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Jealous females? Female competition and reproductive suppression in a wild promiscuous primate

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Abstract

Female-female competition over paternal care has rarely been investigated in promiscuous mammals, where discreet forms of male care have recently been reported despite low paternity certainty. We investigated female competition over paternal care in a wild promiscuous primate, the chacma baboon (*Papio ursinus*), where pregnant and lactating females establish strong social bonds ("friendships") with males that provide care to their offspring. We tested whether pregnant and lactating females interfere with the sexual activity of their male friend to prevent new conceptions that might lead to the subsequent dilution of his paternal care. We found that pregnant and lactating females were more aggressive towards oestrous females when they had recently conceived themselves, and when the oestrous female was mate-guarded by, and showed greater sexual activity with, their male friend. This aggression also reduced the likelihood of conception of the targeted female. These findings indicate that females can aggressively prevent further conceptions with their offspring's carer through reproductive suppression. Competition over access to paternal care may play an important and underestimated role in shaping female social relationships and reproductive strategies in promiscuous mammalian societies.

Keywords: reproductive suppression, paternal care, intrasexual competition, primate, chacma baboon.

1. Introduction

Traditional evolutionary models of paternal care assume that males should only provide care to their offspring when the degree of paternity certainty is high, typically in monogamous species [1,2]. Yet recent empirical studies have indicated that male care can also evolve in promiscuous species where paternity confidence is lower, in particular when the cost of providing care is also low and does not compromise a male's future reproductive success [3,4]. For instance, males of several promiscuous primate species provide discreet forms of care to immatures, such as preferential affiliation, support during conflicts, or tolerance at feeding sites (e.g. Barbary macaques, *Macaca sylvanus*: [5]; yellow baboons, *Papio cynocephalus*: [6]; olive baboons, *P. anubis*: [7]; black-and-white snub-nosed monkeys, *Rhinopithecus bieti*: [8]). While males may provide care to unrelated infants to secure future mating opportunities with the mother [7,9], most studies indicate that males care for their genetic offspring, and assess their paternity probabilistically based on their mating history [10–12], or on their offspring's phenotypic resemblance to themselves [13].

According to evolutionary theories of parental investment [14], the more offspring a male sires the more his care will be diluted between them, potentially leading mothers to compete for exclusive access to their mates [15]. For example, in facultatively polygynous birds, females breeding with polygynous males experience lower male investment and reproductive success than those breeding with monogamous males [15–17], and females that mate first aggressively exclude secondary-mated females from breeding units in order to maintain male monogamous matings [18]. In polygynous and promiscuous species more generally, where multiple females mate with a single male that provides paternal services, females that have already conceived may similarly attempt to prevent further conceptions with their mate, and the subsequent dilution of paternal care. To do so, they may harass those females that attempt to mate with him, either to interrupt copulations directly through mating interference and/or to induce chronic physiological stress that reduces their fertility (the "reproductive suppression hypothesis" [19]).

So far, reproductive suppression has been mostly documented in cooperative breeders, where one or more dominant females use this mechanism to maximise the helper-to-pup ratio for their own offspring [20–22]. Reproductive suppression has been less well studied in groups of plural breeders where multiple females reproduce without helpers, but might similarly represent a manifestation of competition over offspring care provided by males. Mating interference and female-female harassment are commonplace in plural breeders [23], and some studies further suggest that the resulting stress can lower the reproductive success of rivals via physiological mechanisms [24]. For instance, some early studies in yellow baboons and geladas (*Theropithecus gelada*) indicate that subordinate females that are sexually receptive are regularly harassed by dominant females, and are also less fertile [25–27]. However, the determinants of female-female competition remain elusive in such studies, as well as whether the lower fertility of subordinate females is caused by harassment or by other rank-related differences between females.

Here, we tested the hypothesis that females that have already conceived attempt to prevent new conceptions with the carer of their offspring in a promiscuous primate species, the chacma baboon (*Papio ursinus*). Chacma baboons live in stable, multimale-multifemale groups and breed year-round. During pregnancy and lactation, females form a strong social relationship ('friendship') with a particular male [28,29], usually the genetic father of their offspring [11,12]. Male friends will protect females and their offspring against aggression by conspecifics [6], which occasionally leads to infanticide [28] and feticide [30], and subsequently facilitate immature access to ecological resources [31]. Male reproductive skew is high in chacma baboons [32], which means that high-ranking males are usually involved in several simultaneous friendships. Female reproductive competition over paternal care appears likely in such societies, as high ranking females aggressively displace subordinates from the proximity of their male friend [33], and aggression among lactating females peaks in periods of social instability when infanticide risk is elevated [34]. Moreover, alpha males form weaker bonds with their offspring than subordinate males [31], suggesting that each offspring indeed receives less care in the larger paternal sibships of alpha males. We test five predictions of the reproductive suppression over paternal care hypothesis, namely that pregnant and lactating females attempt to prevent oestrous females from copulating with their male friend by harassing them (prediction 1, P1), in particular when they have conceived themselves recently (P2) (given that synchronous females are expected to compete most intensely over access to male care); that the intensity of harassment correlates with the fertility (proximity of ovulation) of the oestrous female (P3) and with the intensity of her sexual activity with the male friend (P4); and that female-female aggression reduces the probability that the oestrous female conceives with the male friend (P5).

2. Material and Methods

(a) Study site and population

We studied wild chacma baboons at Tsaobis Nature Park, Namibia ($22^{o}22'$S $15^{o}44'$E) (for details of the site and population, see [35]). We collected data on two habituated groups of baboons, called ‘J’ and ‘L’, over four different periods: June-December 2005, May 2006-January 2007, June-October 2013 and May-November 2014. Group composition is given in Table S1 (electronic supplementary materials). Dominance ranks of adult males and females were established using both *ad libitum* and focal observations of dyadic agonistic interactions (electronic supplementary materials, Appendix 1).

(b) Female reproductive state & mate-guarding patterns

The reproductive state of each female was monitored on a daily basis and categorised as follows: (1) pregnant, where pregnancy was determined *post hoc* following infant birth, and encompassed the six months since the conceptive cycle; (2) lactation, if she had a dependant infant and had not yet resumed cycling, and (3) in oestrus, if she was sexually receptive with a perineal swelling. Cycling non-swollen females were excluded from the analysis. Every day, trained observers recorded the swelling state (turgescent or deturgescent) and swelling size of oestrous females using a semi-quantitative scoring system (from size 1 to 4). For each cycle, we defined the oestrous period as that time during which a swelling of any size was present, and the peri-ovulatory period (called hereafter 'POP') as that time during which ovulation generally occurs, i.e. the 5-day period preceding (and excluding) the day of swelling detumescence [36]. For each cycle, we determined if it was conceptive or not by identifying *a posteriori* if a pregnancy occurred. The date of conception of pregnant and lactating females was estimated as the day following detumescence of the conceptive cycle (when witnessed) or determined *post hoc* by counting back 6 months from the date of birth, the gestation length of baboons [37]. Mate guarding episodes, defined as periods when oestrous females are constantly followed by a male that mates exclusively with them and prevents others from doing so [38], were monitored *ad libitum* on a daily basis.

(c) Behavioural data

One-hour focal animal samples were conducted on all adult females. In total, our sample comprises 2971 focal observations on 53 females distributed across reproductive states (Table S2, electronic supplementary materials). During focal observations, we continuously recorded aggressive incidents (attacks, chases, threats) and approach-avoid interactions (supplants, displacements) (for definitions, see Appendix 1, electronic supplementary materials) involving the focal female, along with the identity of the receiver and initiator. In total, we observed 370 agonistic interactions initiated by pregnant or lactating females toward oestrous females. In 2013-14, we also recorded all occurrences of male support towards oestrous females following female aggression. In addition, we recorded every occurrence of male-female grooming bouts, sexual solicitations ('presenting', when oestrous females present their hindquarters to males) and copulations, along with the identity of the male. We also noted all approaches and leaves within 1 meter between the focal individual and any other adult female (to calculate the time spent in close proximity between female dyads during a focal observation). Finally, we conducted proximity scans every five minutes to record the identity and distance of the nearest male neighbour.

(d) Identification of heterosexual friendships

The male friend of each pregnant and lactating female was identified using a combination of spatial proximity and grooming allocation indices. Full details can be found in Appendix 2 of the electronic supplementary materials. In short, a male was considered as a friend of a given pregnant/lactating female if he was both her most frequent nearest neighbour and her most frequent grooming partner, and if he had an outstandingly high score in both indices compared to other males (i.e. if his score is at least twice as high as those of other males) [29]. Using this criterion, a female would have either one or two male friend(s) or, in the case of undifferentiated relationships with males, no friend. Overall, we identified at least one male friend for 83% of pregnant and lactating females (*N*=67 out of 81).

(e) Statistical analysis

We ran binomial generalised linear mixed-effect models (GLMMs) using the glmer function of the lme4 package [39] in R version 3.4.1 [40]. Technical details on how GLMMs were run and how the significance of variables was tested are described in Appendix 3, electronic supplementary material.

Are females more likely to exhibit aggression towards oestrous females that are mate-guarded by their male friend?

We first investigated whether pregnant and lactating females involved in a friendship direct more aggression towards oestrous females that are mate-guarded by their male friend, compared to when they are unguarded or mate-guarded by a different male (P1), and when they are in closer reproductive synchrony, compared to when they are less synchronous (P2). For each focal observation, we created a list of all possible dyadic combinations of initiators and receivers involving the focal female (e.g., for female A in an entire group including only two other females, B and C: A→B, A→C, B→A, C→A). We then restricted this dataset to dyads where receivers were in oestrous and initiators were pregnant or lactating. We created a binary variable "Aggression" which recorded whether a directional agonistic interaction occurred in those dyads during the focal observation. We ran a binomial GLMM using the occurrence of aggression received by oestrous females from pregnant/lactating females during a focal observation as the response variable. Random effects comprised the identity of the initiator and receiver, as well as the identity of the focal observation. The fixed effects comprised:

- an index of reproductive synchrony between the initiator and the receiver of the dyad (in days). This index was calculated as the absolute difference in days between the initiator’s conception date and the focal observation date, and measures the potential reproductive synchrony should the oestrous female conceive on that focal day.
- the "mate-guarding status" of the receiver, with three levels: ‘Guarded by the friend’ if the receiver was guarded by the male friend of the initiator, ‘Guarded by a different

male' if the receiver was guarded by another male, and 'Unguarded' if the receiver was not guarded by any male. Cases where the receiver was guarded by a male and the initiator had no friend were categorised as 'Guarded by a different male'.

- the interaction between the index of potential reproductive synchrony and mate-guarding status, in order to test whether potential reproductive synchrony is more important when the receiver is mating with the initiator's friend than in other cases.
- an index of spatial proximity between the initiator and the receiver of the dyad (to control for the fact that two females sharing the same male might attack each other more often just because they spend more time in proximity). This index was calculated as the time spent within 1m of each other during the focal observation (calculated using approaches and leaves within 1m).
- the relative dominance rank of the initiator and receiver (as two fixed effects).
- group identity (by including group identity as a fixed effect, we do not seek to systematically assess group effects, which would require a larger sample with targeted observations, but rather control for such effects should any be present).
- year

Are females more likely to exhibit aggression towards oestrous females that are closer to conception and copulate more frequently with their male friend?

We tested whether aggression received by an oestrous female from the female friends of a male (pregnant or lactating) increased with her probability of conception (P3), and the intensity of her sexual activity with this male (P4), using a binomial GLMM. For each focal observation of an oestrous female, we identified all possible dyads involving this female and all resident males that have at least one female friend, and calculated the response variable as the occurrence of aggression received by that oestrous female from the female friends (pregnant or lactating) of each male (yes/no). Random effects comprised the identity of the focal female, the male and the focal observation. Fixed factors comprised:

- an index of fertility measured by proximity from the peri-ovulatory period ('POP'), as a continuous measure, in days. This measure was used because the probability of ovulation increases gradually through the oestrus period until reaching a peak in the five days preceding the day of detumescence, which is easy to identify visually [36]. This index was therefore set to 0 in the 5 days preceding detumescence (i.e. the POP period), to 1 in the first day preceding the POP, to 2 in the second day preceding the POP, etc. The day of detumescence was set as 1 (i.e. coded similarly to the first day preceding the POP period).
- the rate of sexual activity of the focal female with the male considered (i.e. the number of presentings and copulations per hour).
- the mate-guarding status of the oestrous female (guarded by the male/unguarded: 1/0).
- the interaction between the rate of sexual activity and mate-guarding status, in order to test whether the effect of sexual activity is more important when the oestrous female is mate-guarded by the male friend.
- an index of spatial proximity between the focal female and female friends of a male (to control for the fact that female friends might attack an oestrous female more often because she spends more time around them). This index was calculated as the cumulative time that oestrous females spent within 1m of any female friend of a male during the focal observation.
- the relative rank of the oestrous female.
- the relative rank of the male friend.
- group identity and year.

Can females decrease the chance that their male friend conceives with an oestrous female by harassing her?

We then tested whether the probability of conception between an oestrous female and her mate-guarding male decreased when the oestrous female received higher rates of aggression from the female friends of the male throughout the oestrus period (P5). Only cycles for which we had more than four hours of observations of the oestrus period were included (mean±sd hours of observation per cycle: 16.42±16.42). For each oestrus cycle of each female, we identified the male that mate-guarded her during her POP (i.e. with whom she may conceive). For 17 out of 60 cycles, females had several mate-guarding males in her POP; in these cases we only kept cycles during which one male monopolised 4 days out of 5 of the POP (11/17 cycles) and omitted secondary mate-guarding episodes which were less likely to be conceptive. For females guarded by males who did not have any female friend, the rate of aggression was set at zero. We then ran a binomial GLMM using the probability of conception of each cycle (conceptive/not conceptive: 1/0) as the response variable. Random effects comprised the identities of the oestrous female and the male.

The fixed factors comprised:

- the rate of aggression received by the oestrous female from the female friends of the male throughout the oestrus period (calculated as the total number of aggressive interactions received by the focal female from the female friends of a male throughout her oestrus cycle, divided by the corresponding observation time).
- the rate of aggression received by the oestrous female from any other adult female of the group (calculated as the total number of aggressive interactions received by the focal female from any non-friend female of a male throughout her oestrus cycle, divided by the corresponding observation time) to control for a potential confounding

effect of female-female aggression at the group level on the chance that the focal female conceives.

- whether the cycle was the first postpartum cycle (yes/no) because females experience reduced fertility in the first cycle following lactational amenorrhea [41])
- the relative rank of the oestrous female and of the male (over the oestrus period).

3. Results

Male mating skew was high in both social groups during our study period (see Appendix 4, electronic supplementary material), and male mating success was highly correlated with male dominance rank (see Appendix 5). Moreover, resident males had 0 to 9 pregnant and lactating female friends simultaneously (Table S3), setting-up conditions that may favour female competition over access to male care.

Are females more likely to exhibit aggression towards oestrous females that are mate-guarded by their male friend?

As expected under P1, pregnant and lactating females were more likely to be aggressive towards oestrous females that were mate-guarded by their male friend (mean dyadic rate±sd: 0.07±0.35 time/h), than towards unguarded females (0.03±0.18) or females guarded by another male (0.01±0.13) (Table 1, Figure 1a), even when controlling for the fact that females sharing the same male spend more time in close proximity. Furthermore, pregnant and lactating females that had conceived more recently were more likely to be aggressive towards oestrous females (P2) (Table 1, Figure 1b), though this effect of reproductive synchrony was not greater when the oestrous female was mate-guarded by their male friend than when unguarded or guarded by another male (interaction between reproductive synchrony and male sharing status: χ^2_2=1.45, *p*=0.485).

Are females more likely to exhibit aggression towards oestrous females that are closer to conception and copulate more frequently with their male friend?

Oestrous females were more likely to receive aggression from the pregnant and lactating female friends of their sexual partner when they presented to him and copulated with him more often (P4) (Table 2, Figure 2a). This was true for both mate-guarded and unguarded females (the interaction between mate-guarding status and the rate of sexual activity was not significant: χ^2_1=2.63, *p*=0.105), and when controlling for spatial proximity between the oestrous female and the female friends of her mate. Aggression was also more likely when the male partner had more female friends, but unaffected by the fertility of the oestrous female, estimated via her proximity to ovulation (contrary to P3).

Can females decrease the chance that their male friend conceives with an oestrous female by harassing her?

Oestrous females received twice as much aggression from the female friends of their mate-guarding male in non-conceptive cycles (mean±sd amount of aggression received: 0.13±0.19, *N*=31 cycles) than in conceptive cycles (0.07±0.13 time/h, *N*=20 cycles). The probability of conception of an oestrous female thus decreased when she faced more aggression from the female friends of her mate (P5), but remained unaffected by aggression received from other female group-mates (Table 3, Figure 2d). Females were also more likely to conceive with high-ranking males. The observed association between lower aggression and a greater likelihood of conception might also arise if mate-guarding males more actively protected oestrous females during aggressive interactions with other females during conceptive cycles. However, we assessed the occurrence of male protection of oestrous females (in 2013-14), and male support was involved in only 9 of 144 aggressive incidences initiated by a pregnant or lactating female towards an oestrous female (including 6 from the mate-guarding male and 3 from other males). Moreover, only one of these cases occurred during a conceptive cycle. Males therefore rarely intervened in conflicts among females, regardless of their fertility.

4. Discussion

High rates of female aggression towards oestrous females have previously been reported in this [34,42] and other populations of cercopithecids [25–27], raising the question of whether it represents reproductive suppression. These new analyses extend these studies by showing that the aggressors include the lactating and pregnant females associated with their male mating partner (who is the likely father of, and caregiver to, their offspring). This aggression increases with the sexual activity of the mating couple, and is most likely to occur when the associated females have conceived more recently and are therefore more vulnerable to the future dilution of paternal care, especially protection from infanticidal attacks (which are most common in the first six months of an infant's life [43]). Most importantly, we found that oestrous females were less likely to conceive during those cycles when they received more aggression from the female friends of their mate-guarding male. Taken together, these patterns suggest that females who have already conceived aggressively target oestrous females who attempt to mate with their offspring's father to prevent him from conceiving again, which may lead to the loss of paternal services for their own offspring. In mammals, evidence for reproductive suppression among females primarily comes from cooperative breeders where dominant females monopolise reproduction to maximise the amount of allomaternal care received by their offspring. This study reveals a new form of reproductive suppression in a promiscuous primate society where all females breed and where males provide discreet paternal care, but the ultimate determinant seems to be essentially similar to cooperative breeders: to obtain more help to raise offspring.

Our interpretation assumes the dilution of paternal care among paternal siblings. Although this assumption is central to paternal investment theory [14], it may not hold in promiscuous primates where the cost of paternal care is presumably low, as some forms of paternal care appear essentially passive. For example, spatial proximity between lactating females and their male friend is almost exclusively maintained by the female, while the male simply appears to tolerate their presence [12,28]. However, additional studies suggest that male care may in fact be more costly than it seems. Playback experiments show that males readily respond to a distress call from a female friend by running towards her to provide social support [28] and anecdotal reports show that fathers will engage in severe fights with rivals that pose an infanticidal threat to their offspring [12]. Fights among adult male baboons may incur severe to lethal injuries, suggesting that offspring protection can be associated with life-threatening risks from a male's perspective. It is therefore plausible that males may be less willing to risk their life when they care for several dependent offspring, if only because their capacity to protect the remaining offspring will be compromised if they are injured or die when defending an infant. In line with this, subordinate males, who sire fewer offspring than dominants, also form closer bonds with their offspring [31]. That said, the paternal care dilution hypothesis has never been formally tested in promiscuous primates and certainly deserves further investigation.

The exact mechanisms linking female harassment and reproductive suppression in baboons remain unknown. Reproductive suppression could be mediated by direct mating interference, given that pregnant and lactating females attack oestrous females more frequently when they show higher levels of sexual activity. Such aggression may inhibit the sexual activity of oestrous females, particularly subordinates. However, copulations still occur at a high frequency during mate-guarding episodes, suggesting that mating interference alone is unlikely to explain the observed decline in fertility, and that physiological stress may play a critical role. High rates of aggression and elevated levels of cortisol have been found to disrupt ovulation and the secretion of sex hormones in several captive primates [24,44] and to cause implantation failure in hamsters [45]. This interpretation is also consistent with our finding that pregnant and lactating females harass oestrous females not just at the time of ovulation but throughout the oestrus cycle.

Our results suggest that paternal care may be an important determinant of female competitive relationships in promiscuous primate societies, with wider implications for our understanding of female reproductive competition across mating systems. In the case of demography, the ability of some females to suppress synchronous breeding by others may lead to a staggering of births that could help to explain why some species, like baboons, breed year-round despite living in seasonal environments [46]. Similarly, the prevalence of sexual ornaments in oestrous females from promiscuous primate species (e.g. facial colouration [47], copulatory calls [48] and exaggerated sexual swellings [49]) likely reflects the intensity of competition faced by females to be chosen by males, despite a typically male-biased sex-ratio. This study adds new evidence to the idea that these females ultimately compete over access to male care [50,51].

Ethics. Our research procedures were evaluated and approved by the Ethics Committee of the Zoological Society of London and the Ministry of Environment and Tourism (MET), Namibia, and adhered to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching. Our research was conducted under MET permit numbers 886/2005, 1039/2006, 1786/2013 and 1892/2014.

Data accessibility. Data are available through the public depository GitHub at: https://github.com/AliceBaniel/Reproductive-suppression-chacma-baboon

Author's contributions. A.B. and E.H. designed the study and collected the data. A.B. performed the analyses. All authors contributed to the drafting of the manuscript.

Competing interests. We have no competing interests.

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Table 1. Influence of reproductive synchrony and sharing of the same male partner on the probability of agonistic interactions received by oestrous females from pregnant/lactating females. Parameters and tests are based on 2366 focal observations and 276 occurrence of aggressive interactions distributed among 50 initiators and 40 receivers GLMMs control for focal observation identity, initiator and receiver identity (fitted as random factors). The confidence interval and p-value of statistically significant results are highlighted in bold. SE: Standard error. LRT: statistic of a Likelihood Ratio Test. df: degrees of freedom.

Response variable	Fixed factor	Levels	Estimate	SE	95% confidence interval	LRT	df	P-value
Probability that oestrous females receive aggression from the female friends of a male (0/1), by female-female dyad	Reproductive synchrony		-0.45	0.22	**[-0.89 ; -0.03]**	4.51	1	**0.034**
	Male-sharing status	Same male (ref: no male)	0.75	0.18	**[0.40 ; 1.10]**	38.65	2	**<0.001**
		Same male (ref: different male)	1.46	0.24	**[0.99 ; 1.94]**			
		Different male (ref: no male)	-0.70	0.20	**[-1.11 ; -0.32]**			
	Spatial proximity		0.24	0.07	**[0.08 ; 0.37]**	7.91	1	**0.005**
	Rank initiator		1.54	0.25	**[1.05 ; 2.07]**	29.63	1	**<0.001**
	Rank receiver		-1.06	0.21	**[-1.57 ; -0.69]**	25.64	1	**<0.001**
	Group[a]	L	0.57	0.27	**[0.03 ; 1.13]**	4.27	1	**0.039**
	Year[b]	2006	0.37	0.35	[-0.30 ; 1.09]	14.38	3	**0.002**
		2013	-0.70	0.42	[-1.54 ; 0.12]			
		2014	0.29	0.36	[-0.43 ; 1.00]			

[a] Reference category: J group

[b] Reference category: 2005

Table 2. Influence of the sexual activity of oestrous females with a male on the probability that they receive aggression from the pregnant/lactating females involved in a friendship with him. Parameters and tests are based on 1262 focal observations of oestrous females, distributed among 35 focal females and 27 males. We observed 1569 occurrences of sexual activity (587 copulations, 982 presentings), and 199 occurrences of aggression between oestrous females and pregnant/lactating female friends. GLMMs control for focal observation identity, focal female and male identity (fitted as random factors).The confidence interval and p-value of statistically significant results are highlighted in bold. SE: Standard error. LRT: statistic of a Likelihood Ratio Test. df: degrees of freedom.

Response variable	Fixed factor	Levels	Estimate	SE	95% confidence interval	LRT	df	P-value
Probability that oestrous females receive aggression from the female friends of a male (0/1), across male friends	Sexual activity (presentings, copulations)		0.27	0.13	**[0.00 ; 0.53]**	3.87	1	**0.049**
	Mate-guarding with the male[a]		0.71	0.27	**[0.18 ; 1.24]**	6.83	1	**0.009**
	Proximity to ovulation		0.23	0.20	[-0.16 ; 0.62]	1.35	1	0.246
	Number of female friends of male		1.32	0.24	**[0.86 ; 1.80]**	30.76	1	**<0.001**
	Spatial proximity with female friends		0.21	0.10	[-0.00 ; 0.41]	3.70	1	0.054
	Rank of focal female		-1.03	0.26	**[-1.65 ; -0.58]**	18.50	1	**<0.001**
	Rank of male		0.14	0.30	[-0.45 ; 0.74]	0.23	1	0.635
	Group[b]	L	0.73	0.47	[-0.26 ; 1.69]	2.20	1	0.138
	Year[c]	2006	0.34	0.41	[-0.45 ; 1.22]	9.04	3	**0.029**
		2013	-0.69	0.72	[-2.13 ; 0.75]			
		2014	0.70	0.58	[-0.46 ; 1.91]			

[a] Reference category: not mate-guarded by the male

[b] Reference category: J group

[c] Reference category: 2005

Table 3. Influence of aggression received by oestrous females from the female friends of a male throughout their oestrus periods on the probability of conceiving with this male subsequently. Parameters and tests are based on 51 oestrous cycles (out of which 20 were conceptive) distributed among 29 focal oestrous females and 18 males. GLMMs control for focal female and male identity (fitted as random factors). The confidence interval and p-value of statistically significant results are highlighted in bold. SE: Standard error. LRT: statistic of a Likelihood Ratio Test. df: degrees of freedom.

Response variable	Fixed factor	Estimate	SE	95% confidence interval	LRT	df	P-value
Probability of conception during a given cycle (0/1)	Aggression received from female friends during oestrus cycle[a]	-1.72	1.02	**[-4.06 ; -0.04]**	4.07	1	**0.044**
	Aggression received from other females during oestrus cycle[a]	1.01	0.82	[-0.48 ; 2.84]	1.76	1	0.185
	First postpartum cycle (yes/no)	-0.62	0.82	[-2.36 ; 0.94]	0.59	1	0.441
	Rank of focal female	-0.10	0.74	[-1.59 ; 3.12]	0.02	1	0.889
	Rank of the male	2.65	1.05	**[0.91 ; 5.68]**	10.51	1	**0.001**

[a] Aggression has been calculated as the number of aggressive interactions that the focal female received throughout her oestrus period divided by the corresponding observation time.

Figure 1: Predicted probability that oestrous females receive aggression from pregnant and lactating females, according to **(a)** their male sharing status and **(b)** their reproductive synchrony. In (a), boxplots are drawn from the distribution of the predicted probabilities, while varying the rank of actors and receivers between 0 and 1, and using the mean for other numerical values (for a reproductive synchrony of 259 days and a time in proximity of 0.21 minutes), in J troop in 2014 for categorical variables. Comparisons between the different levels of the variable “male sharing status” are denoted by "*" if statistically significant. In (b) the solid line is the model prediction, and the dotted lines represent the 95% confidence interval. The prediction line is drawn for a dyad sharing a male, that spends 0.21 minutes in proximity, where the initiator has rank 1 and receiver has rank 0.5, in J group, in 2014. The grey dots represent the raw data of whether an aggression was exchanged (1) or not (0) within the dyad, and their size is proportional to the number of occurrences in the dataset.

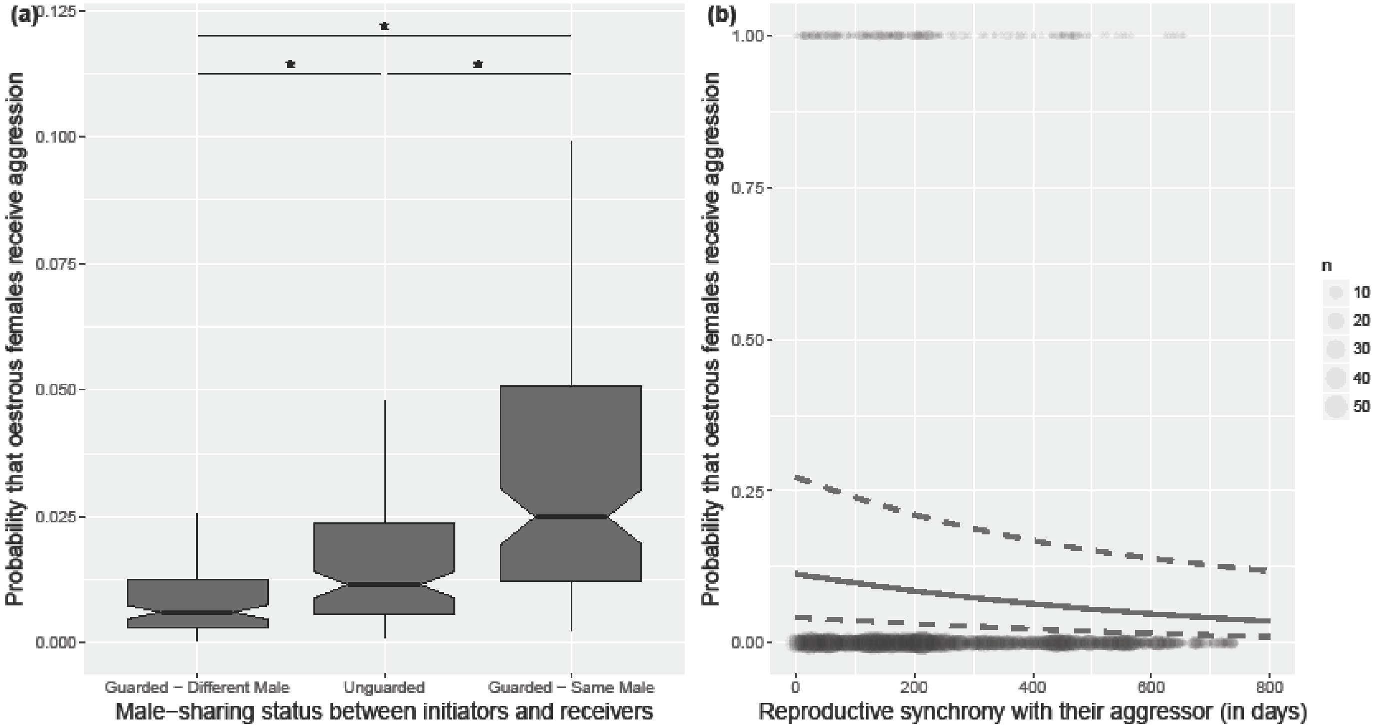
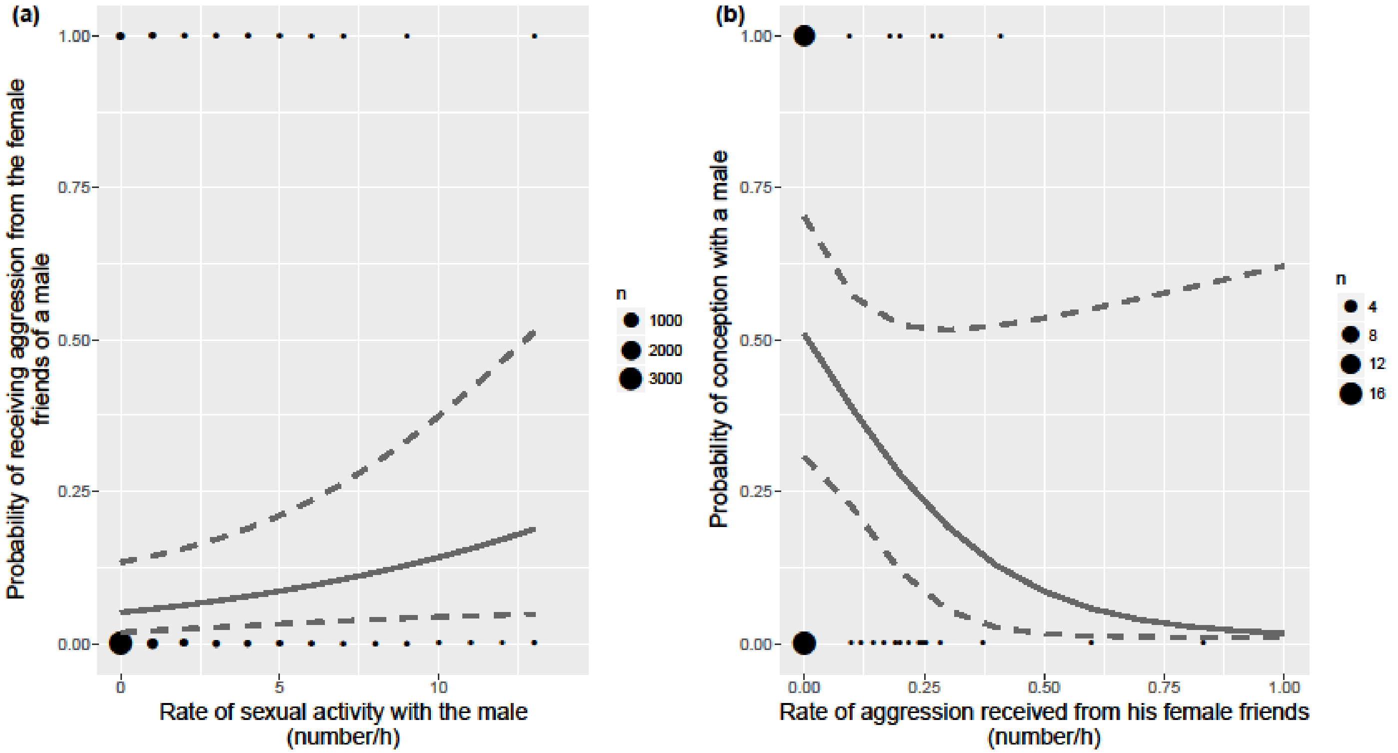


Figure 2: Predicted probability that oestrous females **(a)** receive aggression from the female friends of a male, according to their sexual activity with the male and **(b)** conceive with a male according to the rate of aggression received from the female friends during the oestrus period. Solid lines represent the model predictions and the dotted lines the 95% confidence interval. In (a) the prediction line is drawn holding all other fixed effects constant, using the mean for numeric variables (for a mate-guarded oestrous female of rank 0.53, that spends 0.37 minutes in proximity of the female friends, 7 days before the peri-ovulatory period, and a male of rank 0.67, having 2.15 female friends), in J group, in 2014 for categorical variables. In (b) the prediction line is drawn using the mean ranks for female and male (0.57, and 0.79 respectively) and the mean rate of aggression from other females (0.28 aggressive act/hour). The black dots represent the raw data: whether aggression was exchanged (1) or not (0) in (a), and whether conception occurred (1) or not (0) in (b), and their size is proportional to the number of occurrences in the dataset.



Electronic Supplementary Material Files

Table S1: Demography of J and L groups in the four study periods.

Year	Number of adult males		Number of adult females		Number of juveniles*	
	J group	L group	J group	L group	J group	L group
2005	6-9	3	17	9	26	5-9
2006	4-5	4-5	17	9-11	36	18
2013	7-10	9-11	17	18-19	29-32	31-33
2014	7-8	9	18	17-19	35	29

Demography varies due to emigrations, immigrations, births, deaths, and maturations.

*Subadult males (i.e. between 4 and 8 years old) are counted as juveniles in this study.

Table S2. Sample size of behavioural observations. One-hour focal observations were conducted on all adult females and spread equally across the day (divided into four 3h-time blocks) for each individual. We included only focal observations that lasted at least 45 minutes (mean focal length±standard deviation [sd]: 59.7±3.5 min). The choice of a focal individual was semi-randomised, in order to balance observations equally across individuals, time blocks and reproductive states. The same individual was not sampled more than once per half day to ensure independence between focal observations. In total, our sample comprises 2971 focal observations on 53 females across the following reproductive states.

Reproductive state of focal female	Sample size of focal observations
Lactating	884 observations, 45 females, mean±sd per individual: 19.6±10.5, range: 1–45
Pregnant	714 observations, 47 females, mean±sd per individual: 15.2±9.7, range: 1–46
Oestrous (unguarded)	882 observations, 39 females, mean±sd per individual: 22.6±21.5, range: 1-81
Oestrous (mate-guarded)	491 observations, 32 females, mean±sd per individual: 15.3±14.5, range: 1-53

Table S3. Number of pregnant and lactating females, oestrous females and of female friends per adult male, in J and L groups in the four study periods.

Year	Mean±SD daily number of pregnant and lactating females (range)		Mean±SD daily number of oestrous females (range)		Mean±SD daily number of female friends per male (range)*	
	J group	L group	J group	L group	J group	L group
2005	12.1±2.1 (2-14)	7.3±0.9 (2-8)	1.1±1.2 (0-4)	0.4±0.6 (0-2)	0.9±1.3 (0-5)	3.1±1.7 (0-5)
2006	12.3±3.5 (1-15)	5.8±2.1 (1-8)	1.1±1.4 (0-6)	1.6±1.5 (0-5)	2.5±2.8 (0-9)	1.0±1.0 (0-3)
2013	14.2± 0.7 (13-15)	10.1±0.6 (9-11)	0.9±0.7 (0-3)	2.9±2.1 (0-7)	1.1±1.8 (0-7)	0.7±0.8 (0-3)
2014	13.4±0.9 (11-15)	11.2±1.8 (8-14)	2.6±1.5 (0-5)	3.0±1.6 (0-6)	1.8±1.3 (0-5)	1.2±1.1 (0-4)

* we calculated the daily number of female friends (pregnant and lactating) for each resident male and averaged it over the time period. This mean daily number of friends per male was then averaged across all males of the period.

Appendix 1. Dominance ranks of males and females

Individual dominance ranks were assessed through focal and *ad libitum* observations of approach-avoid interactions (*supplants,* when one animal actively displaces another to take its place; *displacements,* when one animal passes close to another and makes it move away) and agonistic interactions (*attacks,* any agonistic physical contacts including hits, bites, or grabbing movements; *chases,* when one animal chases another for a distance of at least 3 m; and *threats*, including staring, head bobbing, and ground sweeping while oriented toward the targeted individual). Female dominance hierarchies were calculated separately in each year using Matman 1.1.4 (Noldus Information Technology 2003) and were always linear (N_{2005} = 412 interactions, N_{2006} = 576, N_{2013} = 367, N_{2014} = 1259 in group L; N_{2005} = 184, N_{2006} = 460, N_{2013} = 590, N_{2014} = 978 in group J, Landau's linearity index h: $p< 0.05$ in all cases). In the analyses, we used relative female rank to control for variation in group size, where absolute ranks were standardised to vary between 0-1 using the formula: $1-((1-r)/(1-n))$, where r is the absolute rank of an individual (ranging from 1 to the group size, n). In contrast to females, the male hierarchies were much less stable within a year [1], so male ranks were established using an Elo-rating procedure implemented in the R package EloRating (version 0.43) [2]. Compared to matrices of dyadic interactions where ranks are calculated over a given time period, an Elo-rating procedure continuously updates rankings according to the temporal sequence of interactions, and is better adapted to situations of unstable social dominance [2,3]. This gives a score for each individual on each day of observation. We derived a daily standardised rank by scaling the Elo-rating score of each individual proportionally between 0 (corresponding to the minimal score and thus the lowest ranking male) and 1 (corresponding to the maximal score and the highest ranking male).

Appendix 2. Details on the identification of heterosexual friendships

The male friend of each pregnant and lactating female was identified using a combination of spatial proximity and grooming allocation indices, following an established method [1]. First, we calculated dyadic proximity and grooming scores between all pregnant or lactating females and resident males. The grooming allocation index was calculated as the number of grooming bouts that a female gives to a male divided by the total number of grooming bouts given by that female to any male of the group. The dyadic spatial proximity index was calculated as the number of scans where the male was the female's nearest neighbour divided by the total number of scans collected for that female. Second, for each behavioural index (grooming and spatial proximity), we investigated if one or two males had an outstandingly high score compared to other males, hereafter referred as the “preferred male(s)”: we ranked males from the highest to the lowest score, then calculated the ratio of the highest index divided by the second highest index and the ratio of the second highest index divided by the third highest index. If the first ratio was higher than two (i.e. the male with the highest index had twice as many interactions with the female than the second male), we assigned only one preferred male - the one with the highest score - to the female. If the second ratio was also higher than two, we assigned two preferred males - the ones with first and second highest indices - to the female. Otherwise, we considered that the female had no preferred male for this reproductive state. Thus, pregnant/lactating females could have one, two or no preferred male(s) if no male had a highly differentiated score compared to the others. Then, we compared the preferred male(s) designated by each behavioural index and considered as "male friend" the male that was preferred according to both grooming and proximity indices.

Appendix 3. Details on the GLMM procedure

All GLMMs were run using the glmer function of the lme4 package [4] in R version 3.4.1 [5]. All quantitative variables were z-transformed to have a mean of zero and a standard deviation of one (by subtracting the mean from each value and dividing the result by the standard deviation) to facilitate model convergence. The significance of the fixed factors was tested using a likelihood ratio test (LRT), assuming an asymptotic chi-square distribution of the test statistic and using the full model (to avoid problems arising from stepwise model selection procedures: [6,7]). Only interactions for which we had clear predictions were included. We tested their significance by comparing the fit of the models with and without the interaction using a LRT. Non-significant interactions were omitted from the model to avoid over-parameterization. To test for the significance of fixed effects, we computed their 95% profile-likelihood based confidence intervals using confint.merMod, and checked that they did not cross zero. To test for all differences between levels of multilevel categorical variables (e.g., “mate-guarding status"), we changed the reference category sequentially and refitted the model [8]. To diagnose the presence of multicollinearity, we calculated the variance inflation factor for each of the predictors in each model. These VIFs varied between 1.02 and 2.79, which are below 3, and thus do not indicate serious multicollinearity [9].

Appendix 4. Calculation of male mating skew

The extent of female competition over male care is influenced by how matings (and thus paternity) are distributed across males. If there is a high reproductive skew among males, then the intensity of reproductive competition among females is also likely to be high. To assess the potential for paternal care dilution (and female competition), we calculated the extent of mating skew among males during our study period, using the binomial skew index (B) [10]. For each study group and across all study years, we listed all the observation days where at least one female was in her peri-ovulatory period (POP) and mate-guarded, and established a list of all adult males that were present during each of these days. We then recorded which male mate-guarded a given female on a given POP day. If a male mate-guarded a female the entire day, he was awarded one point. If he mate-guarded her for less than a full day (e.g., if there was a switch of mate-guarding between two males during the day), he was awarded 0.5 point. We then calculated (1) the total number of points that each male acquired in a given group (i.e. the number of mate-guarding episodes captured by each male) across all years, noted M_{POP}, (2) the total number of POP days where mate-guarding occurred in a given group across all years, noted POP_{MG} (thus, if there are two POP females who are mate-guarded on the same day, this would count as two days), and (3) the total number of POP_{MG} days during which each male was present across years (i.e. a proxy for the number of mate-guarding opportunities of each male). We then calculated the B index separately for each group (L and J) but across all study years as follows:

$$B = \sum_{i=1}^{N} (p_i - \frac{n_i}{n_t})^2 - \frac{(1 - \frac{1}{\check{N}})}{K}$$

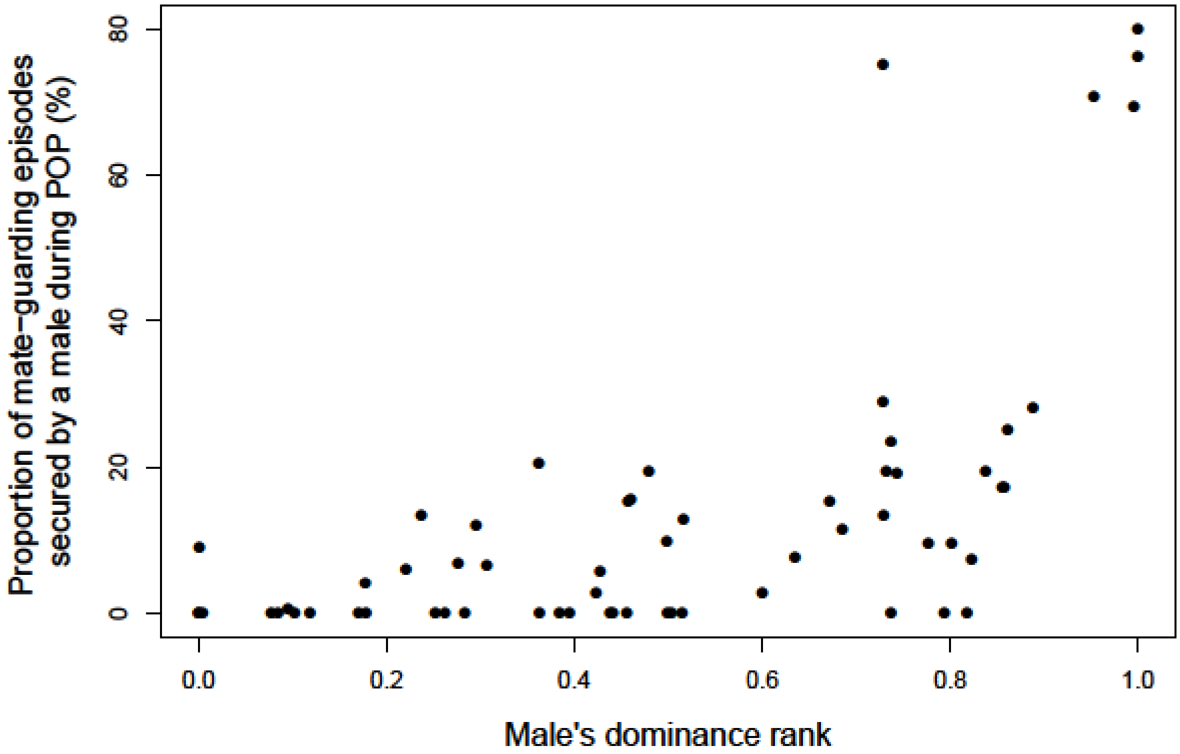
where N is the total number of males observed in the group across all years, p_i is the proportion of the total mate-guarding success gained by male i, calculated as M_{POP} divided by n_i, the total number of POP_{MG} days where he was present, n_t is the sum of n_i across all males of the troop, K is POP_{MG} (i.e. the total number of mate-guarding opportunities across all years), $\check{N}$ is calculated as n_t divided by the total number of POP_{MG} days of a group across years.

B index values that stand close to one indicate a high reproductive skew, while values that stand close to zero indicate a low skew, with zero indicating a random distribution. Negative values indicate a more even distribution of paternity than would be expected by chance. We found a value of 0.63 in L troop and 0.70 in J troop, indicating an important mating skew among males. These values are larger than those previously found in savanna baboons (i.e. *P. ursinus*: 0.05, *P. anubis*: 0.12) [11]. This might be due to the fact that we are using mate-guarding success during peri-ovulatory periods instead of the number of copulations obtained throughout the fertile phase (which is less biased toward high ranking males).

Appendix 5. Calculation of the correlation between male mating success and rank

To further assess the extent of male mating skew among males during our study period, we measured the correlation between the proportion of mate-guarding episodes captured by a male during the POP periods and his dominance rank. Similarly, we calculated (1) the number of mate-guarding episodes captured by each male, like $M_{POP,}$ but per group and per year, (2) the corresponding total number of POP_{MG} days where each male was present per group and per year and (3) the mean dominance rank of each male over the POP_{MG} days in a given year (using the daily estimate of male rank - see Appendix 1). We then ran a linear mixed model using the male M_{POP} scores as the response variable. Fixed effects comprised mean male dominance rank, the number of POP_{MG} days where the male was present (to control for variation in the time spent by each male in the group), year and group. We also included one random effect, the identity of the male (to control for male pseudoreplication across years). We found that the proportion of all mate-guarding episodes secured by a male during the fertile window (POP) of any female was strongly correlated with his dominance rank: β±SE=13.44±2.23, 95% CI=[9.02;17.74], χ^2_1=29.26, p<0.001, N=62 male-year-group combinations, see Figure S1), indicating a high male mating skew. The conditional coefficient of determination (representing the variance explained by the entire model, including both fixed and random effects) is 0.76 and the marginal coefficient of determination (representing the variance explained by the fixed effects only) is 0.57. On average across the 8 combinations of year and troop, males with the highest rank position across the POP_{MG} days monopolize 48.20% (min=17.26%, max=80.00%) of the possible mate-guarding events.

Figure S1. Influence of male dominance rank on the proportion of all mate-guarding episodes secured during the fertile window (POP) of females. We present the raw data over the four study periods and the two social groups.



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