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ORIGINAL ARTICLE

Socio-sexual behaviors and fecal hormone metabolites but not age predict female aggressive interactions in *Macaca arctoides*

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Abstract

The role of androgens, age, and rank position in the regulation of intrasexual competition and aggression in primate males has been widely addressed but understudied in females. We studied whether fecal testosterone (fTm) and estradiol (fEm) metabolites, dominance rank, age, and male-to-female sexual behavior (a proxy for female sexual attractiveness) are predictors of aggression in eight focal females of stump-tailed macaques (*Macaca arctoides*). We analyzed the following aggressive interactions: focal female to female, focal female to male, and male to focal female aggression. We collected fecal samples of the eight adult focal females over a 1-year period along with observational sampling of aggressive and sexual behaviors. We measured hormone metabolites using a validated methanol extraction technique and ^{125}I radioimmunoassay kits. Our results showed that factors positively associated with increased female-to-female aggression were fEm levels, whereas female-to-male aggression was negatively associated with fTm levels and positively related with dominance rank. Social rank increased with age, but age did not affect any recorded aggressive behaviors. Male-to-female aggression was predicted by sexual behaviors but not by female hormonal levels. Further studies are needed to explore the role of age in female antagonistic interactions.

Significance statement

Proximate mechanisms (e.g., hormonal mechanisms) behind sexual selection processes (i.e., intrasexual competition and intersexual selection) are widely reported in the literature. However, studies on these mechanisms in primate females remain scarce. It is possible that steroid hormones and their metabolites in conjunction with individual attributes such as rank position and age may be involved in regulating socio-sexual behaviors in primate females. Using a validated methanol extraction method, we demonstrated that dynamics of fecal estradiol and fecal testosterone metabolites are associated with selective aggression against males or females as well as with sexual behaviors received from males. Moreover, we showed that the oldest females held the highest rank positions, probably facilitating social and sexual resources acquisition. The inclusion of steroid hormones and rank position may help to explain potential differences in both mate choice and mate competition between males and females of *Macaca arctoides*.

Keywords Aggression · Estradiol · Testosterone · Dominance · Females · *Macaca arctoides*

Introduction

In 1871, Darwin developed the sexual selection theory (Darwin 1871), an evolutionary process that accounts for the presence of elaborate weapons and ornaments found in males, and less commonly, in females. He suggested that these weapons and ornaments are not related to the survival of the individual but are the result of intrasexual competition and intersexual selection processes, either for breeding opportunities or to attract potential mates (see Clutton-Brock

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2007 for a review). Since the publication of Darwin's sexual selection theory, several lines of research have described physiological and behavioral traits that are associated with intrasexual competition and intersexual selection processes in nature (e.g., Trivers 1972, 1988; Hillgarth et al. 1997; Dixson and Anderson, 2002).

For example, in primates, aggressive behavior plays a key role in both intrasexual competition and intersexual selection processes, increasing self-protection, resource acquisition (e.g., food, sexual partners, territories), and in building social relationships such as dominance-subordination interactions (Bernstein and Gordon 1974; Drews 1993; Higley 2003). Aggression also represents one of the multiple options to set socio-sexual conflicts, sometimes promoting rather than disrupting social cohesion (Harcourt and de Waal 1992). Besides behavioral studies, many lines of research have focused on the study of the endocrine mechanisms underlying aggressive interactions, particularly the role of steroid hormones such as testosterone (T) and its metabolites (Hillgarth et al. 1997; Sinervo et al. 2000; Enbody et al. 2018). For instance, the "challenge hypothesis" proposes that male T levels increase before intrasexual competition for mating with receptive females (Wingfield et al. 1990). In primates, this hypothesis applies depending on the seasonal patterns of the species. For example, in seasonally breeding primates, an elevation of T levels prepares the organism for succeeding in agonistic interactions during the limited mating season, contributing to maintenance of metabolic function and muscle strength (Wingfield 1994). In the case of a poorly defined breeding season, T levels could rise in response to the presence of receptive females (e.g., Muller and Wrangham 2004; Higham et al. 2013). It has also been reported that dominant primate males undergo a rise in T levels, mostly during unstable situations to defend their position in the hierarchy (Sapolsky and Ray 1989). Although a number of studies have examined this endocrine-behavior relationship in primate males (Cavigelli and Pereira 2000; Muller and Wrangham 2004; Girard-Buttoz et al. 2009), its study in females remains scarce (e.g., von Engelhardt et al. 2000; Beehner et al. 2005; Rosvall 2013a).

In primates, female-to-female aggression occurs in different contexts such as competing for space use, during feeding contests, competing for sexual or social benefits (e.g., grooming partners, mating with high-quality males), in defense of their offspring or a close associate, and when defending their rank position (Hinde and Stevenson-Hinde 1976; Bernstein and Ehardt 1985; Cords 2000; Silk et al. 2010; Beisner and Isbell 2011; Miller et al. 2014). Females can also be aggressive toward males in a variety of social situations, for example, when strange males try to enter the group (Packer and Pusey 1979), or in response to coercive sexual behaviors. When sexual coercion occurs, females could reject aggressively any attempt of copulation with a male, if this situation represents future punishment from higher-ranked males or when females are not receptive (de Waal 1989; Muller et al. 2007). However, the function of high T levels in facilitating aggressive and sexual behaviors in primate females has not been comprehensively explored.

Androgens and estrogens—mainly estradiol (E)—are necessary for the correct functioning of female's reproductive physiology and play a major role in sexual and social behaviors of most mammalian females (Jones et al. 2017). E regulates sexual receptivity whereas T affects sexual desire, mood, normal metabolic function, and well-being (Goldstein et al. 2004). Therefore, some lines of evidence suggest that the well-known male T-mediated mechanisms on aggressive and sexual behaviors may apply to females as well (von Engelhardt et al. 2000; Beehner et al. 2005; Rosvall 2013a). For instance, ring-tailed lemur females display an elevation of fecal androgens (including T) during the mating season, similar to that exhibited during social conflicts (von Engelhardt et al. 2000). Beehner et al. (2005) showed seasonal and reproductive variations in fecal T metabolite levels as well as a positive correlation between T and aggression in females of hybrid baboons. Even though androgens are important for female sexual function, the secretion of high concentrations of T can be costly in terms of health and survival, being a risk factor for cardiovascular, menstrual, and immune impairments (Alberts et al. 1992; Tan and Teoh 2013). Hence, female primate agonistic behavior has also been related to high E levels (although the first evidence comes from ovariectomized models with variable results). For example, in pair-housing conditions female rhesus monkeys (*Macaca mulatta*) increased the frequency of threatening-away behavior toward males after the administration of E (Zumpe and Michael 1970). Contrastingly, unreceptive ovariectomized females of greater galago (*Galago crassicaudatus crassicaudatus*) showed high aggression toward males, reversing the situation after E administration (Dixson 1978). More recently, Ross and French (2011) exposed female marmosets to unfamiliar intruders and found that the high frequency of aggression in resident females was associated with a rapid increase in E levels, measured in urine samples, whereas the received aggression was associated with an increase in T levels after 24 h after the encounter. Reding et al. (2012) showed that E administration in rhesus females attenuated aggression, whereas increased male affiliation and sexual behaviors, but only in the highest- and middle-ranking females. Accordingly, the authors suggested that the effects exerted by E levels on female socio-sexual behaviors could be context-dependent or a side effect of the increased sexual attractiveness promoted by the hormonal replacement (Reding et al. 2012). Contrastingly, Walker et al. (1983) described changes in aggressive behaviors across the menstrual cycle associated with changes in dominance rank, but without any direct correlation with serum concentrations of E or T in intact female rhesus monkeys under colony housing conditions.

Another variable that could explain these previous discrepancies in the influence of hormones on female sociosexual behaviors, besides social rank, is age. For example, it has been suggested that males may prefer older females of high parity since younger females of lower parity are found to have lower reproductive success than older females (Anderson 1986). This can also be explained by the relatively late age at first reproduction in females (Jones 2011), or by the lower behavioral experience observed in young females (e.g., in *M. mulatta*, Mas-Rivera and Bercovitch 2008). In contrast to males, in most Macaca species the oldest females, within kin groups, tend to maintain the higher rank positions, at least until they are reproductive (Chapais 2004; see also Cords 2012). In species such as Langurs (Presbytis entellus) rank progressively decrease with reproductive senescence (Borries et al. 1991). In some other species, late onset of senescence in females relative to males is found in traits such as the rank and body condition (Altmann et al. 2010). Regarding hormones, in some primates, male androgen levels increase with age until a peak, after which androgen levels decrease during old age (i.e., senescence) (Beehner et al. 2009). This maximum occurs around 6–9 years, depending on the species, and represents a potential opportunity to compete for mating opportunities (Beehner et al. 2009). In general, the extent to which factors such as age, social rank, and steroid hormones affect some patterns of agonistic interactions among primate females has not been well investigated.

In the present study, we explored the influence of sexual behavior, age, rank, and fecal hormone metabolites on aggressive interactions in stump-tailed macaque females (*Macaca arctoides*) (hereinafter *M. arctoides*) belonging to a captive colony in Mexico City, Mexico. Specifically, we analyzed the following aggressive interactions in eight adult stump-tailed females (hereinafter focal females): focal female-to-female, focal female-to-male, and male-to-focal female, to explore their associations with fecal testosterone (fTm) and fecal estradiol metabolites (fEm), age, dominance rank, and male-to-female sexual behavior (a proxy for female sexual attractiveness). Stump-tailed macaques are nonseasonally breeders and live in highly cohesive multimale-multifemale social groups (Fooden 1990). They form linear dominance hierarchies in both free-ranging (Richter et al. 2009; de la O-Rodríguez et al. 2013) and captive conditions (Nieuwenhuijsen et al. 1987; López-Vergara et al. 1989). In addition, some literature has shown an increased frequency of male sexual behaviors, along with male-to-male agonistic encounters around mid-cycle of females (Shively et al. 1982; Murray et al. 1985), or an increase in coercive behavior after males were exposed to follicular and periovulatory vaginal scents (Cerda-Molina et al. 2006).

Due to the lack of mating seasonality and to the abovementioned costly androgen effects on health and reproduction, we might hypothesize that fEm levels will be positively associated with female-to-female aggressive behavior. Since the well-known E role in inducing female attractiveness and the T role in sexual desire (Dixson 1998), we might also expect a positive relationship between focal female hormone levels, age, and male-to-female sexual behaviors. Regarding focal female to male aggression, we expected a negative relationship with both, fTm and fEm levels, since the lowest levels of steroid hormones are associated with non-sexually receptive days leading to a high frequency of female aggression against males. Sexual conflict can arise from attractive females with high hormonal levels rejecting some males, who in response can harass such females in order to force mating opportunities (i.e., sexual coercion). Then, we hypothesize a positive relationship between focal female hormone levels and male-to-female aggression.

Methods

Subjects and housing conditions

Our sample included eight adult stump-tailed macaque females (Table 1). These monkeys are part of a primate colony consisting of 28 individuals, at the time of the study, none of them infants (17 females, 11 males), located at the Department of Ethology at the Instituto Nacional de Psiquiatría "Ramón de la Fuente Muñiz," in Mexico City, Mexico. The monkeys live in four large trapezoidal outdoor facilities (6.2 m length × 1.7 m minor side × 6 m major side × 6 m height each) connected to each other and are exposed to ambient conditions (i.e., temperature, humidity, and photoperiod). The space has eight platforms (1.5 m deep × 6 m long), some chains, a swing, and kindergarten playground

Table 1 Age (years), dominance rank (based on normalized David scores), and female reproductive history of stumptail macaques at the Instituto Nacional de Psiquiatría "Ramón de la Fuente Muñiz," in Mexico City

Females	Age	NormDS/ordinal rank	Reproductive history
JA	26	14.23 (1)	Multiparous
SO	15	13.25 (2)	Multiparous
AU	24	12.19 (3)	Multiparous
CL	12	10.79 (4)	Primiparous
KT	11	9.66 (5)	Primiparous
EL	14	8.88 (6)	Multiparous
MU	16	7.92 (7)	Nulliparous
RI	21	7.58 (8)	Multiparous

Linearity h' 0.56, $p < 0.001$, *NormDS* normalized David scores objects such as a slide and a running wheel. The outdoor facilities are cleaned daily from 08:00 to 09:00 h; afterward, animals are fed with fresh fruit, vegetables, and processed monkey food (Lab Diet 5038, PMI Feeds, Inc., St Louis, MO, USA). Water is available ad libitum.

Behavior and dominance hierarchy

Data were collected between February 2012 and January 2013, from Monday to Friday. August was not included because the daily intense rainy days prevented the proper collection of samples. A research assistant conducted two daily sessions of animal focal sampling (Martin and Bateson 1993), from 11:00 to 12:30 h and 15:00 to 16:30 h., simultaneously, ad libitum data on agonistic and sexual interactions (only male-to-female) were also collected. Agonistic interactions included both aggressive (stare, open mouth, grab, slap, push, pull, mock bite, bite, lunge, pretend slap, chase) and submissive (avoiding, flee, crouch, teeth chatter, silent bared teeth, and hip presentation when preceded by aggression) behaviors (Bertrand 1969; Santillán-Doherty et al. 1991). Male-to-female sexual behavior included genital inspection (visual, olfactory, and tactile) and copulation. For each interaction, the identity of both actors involved was scored as well as their behavior. In this study, it was not possible to record data blind because our study involved focal animals.

Fecal sample collection and hormone quantification

We collected 794 fecal samples (mean ± SD = 99.25 ± 15.01, range 78–114 samples per individual) within the first hour after defecation to avoid contamination with urine (visibly wet feces). Samples were placed in 15-mL polypropylene tubes, labeled according to the date, hour, and monkey ID, and then stored at − 20 °C. The next day after collection, we dried the samples in a Thermo Scientific Savant Vacuum Concentrator (Thermo Scientific, USA) at 50 °C (around 6–8 h) and froze them (− 20 °C) for approximately 6 months until assayed. We employed the methanol extraction method proposed by Khan et al. (2002) and slightly modified by Pineda-Galindo et al. (2017).

In brief, we mixed 0.5 g of dried, pulverized, and sieved feces with 5 ml of 100% methanol; shook the tubes in a vortex for 3 min; and left them for 24 h in a vertical shaker. The next day, we centrifuged the samples (1500 × *g* for 30 min at 4 °C) and recovered the supernatants in glass tubes (10 ml). We added 1 ml of methanol to the remaining fecal pellets, centrifuged them again, and mixed both supernatants. We evaporated the samples to dryness in a water bath (around 20–35 min) and reconstituted in 1 ml of phosphate buffer 0.01 M, pH 7 (diluted with absolute ethanol 2:1 and Tween 20, 0.02%). We measured fTm and fEm by using commercially available radioimmunoassay kits (^{125}I RIA Estradiol Kit ESTR-CTRIA, Cisbio Bioassays France, and ^{125}I RIA Testosterone Kit Coat-A-Count, Siemens, Munich, Germany). As per kit instructions, we added 100 µl of the extracts to each antibody-coated tube and then 1 ml of radiolabeled ^{125}I hormone and vortex-mixed the samples. After that, we incubated the samples in a water bath at 37 °C for 1 h. We aspirated the remaining tracer until dry by using vacuum aspiration and radioactivity associated to hormone sample was counted in a gamma counter (Wizard 2470 Automatic Gamma Counter, Perkin Elmer). We ran all the fecal samples in duplicate and calculated concentrations from a logit-log regression slope. Concentrations were corrected for this extraction to report concentrations as nanograms per gram (ng/g) of dry fecal matter (multiplying by the dilution factor). fEm samples were diluted 1:30 and fTm 1:40. The measurement of fTm for *M. arctoides* has been previously validated (Pineda-Galindo et al. 2017). For fEm, we performed the analytical validation that we reported as Supplementary Material.

Data analyses

Hierarchy

We calculated normalized David scores (NormDS) for females (de Vries et al. 2006; see Table 1) and the corrected Landau Index *h′* of linearity accounting for the number of unknown relationships (de Vries 1995, 1998). Here, more dominant animals hold higher NormDS values, while Landau Index *h′* informs on the predictability of dominance relationships among individuals (de la O-Rodríguez et al. 2013). We built a dominance matrix including the frequency of directed aggressions and the submissions received between each pair of females as won encounters. Dominance ranks were calculated based on all the year data. We calculated the hierarchy using the “compete” libraries designed by Curley (2016) for R package 0.1, computed in R 3.5.1 (R Development Core Team 2018).

Female aggressive interactions

Following other authors’ data analysis approach (e.g., Girard-Buttoz et al. 2009; Ostner et al. 2011; Onyango et al. 2013) and trying to make our results comparable, we calculated monthly means of each female’s fecal hormones along with monthly means of aggression rates (aggression per h, given and received) and male sexual behaviors directed to focal females, constructing a database of $n = 88$. We performed a Spearman correlation between age and NormDS of the eight females, as well as a paired *t*-test to compare the mean frequency of aggressions emitted to other females and males. We built three linear mixed models (LMM), one for each behavioral interactions: (1) female-to-female aggression = focal female aggression directed to all females in the group, (2) female-to-male aggression = focal female aggression directed to males, and (3) male-to-female aggression = focal female aggression received by males. All the independent variables were continuous and introduced as covariates: fEm and fTm levels (log-transformed values to reach a normal distribution), NormDS, sexual behavior (i.e., copulations and the frequency of male genital inspections towards focal females), and age (in years). We performed two additional LMM, one to search whether fTm is associated with rank and age, and a second one to search whether sexual behaviors are associated with fEm and fTm levels. For all LMM models, we included female's ID as random variable; month was entered as the repeated variable and selected the auto-regressive correlation structure due to the repetitive nature of the data (monthly means of the same subjects). Because of the low frequency of contact aggression displayed by females, contact and non-contact aggressive behaviors were combined into a single category. All the analyses were performed in SPSS version 21; all tests were two-tailed, and we set the alpha level at 0.05.

Results

Despite the small sample size of females, a moderate positive correlation was found between age and NormDS (Spearman correlation: $r = 0.49$, $n = 8$, $p < 0.001$) indicating that rank position increases with age. Focal females directed significantly more aggression to other females (mean ± SD = 1.48 ± 1.67, range 0–12.50) than to males (0.80 ± 0.74, range 0–3.57; $t = -3.18$, $df = 87$, $p = 0.002$).

Female-to-female aggression

As can be seen on Table 2, the only significant predictor of female-to-female aggression was fEm levels (Est. = 0.450, error = 0.166, $t = 2.703$, $df = 1$, 78.748, $p = 0.008$). Aggression from focal females towards other females increased with fEm levels (see Fig. 1).

Female-to-male aggression

Results of the LMM indicated that NormDS and fTm levels predicted female-to-male aggression (NormDS: Est. = 0.666,

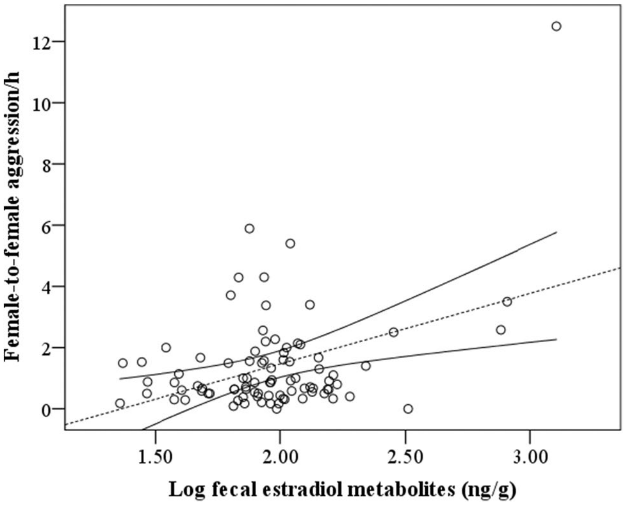

Fig. 1 Positive correlation between the rates of aggression per hour of eight focal females directed to other females and fecal estradiol metabolites (ng/g). Dashed line indicates the model-predicted line; solid lines indicate 95% CI from the mean

Table 2 Summary of mixed model results from regressing age, rank, fecal hormone metabolites, and male sexual behavior on female aggression. Focal females were the actors

Factor	Est	Error	*F*	*t*	*df* Num	*df* Denom	Sig
Model 1. Female-to-female aggression							
Intercept	−0.663	0.456	2.11	−1.45	1	14.865	0.167
Age	−0.004	0.015	0.094	−0.307	1	5.489	0.770
NormDS	0.005	0.036	0.019	0.137	1	14.516	0.893
SexBehav	0.009	0.019	0.261	−0.511	1	69.941	0.611
fEm	0.450	0.166	7.306	2.703	1	78.748	**0.008**
fTm	−0.137	0.123	1.247	−1.117	1	76.249	0.268
Model 2. Female-to-male aggression							
Intercept	3.447	0.728	0.045	0.211	1	18.001	0.835
Age	−0.211	0.104	4.080	−2.020	1	6.426	0.087
NormDS	0.666	0.266	6.228	2.496	1	13.739	**0.026**
SexBehav	−0.026	0.206	0.016	−0.127	1	78.737	0.900
fEm	−0.449	1.468	0.094	−0.306	1	67.137	0.760
fTm	−2.410	1.100	4.797	−2.190	1	61.338	**0.032**

NormDS normalized David score, *SexBehav* sexual behavior received from males, *fTm* fecal testosterone metabolites, *fEm* fecal estradiol metabolites error = 0.266, $t = 2.496$, $df = 1$, 13.739, $p = 0.026$; fTm: Est. = − 2.420, Error = 1.100, t =—2.190, $df = 1$, 61.338, $p = 0.032$; see Table 2). As expected, higher-ranking females directed more aggression to males (Fig. 2A). Contrastingly, the association between fTm and aggression toward males was negative (Fig. 2B); when fTm levels were high, aggression against males was low. Since this result is coincident with the observation that the oldest females are also the most dominant, we performed a separate LMM to search for an association between fTm and both, age, and rank. However, we did not find a significant effect of age or rank on fTm (Est. = − 0.021, error = 0.018, $t = -1.150$, df = 1, 6.483, $p = 0.291$; Est. = 0.012, error = 0.040, $t = 0.310$, $df = 1$, 18.52, $p = 0.760$, respectively; see Table 3).

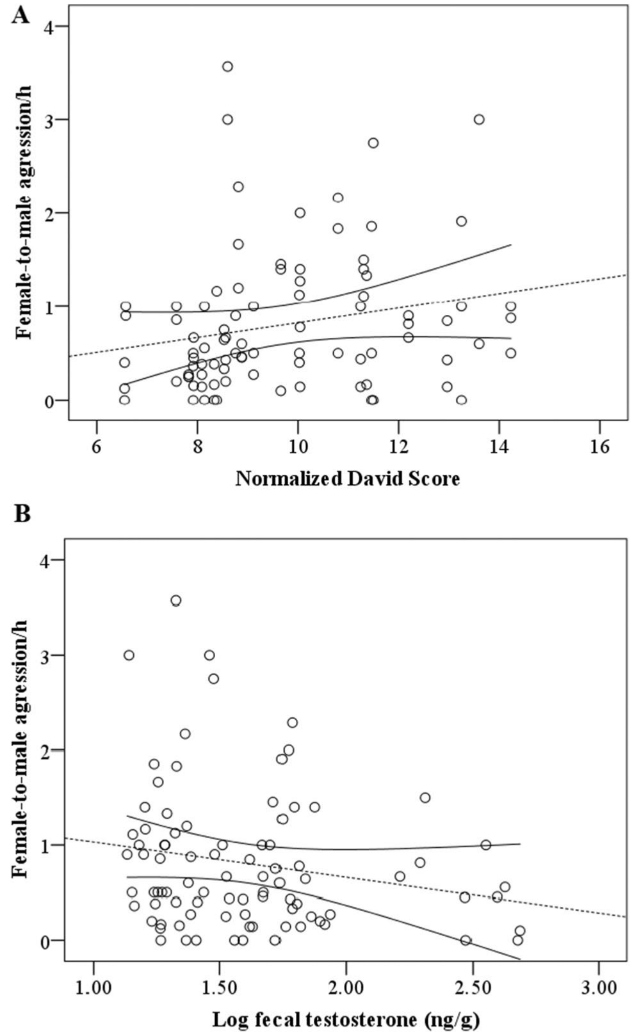

Fig. 2 A Positive correlation between rates of aggression per hour of eight focal females directed to males and the normalized David score. B Negative correlation between rates of aggression per hour of eight focal females directed to males and female fecal testosterone metabolites (ng/g). Dashed line indicates the model-predicted line; solid lines indicate 95% CI from the mean

Male-to-female aggression and sexual behavior

Male sexual behavior directed to females (i.e., genital inspection and copulation) was the only significant predictor of male-to-female aggression (Est. = 0.081, error = 0.021, $df = 1$, 73.733, $t = 3.464$ $p < 0.001$; see Table 4). Figure 3 A illustrates that male aggression directed to females was positively related to sexual behaviors. We performed a separate LMM to test whether sexual behaviors (as dependent variable) are associated with fEm or fTm levels, as indirect evidence of female attractiveness. The analyses indicated that fTm was negatively associated with sexual behavior (Est. = − 1.596, error = 0.585, $t = -2.725$, $df = 1$, 63.70, $p = 0.008$, Fig. 3B) but fEm was not (Est. = 0.900, Error = 0.795, $t = 1.133$, df = 1, 69.400, $p = 0.261$; Table 3).

Discussion

In this research, we studied female aggressive behavior in relation to hormonal levels, individual attributes such as age and dominance rank, as well as sexual behaviors in a captive colony of stump-tailed macaques. As we expected, female fEm levels were associated with an increase of aggression toward other females in the group—i.e., focal

Table 3 Summary of mixed model results from regressing (1) rank and age on fecal testosterone metabolites of females and (2) fecal hormone metabolites on sexual behavior received from males

Factor	Est	Error	*F*	*t*	*df* Num	*df* Denom	Sig
Fecal testosterone metabolites							
Intercept	1.898	0.404	22.039	4.695	1	8.488	0.001
Age	− 0.021	0.018	1.322	− 1.150	1	6.483	0.291
NormDS	0.012	0.040	0.096	0.310	1	18.52	0.760
Sexual behaviors							
Intercept	2.374	1.639	2.097	1.448	1	58.032	0.153
fTm	− 1.596	0.585	7.428	− 2.725	1	63.705	**0.008**
fEm	0.901	0.795	1.284	1.133	1	69.400	0.153

NormDS normalized David score, *fTm* fecal testosterone metabolites, *fEm* fecal estradiol metabolites

Table 4 Summary of mixed model results from regressing age, rank, fecal hormone metabolites, and sexual behavior on female received aggression from males. Focal females were the receptors

Factor	Est	Error	*F*	*t*	*df* Num	*df* Denom	Sig
Model 3. Male-to-female aggression							
Intercept	−0.703	0.494	2.022	−1.422	1	15.384	0.175
Age	−0.007	0.016	0.204	−0.452	1	6.023	0.667
NormDS	0.045	0.039	1.321	1.149	1	14.128	0.270
SexBehav	0.081	0.021	14.600	3.464	1	73.733	**0.000**
fEm	−0.183	0.176	1.073	−1.036	1	75.772	0.304
fTm	0.165	0.143	1.335	1.156	1	73.444	0.252

NormDS normalized David score, *SexBehav* sexual behavior received from males, *fTm* fecal testosterone metabolites, *fEm* fecal estradiol metabolites

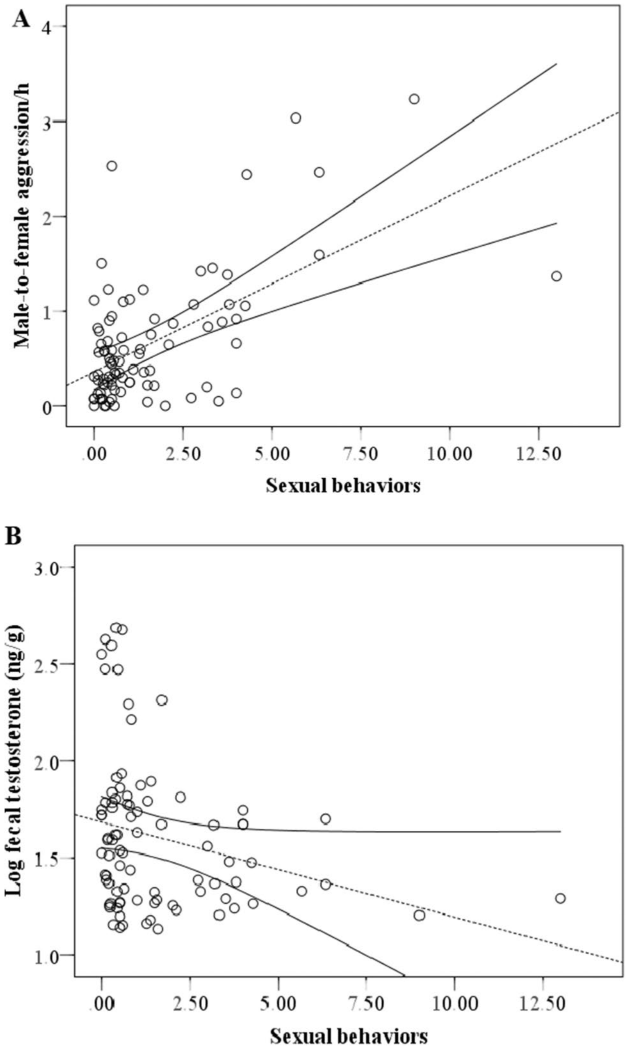

Fig. 3 **A** Positive correlation between sexual behaviors and the rate of male aggression per hour toward females. **B** Negative correlation between sexual behaviors and fecal testosterone metabolites (ng/g). Dashed line indicates the model-predicted line; solid lines indicate 95% CI from the mean

female to female aggression model—suggesting an active role of fEm in intrasexual competition processes in female *M. arctoides.* These results are similar to those reported by Ross and French (2011) in female marmosets (*Callithrix kuhlii*) where increases in E levels and aggressive behavior towards unfamiliar intruders were found. The fact that fEm levels, but not fTm (as it happens in males according to the challenge hypothesis), were associated with female-to-female aggressive behaviors suggests that selection could favor mechanisms that (i) minimize the cost of increases in T levels (e.g., menstrual or immune impairments) and (ii) increase the sensitivity of T effects on the expression of aggression, at least among females (Rosvall 2013b). Alternatively, the role of T in aggressive behavior of females might be indirect, being an important precursor of E synthesis, not only in the ovary, but also in certain peripheral tissues (Tan and Teoh 2013). On the other hand, literature has shown that aggression among females could be driven by intersexual selection processes such as sexual activity and mating partners, in contrast to their needs for food or care of infants (Huchard and Cowlishaw 2011). Then, the association found in this study between higher levels of fEm and aggression toward other females could be a consequence of female-female competition and mate choice, where receptive and attractive females try to keep others away from the reproductive opportunities (Stockley and Campbell 2013).

Furthermore, high E levels might confer some advantage under strong intrasexual competition, as expected when adult sex ratio is female-biased. In fact, theoretical models on the evolution of sex roles predict low intrasexual competition among females in male-biased societies (Kappeler 2017). In our studied group, adult sex ratio is female-biased. Although we do not have direct evidence, we suggest that female-to-female aggression might be mediated by variations in fEm levels consistent with menstrual fluctuations, which may represent a response to enhance reproductive competition (Huchard and Cowlishaw 2011; Stockley and

Campbell 2013). Female intrasexual competition for mates has been reported in some primate species living in multimale groups. For instance, female *Pan paniscus*, who interrupt mating attempts of others, tend to be around their midcycle, and such interferences are associated with increasing mating rates (Hohmann and Fruth 2003). Unfortunately, we did not find a correlation between fEm levels and male-to-female sexual behaviors. However, this lack of association could be due to the limitation of having a small sample size of females and monthly means of fecal samples.

Contrary to our expectations, fTm were negatively related with female aggression toward males. Research on hormonal fluctuations in primates has shown that maximum levels of E and T are characteristic of the mid-cycle (e.g., Dixson 1998). In contrast, minimum levels of both hormones are coincident with early follicular and pre-menstrual phases just when females might refuse any sexual activity (Nadler et al. 1985; Bielert 1986). Thus, we might suggest that females with low fTm levels could have been less receptive and consequently turned more aggressive toward males, i.e., refusing any sexual interaction. Forced copulations occur when males try to mate with reluctant or non-receptive females, and even subordinate males might try to copulate with these females as the only chance to increase their opportunities of fathering offspring. This situation increases agonistic conflicts with females (Smuts and Smuts 1993). In fact, we also found an association between social rank and female aggression toward males. This result was expected because literature has shown that especially the highest-ranked females could direct more aggression toward males, despite their physical disadvantages in strength, size, or age, without retaliation (Smuts and Smuts 1993). Among primates, it is well known that females in the top-ranking position consistently win in intrasexual competition processes, largely due to the kin support they have received (Bernstein and Gordon 1974; Chapais 2004). Then, dominant females—contrary to subordinates—could even attack or threaten a male without incurring in high physical costs, which could also be associated with mating selectivity (Bernstein and Gordon 1974). Females have the chance to increase their rank when they give birth, and in some species, the oldest females compete intensely to reach better positions than the younger (e.g., hanuman langurs, Borries et al. 1991). The fact that rank increases with age, in the present study, can support this explanation. This result agrees with the literature, showing that, in some primate species, old and dominant females may achieve access to better quality resources than subordinates such as food, high-quality mates, and male protection (van Noordwijk and van Schaik, 1987; Murray et al. 2006). It has been previously reported that aggressive interactions in *M. arctoides* are affected by factors such as age, kinship, and dominance rank, being the highest-ranking subjects the most aggressive towards the lowest-ranking subjects (de Waal and Luttrel 1989; Santillán-Doherty et al. 1991). In some cases, kinship intensifies aggressive interactions, for example, higher-ranking females were significantly more aggressive toward lower-ranking kin females, but in contrast, higher-ranking females were more aggressive toward lower-ranking males, irrespective of the kinship (Santillán-Doherty et al. 1991).

Regarding the negative association between fTm and aggression directed to males, it is contrary to that reported by other authors; for example, Beehner et al. (2005) found a positive relationship between female aggressive behavior and fTm levels. Nevertheless, Beehner's research did not indicate the receptor of the aggressive interaction, and they included pregnant females, which had the highest fTm levels. The finding that sexual behavior received from males was the most important predictor of male-to-female aggression could also be indicative of sexual coercion which is well documented in stump-tailed macaques. For example, de Waal (1989) described that stump-tailed males could harass females with a mixture of sexual and aggressive behaviors, that might occur during tension in the group, or when the male's rank position is at stake. Unexpectedly, we did not find an association between fEm levels, and sexual behaviors that support a receptive condition in females, but the fact that fTm levels showed a negative association with sexual behavior could explain a decrease in female sexual desire leading to male coercion.

Contrary to our expectations, age was not an important predictor for the aggressive interactions in our sample of stump-tailed females, even though it was an important factor to be associated with other social behaviors displayed for the establishment of group hierarchies. We might suggest that other factors could influence female aggression such as kinship or unstable social conditions where dominance rank is being threatened.

Overall, our results show the importance of including rank, E and T levels when studying aggressive behaviors in female stump-tailed macaques. Contrary to what has been described in males, fEm is more relevant than fTm on the expression of aggression among females. Further studies need to explore the aging role in the social dynamics of the primate groups as well as the physiological variables and behavioral traits associated with sexual selection processes.

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Data Availability All data generated or analyzed during this study are included in this published article [and its supplementary information files].

Code availability Not applicable.

Declarations

Ethics approval This study was completely non-invasive; the present study was approved by the Institutional Ethical Committee and by the Biosecurity Committee of the Instituto Nacional de Psiquiatría "Ramón de la Fuente Muñiz." This study also followed the National Official Norm of Technical Specifications for the Production, The Guide for the Care and Use of Laboratory Animals Eighth Edition, and the Ethical Standards of the Animal Behavior Society.

Conflict of interest The authors declare no competing interests.

References

Alberts SC, Sapolsky RM, Altmann J (1992) Behavioral, endocrine, and immunological correlates of immigration by an aggressive male into a natural primate group. Horm Behav 26:167–178. https://doi.org/10.1016/0018-506X(92)90040-3

Altmann J, Gesquiere L, Galbany J, Onyango PO, Alberts SC (2010) Life history context of reproductive aging in a wild primate model. Ann NY Acad Sci 1204:127–138. https://doi.org/10.1111/j.1749-6632.2010.05531.x

Anderson CM (1986) Female age: Male preference and reproductive success in primates. Int J Primatol 7:305–326. https://doi.org/10.1007/BF02736394

Beehner JC, Gesquiere L, Seyfarth RM, Cheney DL, Alberts SC, Altmann J (2009) Testosterone related to age and life-history stages in male baboons and geladas. Horm Behav 56:472–480. https://doi.org/10.1016/j.yhbeh.2009.08.005

Beehner JC, Phillips-Conroy JE, Whitten PL (2005) Female testosterone, dominance rank, and aggression in an Ethiopian population of hybrid baboons. Am J Primatol 61:101–119. https://doi.org/10.1002/ajp.20172

Beisner BA, Isbell LA (2011) Factors affecting aggression among females in captive groups of rhesus macaques (*Macaca mulatta*). Am J Primatol 73:1152–1159. https://doi.org/10.1002/ajp.20982

Bernstein IS, Ehardt CL (1985) Agonistic aiding: kinship, rank, age, and sex influences. Am J Primatol 8:37–52. https://doi.org/10.1002/ajp.1350080105

Bernstein IS, Gordon TP (1974) The function of aggression in primate societies: uncontrolled aggression may threaten human survival, but aggression may be vital to the establishment and regulation of primate societies and sociality. Am Sci 62:304–311

Bertrand M (1969) The behavioral repertoire of the stumptail macaque: a descriptive and comparative study. S. Karger, Basel

Bielert C (1986) Sexual interactions between captive adult male and female chacma baboons *(Papio ursinus)* as related to the female's menstrual cycle. J Zool 209:521–536. https://doi.org/10.1111/j.1469-7998.1986.tb03608.x

Borries C, Sommer V, Srivastava A (1991) Dominance, age, and reproductive success in free-ranging female Hanuman langurs (*Presbytis entellus*). Int J Primatol 12:231–257. https://doi.org/10.1007/BF02547586

Cavigelli SA, Pereira ME (2000) Mating season aggression and fecal testosterone levels in male ring-tailed lemurs (*Lemur catta*). Horm Behav 37:246–255. https://doi.org/10.1006/hbeh.2000.1585

Cerda-Molina AL, Hernández-López L, Rojas-Maya S, Murcia-Mejía C, Mondragón-Ceballos R (2006) Male-induced sociosexual behavior by vaginal secretions in *Macaca arctoides*. Int J Primatol 27:791–807. https://doi.org/10.1007/s10764-006-9045-0

Chapais B (2004) How kinship generates dominance structures: a comparative perspective. In: Thierry B, Singh M, Kaumanns W (eds) Macaque societies: A Model for the Study of Social Organization. Cambridge University Press, Cambridge, UK, pp 186–203

Clutton-Brock T (2007) Sexual selection in males and females. Science 318:1882–1885. https://doi.org/10.1126/science.1133311

Cords M (2000) Agonistic and affiliative relationships in a blue monkey group. In: Whitehead PF, Jolly CJ (eds) Old World Monkeys. Cambridge University Press, Cambridge, pp 453–479

Cords M (2012) The behavior, ecology, and social evolution of cercopithecine monkeys. In: Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB (eds) The evolution of primate societies. University of Chicago Press, Chicago, pp 91–112. https://doi.org/10.7208/9780226531731-008

Curley JP (2016) Compete: organizing and analyzing social dominance hierarchy data. R package version 0.1, https://www.r-pkg.org/pkg/compete

Darwin C (1871) The descent of man and selection in relation to sex. The Modern Library, New York

de la O-Rodríguez C, Mevis L, Richter C, Malaivijitnond S, Ostner J, Schülke O (2013) Reconciliation in male stump-tailed macaques (*Macaca arctoides*): intolerant males care for their social relationships. Ethology 119:39–51. https://doi.org/10.1111/eth.12034

de Vries H (1995) An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Anim Behav 50:1375–1389. https://doi.org/10.1016/0003-3472(95)80053-0

de Vries H (1998) Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Anim Behav 55:857–843. https://doi.org/10.1006/anbe.1997.0708

de Vries H, Stevens J, Vervaecke H (2006) Measuring and testing the steepness of dominance hierarchies. Anim Behav 71:585–592. https://doi.org/10.1016/j.anbehav.2005.05.015

de Waal FBM (1989) Pacemaking among primates. Harvard University Press, Cambridge, MA

de Waal FBM, Luttrel LM (1989) Toward a comparative socioecology of the genus: Different dominance styles in rhesus and stumptail monkeys. Am J Primatol 19:83–109. https://doi.org/10.1002/ajp.1350190203

Dixson AF (1978) Effects of ovariectomy and estradiol replacement therapy upon the sexual and aggressive behavior of the greater galago (*Galago crassicaudatus crassicaudatus*). Horm Behav 10:61–70. https://doi.org/10.1016/0018-506X(78)90025-9

Dixson AF (1998) Primate sexuality. comparative studies of the prosimians, monkeys, apes, and human beings. Oxford University Press, Oxford

Dixson AF, Anderson MJ (2002) Sexual selection, seminal coagulation and copulatory plug formation in primates. Folia Primatol 73:63–69. https://doi.org/10.1159/000064784

Drews C (1993) The concept and definition of dominance in animal behaviour. Behaviour 125:283–313. https://doi.org/10.1163/156853993X00290

Enbody ED, Boersma J, Schwabl H, Karubian J (2018) Female ornamentation is associated with elevated aggression and testosterone in a tropical songbird. Behav Ecol 29:1056–1066. https://doi.org/10.1093/beheco/ary079

Fooden J (1990) The bear macaque, *Macaca arctoides*: a systematic review. J Hum Evol 19:607–686. https://doi.org/10.1016/0047-2484(90)90002-S

Girard-Buttoz C, Heistermann M, Krummel S, Engelhardt A (2009) Seasonal and social influences on fecal androgen and glucocorticoid excretion in wild male long-tailed macaques (*Macaca fascicularis*). Physiol Behav 98:168–175. https://doi.org/10.1016/j.physbeh.2009.05.005

Goldstein I, Traish A, Kim N, Munarriz R (2004) The role of sex steroid hormones in female sexual function and dysfunction. Clin Obstet Gynecol 47:471–484. https://doi.org/10.1097/00003081-200406000-00022

Harcourt AH, de Waal FBM (1992) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford

Higham JP, Heistermann M, Maestripieri D (2013) The endocrinology of male rhesus macaque social and reproductive status: a test of the challenge and social stress hypotheses. Behav Ecol Sociobiol 67:19–30. https://doi.org/10.1007/s00265-012-1420-6

Higley JD (2003) Aggression. In: Maestripieri D (ed) Primate psychology. Harvard University Press, Cambridge, MA, pp 17–40

Hillgarth N, Ramenosfsky M, Wingfield J (1997) Testosterone and sexual selection. Behav Ecol 8:108–109

Hinde RA, Stevenson-Hinde J (1976) Towards understanding relationships: dynamic stability. In: Bateson PPG, Hinde RA (eds) Growing Points in Ethology. Cambridge University Press, Oxford, England, pp 451–479

Hohmann G, Fruth B (2003) Intra- and inter-sexual aggression by bonobos in the context of mating.Behaviour 1389–1413https://doi.org/10.1163/156853903771980648

Huchard E, Cowlishaw G (2011) Female–female aggression around mating: an extra cost of sociality in a multimale primate society. Behav Ecol 22:1003–1011. https://doi.org/10.1093/beheco/arr083

Jones JH (2011) Primates and the evolution of long, slow life histories. Curr Biol 21:R708–R717. https://doi.org/10.1016/j.cub.2011.08.025

Jones SL, Ismail N, Pfaus JG (2017) Facilitation of sexual behavior in ovariectomized rats by estradiol and testosterone: a preclinical model of androgen effects on female sexual desire. Psychoneuroendocrinology 79:122–133. https://doi.org/10.1016/j.psyneuen.2017.02.018

Kappeler PM (2017) Sex roles and adult sex ratios: insights from mammalian biology and consequences for primate behaviour. Phil Trans R Soc B 372:20160321. https://doi.org/10.1098/rstb.2016.0321

Khan MZ, Altmann J, Isani SS, Yu J (2002) A matter of time: evaluating the storage of fecal samples for steroid analysis. Gen Comp Endocrinol 128:57–64. https://doi.org/10.1016/S0016-6480(02)00063-1

López-Vergara L, Santillan-Doherty AM, Mayagoitia L, Mondragon-Ceballos R (1989) Self and social grooming in stump-tailed macaques: effects of kin presence or absence within the group. Behav Process 18:99–106. https://doi.org/10.1016/S0376-6357(89)80008-7

Martin P, Bateson P (1993) Measuring Behaviour. Cambridge University Press, Cambridge, UK

Mas-Rivera A, Bercovitch FB (2008) Postpartum recuperation in primiparous rhesus macaques and development of their infants. Am J Primatol 70:1047–1054. https://doi.org/10.1002/ajp.20596

Miller JA, Pusey AE, Gilby IC, Schroepfer-Walker K, Markham AC, Murray CM (2014) Competing for space: female chimpanzees are more aggressive inside than outside their core areas. Anim Behav 87:147–152. https://doi.org/10.1016/j.anbehav.2013.10.023

Muller MN, Kahlenberg SM, Emery Thompson M, Wrangham RW (2007) Male coercion and the costs of promiscuous mating for female chimpanzees. Proc R Soc Lond B 274:1009–1014. https://doi.org/10.1098/rspb.2006.0206

Muller MN, Wrangham RW (2004) Dominance, aggression and testosterone in wild chimpanzees: a test of the 'challenge' hypothesis. Anim Behav 67:113–123. https://doi.org/10.1016/j.anbehav.2003.03.013

Murray CM, Eberly LE, Pusey AE (2006) Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). Behav Ecol 17:1020–1028. https://doi.org/10.1093/beheco/arl042

Murray D, Bour E, Smith O (1985) Female menstrual cyclicity and sexual behavior in stumptail macaques (*Macaca arctoides*). Int J Primatol 6:101–113. https://doi.org/10.1007/BF02693698

Nadler RD, Graham CE, Gosselin RE, Collins DC (1985) Serum levels of gonadotropins and gonadal steroids, including testosterone, during the menstrual cycle of the chimpanzee (*Pan troglodytes*). Am J Primatol 9:273–284. https://doi.org/10.1002/ajp.1350090404

Nieuwenhuijsen K, de Neef KJ, van der Werff ten Bosch JJ, Slob AK (1987) Testosterone, testis size, seasonality, and behavior in group-living stumptail macaques (*Macaca arctoides*). Horm Behav 21:153–169. https://doi.org/10.1016/0018-506X(87)90041-9

Ostner J, Heistermann M, Schülke O (2011) Male competition and its hormonal correlates in Assamese macaques (*Macaca assamensis*). Horm Behav 59:105–113. https://doi.org/10.1016/j.yhbeh.2010.10.017

Onyango PO, Gesquiere LR, Altmann J, Alberts SC (2013) Testosterone positively associated with both male mating effort and paternal behavior in savanna baboons (*Papio cynocephalus*). Horm Behav 63:430–436. https://doi.org/10.1016/j.yhbeh.2012.11.014

Packer C, Pusey AE (1979) Female aggression and male membership in troops of Japanese macaques and olive baboons. Folia Primatol 31:212–218. https://doi.org/10.1159/000155884

Pineda-Galindo E, Cerda-Molina AL, Mayagoitia-Novales L, Matamoros-Trejo G (2017) Biological validations of fecal glucocorticoid, testosterone, and progesterone metabolite measurements in captive stumptail macaques (*Macaca arctoides*). Int J Primatol 38:985–1001. https://doi.org/10.1007/s10764-017-9992-7

R Development Core Team (2018). R: A language and environment for statistical computing: R Foundation for Statistical Computing, Vienna, Austria, https://cran.r-project.org/bin/windows/base/old/3.5.1/

Reding K, Michopoulos V, Wallen K, Sanchez M, Wilson ME, Toufexis D (2012) Social status modifies estradiol activation of sociosexual behavior in female rhesus monkeys. Horm Behav 62:612–620. https://doi.org/10.1016/j.yhbeh.2012.09.010

Richter C, Mevis L, Malaivijitnond S, Schülke O, Ostner J (2009) Social relationships in free-ranging male *Macaca arctoides*. Int J Primatol 30:625–642. https://doi.org/10.1007/s10764-009-9364-z

Ross CN, French JA (2011) Female marmosets' behavioral and hormonal responses to unfamiliar intruders. Am J Primatol 73:1072–1081. https://doi.org/10.1002/ajp.20975

Rosvall KA (2013a) Proximate perspectives on the evolution of female aggression: good for the gander, good for the goose? Phil Trans R Soc B 368:20130083. https://doi.org/10.1098/rstb.2013.0083

Rosvall KA (2013b) Life history trade-offs and behavioral sensitivity to testosterone: an experimental test when female aggression and maternal care co-occur. PLoS One 8:e54120. https://doi.org/10.1371/journal.pone.0054120

Santillán-Doherty AM, Díaz JL, Mondragón-Ceballos R (1991) Synergistic effects of kinship, sex and rank in the behavioural interactions of captive stump-tailed macaques. Folia Primatol 56:177–189. https://doi.org/10.1159/000156546

Sapolsky RM, Ray JC (1989) Styles of dominance and their endocrine correlates among wild olive baboons (*Papio anubis*). Am J Primatol 18:1–13. https://doi.org/10.1002/ajp.1350180102

Shively C, Clarke S, King N, Schapiro S, Mitchell G (1982) Patterns of sexual behavior in male macaques. Am J Primatol 2:373–384. https://doi.org/10.1002/ajp.1350020406

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Cheney DL (2010) Strong and consistent social bonds enhance the longevity of female baboons. Curr Biol 20:1359–1361. https://doi.org/10.1016/j.cub.2010.05.067

Sinervo B, Miles DB, Frankino WA, Klukowski M, DeNardo DF (2000) Testosterone, endurance, and Darwinian fitness: natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. Horm Behav 38:222–223. https://doi.org/10.1006/hbeh.2000.1622

Smuts BB, Smuts RW (1993) Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. Adv Stud Behav 22:1–63

Stockley P, Campbell A (2013) Female competition and aggression: interdisciplinary perspectives. Phil Trans R Soc B 368:20130073. https://doi.org/10.1098/rstb.2013.0073

Tan RS, Teoh SH (2013) Testosterone use in women: how safe is it? Curr Drug Saf 8:120–127. https://doi.org/10.2174/1574886311308020005

Trivers R (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual Selection and the Descent of Man, 1871–1971. Aldine de Gruyter, New York, pp 136–179

Trivers R (1988) Sex differences in rates of recombination and sexual selection. In: Michod RE, Levin BR (eds) The Evolution of Sex. Sinauer Press, Sunderland, MA, pp 270–286

van Noordwijk MA, van Schaik CP (1987) Competition among female long-tailed macaques, *Macaca fascicularis*. Anim Behav 35:577–589. https://doi.org/10.1016/S0003-3472(87)80284-1

von Engelhard N, Kappeler PM, Heistermann M (2000) Androgen levels and female social dominance in *Lemur catta*. Proc R Soc Lond B 267:1533–1539. https://doi.org/10.1098/rspb.2000.1175

Walker ML, Wilson ME, Gordon TP (1983) Female rhesus monkey aggression during the menstrual cycle. Anim Behav 31:1047–1054. https://doi.org/10.1016/S0003-3472(83)80011-6

Wingfield JC (1994) Control of territorial aggression in a changing environment. Psychoneuroendocrinology 19:709–721. https://doi.org/10.1016/0306-4530(94)90052-3

Wingfield JC, Hegner RE, Dufty AM, Ball GF (1990) The “challenge hypothesis”: theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. Am Nat 136:829–846. https://doi.org/10.1086/285134

Zumpe D, Michael RP (1970) Redirected aggression and gonadal hormones in captive rhesus monkeys (*Macaca mulatta*). Anim Behav 18:11–19. https://doi.org/10.1016/0003-3472(70)90063-1

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