in both strepsirrhine and haplorhine female primates. We investigated variation in 2D:4D ratio in female primates using improved 2D:4D measurement methods and quantitative measures of female social structure. We aimed to investigate the relationship between variation in PAEs (inferred from 2D:4D ratios) and female intrasexual competition and intersexual dominance relationships across primates. We tested five hypotheses, based on the assumption that 2D:4D ratio correlates negatively with PAEs. First, if food contestability affects female competitive relationships, females in species that depend on foods thought to elicit contest competition should face selection for higher PAEs than females in species that do not depend on such foods. Thus, we predict that highly frugivorous species have lower 2D:4D ratios than less frugivorous species. Second, if direct competition increases with group size, we predict that species that live in larger groups will display lower 2D:4D ratios than those that live in smaller groups. Third, if behavioral traits associated with higher PAEs are favored in females in species characterized by a high degree of despotism and high rates of female–female agonism, then we predict that the directional consistency in dominance interactions and rate of agonism will both be negatively related to 2D:4D ratio. Fourth, if species in which females experience higher competition for mates are likely to benefit from higher PAEs, we predict that monogamous females will have the highest 2D:4D ratios, followed by polyandrous females, with polygynous and polygynandrous females having the lowest 2D:4D ratios. Finally, PAEs play a vital role in the masculinization of behavioral tendencies (Goy *et al.* 1988; Pomerantz *et al.* 1985, 1986; Wallen 2005; Wallen and Hassett 2009), so we hypothesize that higher PAEs may be important for the maintenance of intersexual dominance relationships among primates (particularly female dominance) and predict that female 2D:4D ratios will be lowest in species in which females are the dominant sex (Table 1).

Methods

Study Subjects

We collected hand images between March 2016 and November 2017 on 488 individual female primates across 71 species housed in 29 zoos, wildlife/safari parks, and primate research centres in the UK, Germany, Italy, Netherlands, Spain, and one sanctuary in South Africa. We also included published 2D:4D ratio data from 25 wild female chacma

Table I The socioecological variables investigated and their predicted relationships with PAEs and the 2D:4D ratio in female primates

Socioecological factor	Relationship with PAEs	Relationship with 2D:4D ratio
Percentage of fruit in diet	Positive	Negative
Group size	Positive	Negative
DCI	Positive	Negative
Rate of agonism	Positive	Negative
Mating system	Lower in monogamy/polyandry; higher in polygyny/polygynandry	Higher in monogamy/polyandry; lower in polygyny/polygynandry
Intersexual dominance pattern	Lowest in codominant species; higher in male dominant species; highest in female dominant species	Highest in codominant species; lower in male dominant species; lowest in female dominant species

baboons (*Papio ursinus*) (Howlett *et al.* 2015). Animals included in the study were of juvenile (53 individuals), subadult (21 individuals), and adult (439 individuals) ages. The use of animals that are not fully mature in this study is justified as the 2D:4D ratio is fixed early in prenatal development (Galis *et al.* 2010) and does not change appreciably during puberty (Králik *et al.* 2014; Manning 2002; Manning *et al.* 2003, 2004).

2D:4D Ratio Measurements

We used the digital photographic and computer-assisted image analysis software method as described in Howlett *et al.* (2015) to obtain 2D:4D ratio measurements. We collected images of primate hands using the “free photo” method as described in Howlett *et al.* (2015) and photographs of the ventral surface of the animals’ hands were taken against a clear Perspex® sheet on occasions when animals were being handled for veterinary treatment (Fig. 1). For each individual, we identified three photographs per hand in which digits were in the optimal positions and for purposes of data reliability (Allaway *et al.* 2009), the first author carried out all measurements of 2D:4D ratios from these photographs using the software program ImageJ.

For each individual, we measured the second and fourth digits five times per photograph, giving a total of 15 measurements for each digit, and we used the mean of these 15 measurements as the measurement for that digit. We 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. We calculated the mean 2D:4D ratio (M2D:4D) by averaging the right 2D:4D ratio (R2D:4D) and left 2D:4D ratio (L2D:4D). We then took the mean of individual within species 2D:4D ratio measurements to obtain R2D:4D, L2D:4D, and M2D:4D data for each species. These species means are the 2D:4D ratio measures we used in analyses and the final data set comprised the R2D:4D, L2D:4D, and M2D:4D of 513 individual female primates across 71 species (Table II).

Anatomical Considerations

Variation in primate hand morphology is associated with substrate use (Jouffroy *et al.* 1993; Lemelin and Schmitt 1998; Richmond 2007) and so we collated substrate use



Fig. 1 Image showing an example of computer-assisted measurement of hands using ImageJ software. White 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 anesthetized male coppery titi monkey (*Callicebus cupreus*).

data for each species from the literature. 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, we used categorical classifications given by the authors of the publications (Electronic Supplementary Material [ESM] Table SI).

In humans, it has been suggested that men have lower 2D:4D ratios because they have longer digits than women (Kratovichil and Flegr 2009; Lolli *et al.* 2017; *cf.* 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 (Galis *et al.* 2010; Manning and Fink 2018), 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, we collected mean adult female body mass (in grams) data for each species and controlled for this variable in all analyses (Table II; ESM Table SII).

Diet and Group Size

To test predictions related to frugivory, we collated data from the literature on the percentage of fruit in each species' diet (Table II; ESM Table SIII). 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. We 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. Equivalent methods are those based on

Table II Data set with female right, left and mean 2D:4D with standard deviation (SD) for each primate species, substrate use, mean female body mass (g), mean percentage (%) of fruit in diet, mean group size, female rate of agonism (per hour of observation time), female directional consistency index (DCI), and intersexual dominance patterns

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

Table II (continued)

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

Table II (continued)

Species ^a	N ^b	Right 2D:4D	SD	Left 2D:4D	SD	Mean 2D:4D	SD	Substrate use ^c	Body mass (g)	% Fruit ^{d,e}	Group size	Rate of agonism	DCI	Intersexual dominance ^f
<i>Colobus guereza</i>	2	0.808	0.022	0.766	0.048	0.787	0.035	A	9200	20.8	9.0	xxx	xxx	M
<i>Colobus polykomos</i>	1	0.864	—	0.726	—	0.795	—	A	8300	36.0	13.6	0.600	0.746	M
<i>Macaca fascicularis</i>	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
<i>Macaca fasciata</i>	11	0.815	0.027	0.851	0.036	0.833	0.019	A/T	8030	51.4	45.5	1.020	X	M
<i>Macaca mulatta</i>	80	0.804	0.055	0.831	0.053	0.817	0.044	A/T	5370	8.5	40.8	xxx	xxx	M
<i>Macaca nemestrina</i>	3	0.805	0.033	0.859	0.033	0.832	0.013	A/T	6500	74.2	18.3	xxx	xxx	M
<i>Macaca nigra</i>	18	0.847	0.038	0.850	0.030	0.848	0.026	A/T	5470	65.4	50.0	X	X	M
<i>Macaca silenus</i>	19	0.822	0.029	0.842	0.034	0.832	0.022	A	6100	78.1	21.0	xxx	xxx	M
<i>Macaca sylvanus</i>	11	0.821	0.031	0.832	0.037	0.826	0.029	T	5500	32.0	18.3	xxx	X	M
<i>Mandrillus leucophaeus</i>	6	0.830	0.023	0.803	0.024	0.817	0.008	A/T	12,500	58	58.0	xxx	xxx	M
<i>Mandrillus sphinx</i>	16	0.856	0.049	0.855	0.047	0.851	0.042	A/T	12,500	81	52.0	xxx	xxx	M
<i>Papio hamadryas</i>	20	0.863	0.046	0.840	0.060	0.851	0.042	T	9900	54.1	77.4 ^g	xxx	xxx	M
<i>Papio papio</i>	17	0.865	0.032	0.862	0.030	0.864	0.023	T	12,100	77	62.0 ^h	xxx	xxx	M
<i>Papio ursinus</i>	32	0.885	0.037	0.885	0.039	0.885	0.035	T	14,800	43.3	48.7	1.558	X	M
<i>Theropithecus gelada</i>	7	0.816	0.058	0.838	0.050	0.827	0.047	T	11,700	3.5	113.0 ^g	xxx	X	M
<i>Trachypithecus auratus</i>	5	0.774	0.021	0.762	0.043	0.768	0.030	A	5841	32	14.0	xxx	xxx	M
<i>Trachypithecus obscurus</i>	6	0.769	0.029	0.775	0.019	0.772	0.010	A	6260	35	17.0	xxx	xxx	M
<i>Hylobates agilis</i>	1	1.127	—	1.100	—	1.113	—	A	5820	58	4.4	xxx	xxx	CO
<i>Hylobates lar</i>	1	1.059	—	1.096	—	1.078	—	A	5340	62.7	4.0	xxx	xxx	CO
<i>Hylobates muelleri</i>	1	1.004	—	1.013	—	1.008	—	A	5350	62	3.4	xxx	xxx	CO
<i>Hylobates pileatus</i>	1	1.077	—	1.017	—	1.047	—	A	5440	71	4.1	xxx	xxx	CO
<i>Nomascus leucogenys</i>	2	0.994	0.053	1.021	0.050	1.008	0.001	A	7320	xxx	3.6	xxx	xxx	CO
<i>Symphalangus syndactylus</i>	4	1.071	0.110	1.050	0.058	1.060	0.081	A	10,700	46.7	4.0	xxx	xxx	CO

Table II (continued)

Species ^a	N ^b	Right 2D:4D	SD	Left 2D:4D	SD	Mean 2D:4D	SD	Substrate use ^c	Body mass (g)	% Fruit ^{d,e}	Group size	Rate of agonism	DCI	Intersexual dominance ^f
<i>Gorilla gorilla gorilla</i>	4	0.914	0.023	0.911	0.025	0.913	0.023	A/T	71,500	48	10.0	xxx	xxx	M
<i>Pan paniscus</i>	2	0.886	0.033	0.932	0.009	0.909	0.012	A/T	33,200	55	9.5 ⁱ	xxx	X	F
<i>Pan troglodytes</i>	14	0.887	0.038	0.921	0.036	0.904	0.027	A/T	45,800	62.5	8.3 ⁱ	0.150	X	M

All data are based on wild animals unless otherwise stated. See ESM Tables SI–SVI for the sources of these data.

^aTaxonomy from Groves (2001) with some exceptions (see ESM Table SI).

^bNumber of individuals.

^cSubstrate use: A = arboreal, A/T = arboreal/terrestrial, T = terrestrial.

^dIncludes fruit, nuts, seeds, and seed pods.

^eData presented as percentage of time spent feeding on food items or calculated from equivalent methods (see Methods section: Diet and Group Size).

^fIntersexual dominance: M = males are dominant; F = females are dominant; CO = sexes are codominant/there is no clear dominance relationship between the sexes.

^gGroup size here refers to mean band size.

^hGroup size here refers to mean 3rd level grouping size (analogous to bands).

ⁱGroup size here refers to mean party size.

^jData from captive animals.

X Data are from Koenig *et al.* (*unpubl. data*) and are withheld at the request of the providing author.

xxx Data not available.

scan sampling, where the interval between samples is short relative to the mean duration of the behavior. This method provides estimates of time spent feeding on food items (Martin and 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).

We obtained data on mean species group size (includes both sexes and all age classes) from the literature. If more than one value was available for a species (e.g., representing different populations), we took the mean of these as the mean group size value for the species as a whole. Where data described the size of mixed-species groups, we included only the number of individuals of the species in question. For some species that live in large multilevel groups, mean group size data describes smaller grouping levels, e.g., band level of social structure in *Papio hamadryas* (Table II; ESM Table SIV).

Female Social Variables

We collated data on DCI and rate of agonism from the literature. DCI describes the proportion of interactions in the more common direction in each dyad (i.e., when the outcome of an agonistic encounter is in favor of the individual in the dyad who most often wins) among females in a social group. It 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 and Wensing 1987). We also obtained data on rates of agonism per hour of observation time (rate of agonism). 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), we used the mean 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 8 species in the 2D:4D ratio data set respectively (Table II; ESM Table SV).

Mating System Variables

We collated data from various sources on mating system and mating system subcategory for each species (ESM Table SVI). Categories for mating system are 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 (ESM Table SVII; Howlett and Wheeler *unpubl. data*). 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, we 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.

Intersexual Dominance Patterns

We obtained data on intersexual dominance patterns for all 71 species in the data set from the literature (Table II; ESM Table SVIII). We categorized species as 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 that 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.

Statistical Methods

We 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 were arcsine transformed. All other variables are categorical. We 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.

2D:4D Ratio Measurement Reliability

We used the single measures values of the intraclass correlation coefficient (ICC) set to the ‘absolute agreement’ definition to test intraobserver reliability. ICC values showed that 2D:4D ratio measurements were highly repeatable for both hands (for R2D:4DICC = 0.992, $F_{512, 7168} = 1891.487$, $P < 0.001$; for L2D:4D ICC = 0.992, $F_{512, 7168} = 1774.794$, $P < 0.001$). We 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 we also used M2D:4D in subsequent analyses.

Phylogenetic Signal

We tested for phylogenetic signal 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” and *10kTrees* (version 3) phylogeny with associated taxonomy from GenBank for the phylogenetic trees (Arnold *et al.* 2010). We found statistically significant Pagel’s λ values for all variables other than percentage of fruit in diet, DCI, and rate of agonism (Table III). Since 2D:4D ratio measures had significant amounts of phylogenetic signal, the use of phylogenetically controlled methods is appropriate.

Phylogenetically Controlled Analysis

The 2D:4D ratio is a proposed proxy for PAEs, which in turn are likely modulated by the social and ecological environment. Therefore, in all analyses, we assigned 2D:4D ratio measures as the dependent variables and all other variables as the independent

Table III Phylogenetic signal results using Pagel's λ for each variable in female primates

Variable	Λ	LogL ^a	<i>P</i>	<i>N</i> ^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
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.

variables. 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, mating system, mating system subcategory, and intersexual dominance pattern), we carried out phylogenetic generalized least squares (PGLS) analysis using the package Comparative Analysis of Phylogenetics and Evolution in R (caper). We ran the analysis across a block of 200 phylogenetic trees for each variable. Molecular data were not available for five species in the *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), we added these species into the trees based on their relationships to sister taxa that were present in *10KTrees* phylogeny. *Callicebus moloch* and *Callicebus cupreus* are sister species that diverged *ca.* 3.65 mya (Byrne *et al.* 2016; Perelman *et al.* 2011). *Mico melanurus* is in the *Mico* subgenus and we included it using information on phylogeny from Garbino (2015). We included *Cercocebus chrysogaster* using *Cercocebus torquatus*, from which it diverged *ca.* 3.33 mya. We included *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 (Mittermeier *et al.* 2013; Oates *et al.* 2016). Genetic data suggest that *P. coronatus* and *P. deckenii* are the same subspecies and so we substituted *P. deckenii* for *P. coronatus* in the phylogeny (Pastorini *et al.* 2001; *cf.* Thalmann *et al.* 2002).

Ethical Note

This research was supported by the British and Irish Association of Zoos and Aquariums and all hand images were collected with the permission of the institutions involved. Our method of obtaining digit measurements through digital photographs is noninvasive and

Perpex® images were collected only opportunistically when individuals were undergoing veterinary care. The authors declare that they have no conflict of interest.

Data Availability All data used in this study are available in the Electronic Supplementary Material (Tables SI–SVIII).

Results

Anatomical Considerations

There were no significant relationships between female body mass or substrate use and any of the 2D:4D ratio measures (Table IV). 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.

Other Control Variables

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

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 VI).

Female Social Variables

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

Mating System Variables

There were significant associations between mating system and all female R2D:4D and M2D:4D but not L2D:4D (Table VIII; Fig. 3). There were also significant associations

Table IV Results of a PGLS regression testing for an effect of substrate use and female body mass on female 2D:4D ratio in primates

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

Table V Results of the PGLS regression testing for an effect of group size on mating system and mating system subcategory in female primates while controlling for substrate use and female body mass

Variables	t	P	Estimate	SE	df	Λ	Adj. r^2
Mating system and group size	3.050	<u>0.003</u>	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 subcategory and group size	3.936	<u><0.001</u>	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			

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 underlined.

between mating system subcategory and female R2D:4D and M2D:4D but not L2D:4D (Table VIII; Fig. 4).

Intersexual Dominance Relationships

There were significant relationships between all 2D:4D ratio measures and intersexual dominance pattern (Table IX). Species in which females are the dominant sex had 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 (Fig. 5).

Table VI Results of a PGLS regression testing for an effect of percentage (%) of fruit in diet and mean group size on female primate 2D:4D ratio while controlling for substrate use and female body mass

Variables	T	P	Estimate	SE	df	λ	Adj. r^2
Female R2D:4D and % 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 and % 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 and % 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 and 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 and 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 and 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			

Model variables are indicated in bold with the control variables taken into account; parameters for individual control variables are displayed below these

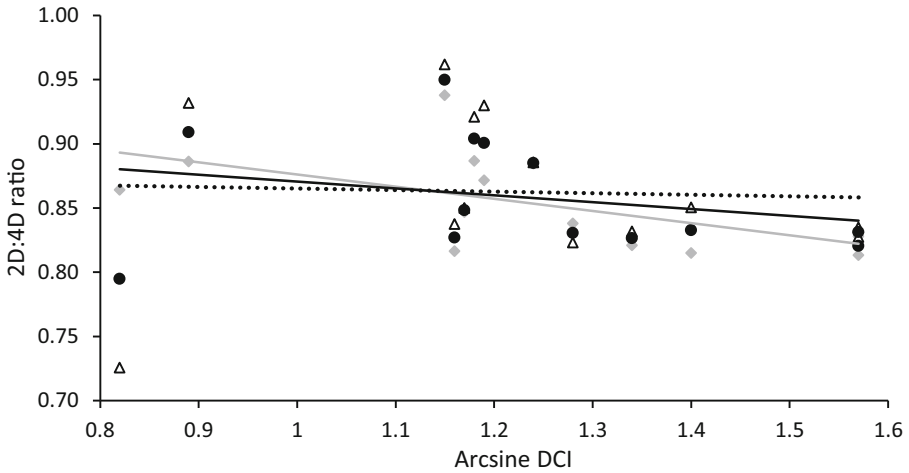


Fig. 2 Association between arcsine dominance consistency index (DCI) and female primate 2D:4D ratio measures. Right 2D:4D, gray diamonds, gray solid trendline; left 2D:4D, white triangles, black dotted trendline; mean, 2D:4D, black circles, black solid trendline.

Discussion

The support for variation in primate socioecology being underpinned by variation in PAEs was mixed. Predictions regarding the relationship between PAEs and female reproductive competition and intersexual dominance patterns were met. However, we

Table VII Results of a PGLS regression testing for an effect of female primate DCI and rate of agonism on female 2D:4D ratio while controlling for substrate use and female body mass

Variables	t	P	Estimate	SE	df	λ	Adj. r^2
Female R2:D4D and 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 and 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 and 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 and rate of agonism	1.132	0.320	6.773	5.980	4	0.000	0.544
Substrate use	3.161	<u>0.034</u>	0.774	0.244			
Body mass	-2.680	<u>0.055</u>	-0.520	0.194			
Female L2D:4D and 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 and 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			

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 underlined.

Table VIII Results of a PGLS regression testing for an effect of mating system variables on female primate 2D:4D ratio while controlling for substrate use, female body mass, and mean group size

Variables	T	P	Estimate	SE	df	λ	Adj. r^2
Female R2D:4D and mating system	-2.650	<u>0.010</u>	-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	<u>0.018</u>	0.460	0.192			
Female L2D:4D and 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	<u>0.026</u>	0.445	0.195			
Female M2D:4D and mating system	-2.436	<u>0.018</u>	-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	<u>0.023</u>	0.446	0.193			
Female R2D:4D and mating system subcategory	-2.970	<u>0.006</u>	-8.328	3.305	65	0.687	0.363
Substrate use	1.019	0.742	0.040	0.484			
Body mass	2.447	<u>0.033</u>	0.534	0.227			
Group size	4.313	<u><0.001</u>	1.448	0.343			
Female L2D:4D and 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	<u><0.001</u>	1.399	0.360			
Female M2D:4D and mating system subcategory	-2.458	<u>0.017</u>	-7.911	3.190	65	0.777	0.314
Substrate use	0.289	0.780	0.144	0.496			
Body mass	2.129	<u>0.042</u>	0.501	0.236			
Group size	3.968	<u><0.001</u>	1.399	0.351			

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 underlined.

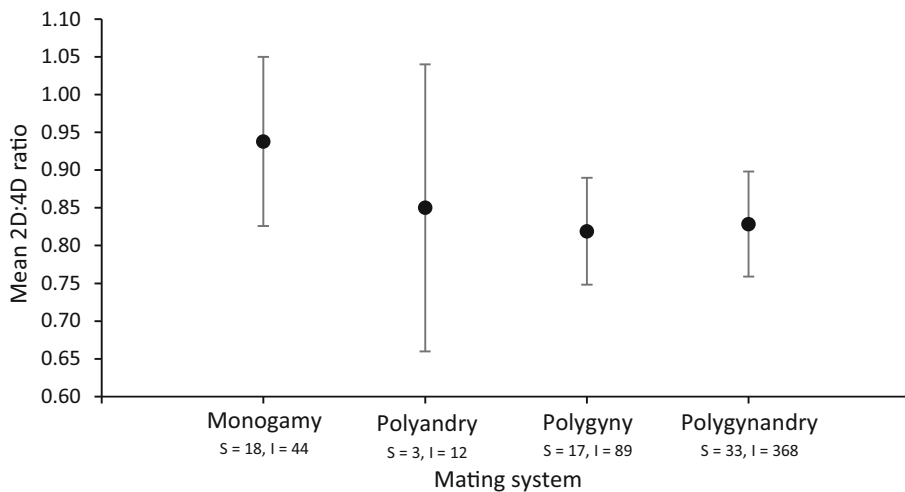


Fig. 3 Relationship between female primate mean 2D:4D (group mean \pm standard deviation) and species mating system. Number of species (S) and number of individuals (I) included in each category are given below the mating system.

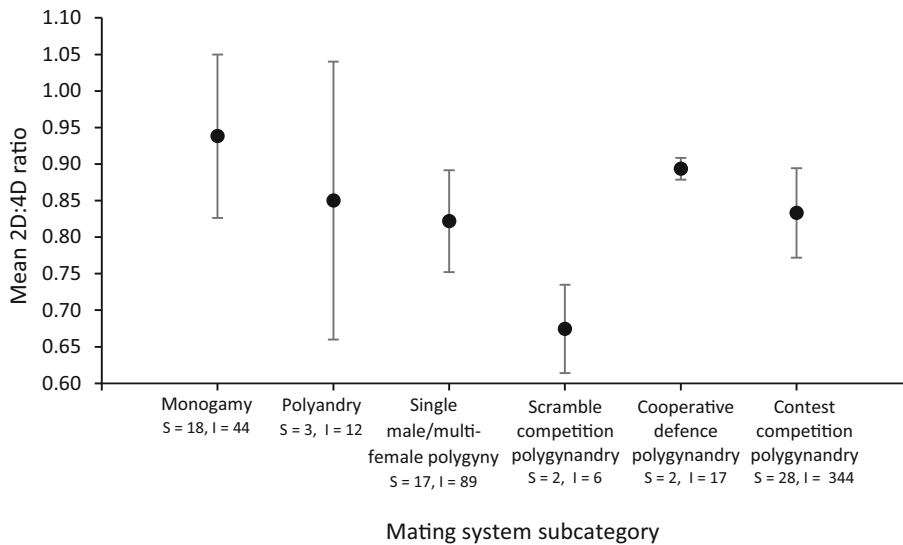


Fig. 4 Relationship between female primate mean 2D:4D ratio (group mean \pm standard deviation) and mating system subcategory. Number of species (S) and number of individuals (I) included in each category are given below the mating system subcategory.

did not find the expected relationships between PAEs and degree of frugivory, group size, or the two quantitative measures of female dominance behavior. This study demonstrates that PAEs may act as a proximate mechanism underlying variation in certain aspects of social behavior in female nonhuman primates but may not be associated with the (potential) effects of diet and group size on social structure. Alternatively, these two factors that 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.

As predicted, monogamous females had the highest 2D:4D ratios, likely as a result of selection for many of the key behaviors underpinning monogamous relationships in primates (e.g., pair bonding and parental care) also requiring selection for reduced

Table IX Results of a PGLS regression testing for an effect of intersexual dominance relationships on female primate 2D:4D ratio while controlling for substrate use and female body mass

Variables	T	P	Estimate	SE	df	λ	Adj. r^2
Female R2D:4D and intersexual dominance	3.106	<u>0.003</u>	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 and intersexual dominance	2.619	<u>0.011</u>	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 and intersexual dominance	3.025	<u>0.004</u>	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			

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 underlined.

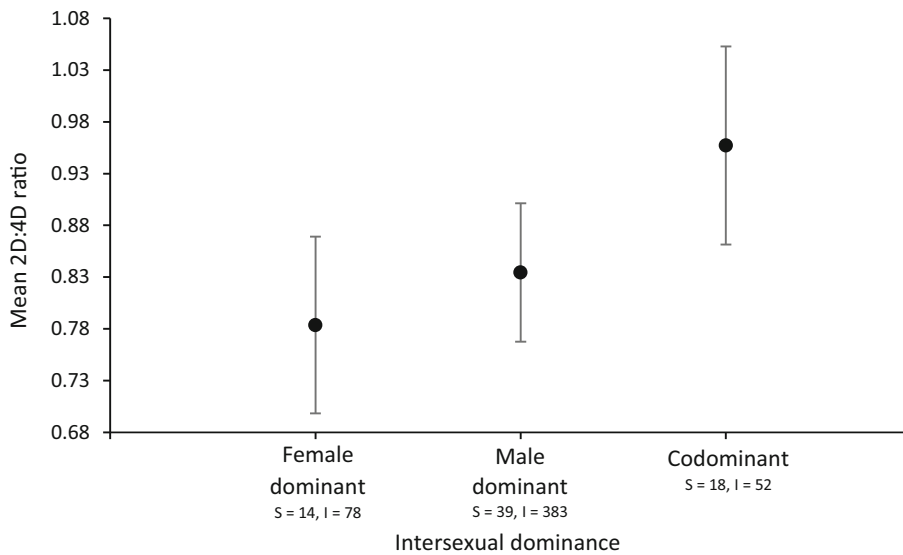


Fig. 5 Association between intersexual dominance patterns and female primate mean 2D:4D (group mean \pm standard deviation). Number of species (S) and number of individuals (I) included in each category are given below the intersexual dominance pattern.

PAEs and/or increased POEs (French *et al.* 2018). Polyandrous females had lower 2D:4D ratios than monogamous females but higher 2D:4D ratios than females characterized by polygyny or polygynandry. Females of species characterized 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 female primates but the pattern may stem from differences in female relationships between the subcategories of the mating systems, if indeed these social differences place differential selective pressures in terms of PAEs. Females characterized 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 characterized by this mating system are needed before any conclusions can be made as to the relationship between PAEs and this mating system. Female 2D:4D ratios in species characterized by single male/multifemale polygyny and contest competition polygynandry were similar, with single male/multifemale polygyny 2D:4D ratios being very slightly lower. This is perhaps unsurprising, as group formation in species characterized 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 characterized by cooperative defence polygynandry. There is evidence that the formation of platonic social bonds is associated with OT in adult primates (Zeigler and Crockford 2017). The species characterized by cooperative defence polygyny in this study (*Pan troglodytes* and *Alouatta caraya*) are likely to experience increased selection for cooperative and affiliative behaviors (moderated by estrogen and its associated neuropeptides) and increased POEs/reduced PAEs, 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.

There was a significant relationship between female 2D:4D ratios and intersexual dominance patterns. Female 2D:4D ratios were lower in species characterized by female dominance than those characterized by both male dominance and codominance. The low 2D:4D ratios in species characterized by female dominance may be due to selection for higher PAEs that could result in the behavioral masculinization necessary for dominating males in these species (Dunham 2008). The results lend support to prenatal sex hormones acting as a proximate mechanism underlying the evolution of female dominance in nonhuman primates (Petty and Drea 2015). Codominant species have the highest 2D:4D ratios (lower PAEs) 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 characterized by monogamy or polyandry (Carpenter 1940; Kinzey 1981; Koba *et al.* 2012).

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

Contrary to our prediction, females with a higher percentage of fruit in their diet did not have lower 2D:4D ratios. The hypothesized greater contestability of fruit relative to other food types led to the suggestion that feeding competition should be greatest among highly frugivorous species and lowest among highly folivorous species (Clutton-Brock and Janson 2012; Snaith and Chapman 2007), which has been corroborated by some studies (Janson and Goldsmith 1995; Steenbeek and van Schaik 2001), but not others. For example, intragroup contest competition was not elevated by increased feeding on fruits in *Macaca 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 that can be patchily distributed and therefore contestable (Koenig *et al.* 1998; Yeager and Kool 2000). 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 seasonal high-quality, contestable foods (Wikberg *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 and Inglett 1989), and

territory (Schülke and Kappeler 2003) and competition between females may occur in reference to these rather than just food. Although these findings were not significant in the Order-wide analysis, the relationship between PAEs and variables relating to competition for food may be apparent between individual females at the species level via the positive impact that PAEs have on an individual's competitive abilities and dominance rank (Hönekopp *et al.* 2006; Howlett *et al.* 2012). For example, in certain conditions, female primates with lower 2D:4D ratios (high PAEs) may be better able to outcompete intragroup rivals with higher 2D:4D ratios (lower PAEs) due to the behavioral predispositions brought about by high PAEs. This is supported by the link between dominance rank and resource acquisition in female primates including olive baboons (*Papio anubis*: Barton and Whiten 1993) and sooty mangabeys (*Cercocebus torquatus atys*: Range and Noë 2002).

Females of species characterized by larger group sizes did not have lower 2D:4D ratios than females of species that live in smaller groups. This is somewhat surprising as females living in larger groups have a greater number of intragroup competitors and an increased likelihood of experiencing contest competition (Koenig and Borries 2006) that 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 intergroup competition in smaller primate groups, for example over territory in pair-living and solitary species, also generates selection for higher levels of PAEs, particularly in species where females are actively involved in territory defence (Anzenberger 1992; Raemaekers and Raemaekers 1985). Additionally, there is likely to be substantial selection for cooperative and affiliative behaviors to facilitate the coexistence of primates in large groups and this is likely to moderate selection for higher PAEs (French *et al.* 2018). Further, depending on relationships between females, larger group sizes could result in increased intragroup scramble competition and, unlike direct contest competition, scramble competition is not likely to result in increased selection for behaviors associated with higher PAEs (e.g., dominance), although there is evidence to suggest that intragroup contest competition also increases with increasing group size (Koenig and Borries 2006; Wheeler *et al.* 2013). This, 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 PAEs.

The hormones underlying competitive and cooperative behaviors are largely conserved across all mammals (Soares *et al.* 2010; Trumble *et al.* 2015) and PAEs may act as a proximate mechanism underlying the expression of certain aspects of behavior in female primates in ways that are adaptive to their social system. The results stress that, to fully understand the relationship between PAEs and competition in female nonhuman primates, it is necessary to consider reproductive competition and intersexual dominance relationships alongside ecological factors and female sociality. The predictions of this study are based on the assumption that the 2D:4D ratio is a negative correlate of PAEs across primate species, such that lower 2D:4D ratios indicate higher PAEs and higher 2D:4D ratios indicate lower PAEs. However, because some studies have observed species in which males have on average higher 2D:4D ratios (lower inferred PAEs) than females (Baxter *et al.* 2018; Roney *et al.* 2004) this suggests that the pattern may not be universal across the Order and in some species for example, higher 2D:4D ratios may indicate higher PAEs. Such reversals in the pattern would bias

against our predictions, and this, and not a lack of PAEs, may explain nonsignificant results. However, the fact that tests based on the broader categories of mating systems and intersexual dominance patterns were significant suggests that the expected trend of lower 2D:4D ratios reflecting higher PAEs likely holds across most species in the data set. Additional research into species specific patterns in 2D:4D ratio with consistent, reliable, and comparable measurement methods is needed to investigate this further.

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Author contributions CH conceived and designed the study, conducted fieldwork, analyzed the data, and wrote the manuscript. BCW contributed to the conception and design of the study and provided editorial advice.

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