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3

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

6

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8

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13

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17 **Abstract**

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

33

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

36 **1. Introduction**

37 Traditional evolutionary models of paternal care assume that males should only provide care
38 to their offspring when the degree of paternity certainty is high, typically in monogamous
39 species [1,2]. Yet recent empirical studies have indicated that male care can also evolve in
40 promiscuous species where paternity confidence is lower, in particular when the cost of
41 providing care is also low and does not compromise a male's future reproductive success
42 [3,4]. For instance, males of several promiscuous primate species provide discreet forms of
43 care to immatures, such as preferential affiliation, support during conflicts, or tolerance at
44 feeding sites (e.g. Barbary macaques, *Macaca sylvanus*: [5]; yellow baboons, *Papio*
45 *cynocephalus*: [6]; olive baboons, *P. anubis*: [7]; black-and-white snub-nosed monkeys,
46 *Rhinopithecus bieti*: [8]). While males may provide care to unrelated infants to secure future
47 mating opportunities with the mother [7,9], most studies indicate that males care for their
48 genetic offspring, and assess their paternity probabilistically based on their mating history
49 [10–12], or on their offspring's phenotypic resemblance to themselves [13].

50 According to evolutionary theories of parental investment [14], the more offspring a
51 male sires the more his care will be diluted between them, potentially leading mothers to
52 compete for exclusive access to their mates [15]. For example, in facultatively polygynous
53 birds, females breeding with polygynous males experience lower male investment and
54 reproductive success than those breeding with monogamous males [15–17], and females that
55 mate first aggressively exclude secondary-mated females from breeding units in order to
56 maintain male monogamous matings [18]. In polygynous and promiscuous species more
57 generally, where multiple females mate with a single male that provides paternal services,
58 females that have already conceived may similarly attempt to prevent further conceptions
59 with their mate, and the subsequent dilution of paternal care. To do so, they may harass those
60 females that attempt to mate with him, either to interrupt copulations directly through mating

61 interference and/or to induce chronic physiological stress that reduces their fertility (the
62 “reproductive suppression hypothesis” [19]).

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

76 Here, we tested the hypothesis that females that have already conceived attempt to
77 prevent new conceptions with the carer of their offspring in a promiscuous primate species,
78 the chacma baboon (*Papio ursinus*). Chacma baboons live in stable, multimale-multifemale
79 groups and breed year-round. During pregnancy and lactation, females form a strong social
80 relationship (‘friendship’) with a particular male [28,29], usually the genetic father of their
81 offspring [11,12]. Male friends will protect females and their offspring against aggression by
82 conspecifics [6], which occasionally leads to infanticide [28] and feticide [30], and
83 subsequently facilitate immature access to ecological resources [31]. Male reproductive skew
84 is high in chacma baboons [32], which means that high-ranking males are usually involved in
85 several simultaneous friendships. Female reproductive competition over paternal care appears

86 likely in such societies, as high ranking females aggressively displace subordinates from the
87 proximity of their male friend [33], and aggression among lactating females peaks in periods
88 of social instability when infanticide risk is elevated [34]. Moreover, alpha males form weaker
89 bonds with their offspring than subordinate males [31], suggesting that each offspring indeed
90 receives less care in the larger paternal sibships of alpha males. We test five predictions of the
91 reproductive suppression over paternal care hypothesis, namely that pregnant and lactating
92 females attempt to prevent oestrous females from copulating with their male friend by
93 harassing them (prediction 1, P1), in particular when they have conceived themselves recently
94 (P2) (given that synchronous females are expected to compete most intensely over access to
95 male care); that the intensity of harassment correlates with the fertility (proximity of
96 ovulation) of the oestrous female (P3) and with the intensity of her sexual activity with the
97 male friend (P4); and that female-female aggression reduces the probability that the oestrous
98 female conceives with the male friend (P5).

99

100 **2. Material and Methods**

101 *(a) Study site and population*

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

109

110 *(b) Female reproductive state & mate-guarding patterns*

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

128

129 ***(c) Behavioural data***

130 One-hour focal animal samples were conducted on all adult females. In total, our sample
131 comprises 2971 focal observations on 53 females distributed across reproductive states (Table
132 S2, electronic supplementary materials). During focal observations, we continuously recorded
133 aggressive incidents (attacks, chases, threats) and approach-avoid interactions (supplants,
134 displacements) (for definitions, see Appendix 1, electronic supplementary materials)
135 involving the focal female, along with the identity of the receiver and initiator. In total, we

136 observed 370 agonistic interactions initiated by pregnant or lactating females toward oestrous
137 females. In 2013-14, we also recorded all occurrences of male support towards oestrous
138 females following female aggression. In addition, we recorded every occurrence of male-
139 female grooming bouts, sexual solicitations ('presenting', when oestrous females present their
140 hindquarters to males) and copulations, along with the identity of the male. We also noted all
141 approaches and leaves within 1 meter between the focal individual and any other adult female
142 (to calculate the time spent in close proximity between female dyads during a focal
143 observation). Finally, we conducted proximity scans every five minutes to record the identity
144 and distance of the nearest male neighbour.

145

146 *(d) Identification of heterosexual friendships*

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

156

157 *(e) Statistical analysis*

158 We ran binomial generalised linear mixed-effect models (GLMMs) using the glmer function
159 of the lme4 package [39] in R version 3.4.1 [40]. Technical details on how GLMMs were run

160 and how the significance of variables was tested are described in Appendix 3, electronic
161 supplementary material.

162

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

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

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

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

188 • the interaction between the index of potential reproductive synchrony and mate-
189 guarding status, in order to test whether potential reproductive synchrony is more
190 important when the receiver is mating with the initiator's friend than in other cases.

191 • an index of spatial proximity between the initiator and the receiver of the dyad (to
192 control for the fact that two females sharing the same male might attack each other
193 more often just because they spend more time in proximity). This index was calculated
194 as the time spent within 1m of each other during the focal observation (calculated
195 using approaches and leaves within 1m).

196 • the relative dominance rank of the initiator and receiver (as two fixed effects).

197 • group identity (by including group identity as a fixed effect, we do not seek to
198 systematically assess group effects, which would require a larger sample with targeted
199 observations, but rather control for such effects should any be present).

200 • year

201

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

204 We tested whether aggression received by an oestrous female from the female friends of a
205 male (pregnant or lactating) increased with her probability of conception (P3), and the
206 intensity of her sexual activity with this male (P4), using a binomial GLMM. For each focal
207 observation of an oestrous female, we identified all possible dyads involving this female and
208 all resident males that have at least one female friend, and calculated the response variable as
209 the occurrence of aggression received by that oestrous female from the female friends

210 (pregnant or lactating) of each male (yes/no). Random effects comprised the identity of the
211 focal female, the male and the focal observation. Fixed factors comprised:

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

234

235

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

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

251 The fixed factors comprised:

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

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

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

265

266 **3. Results**

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

272

273 *Are females more likely to exhibit aggression towards oestrous females that are mate-* 274 *guarded by their male friend?*

275 As expected under P1, pregnant and lactating females were more likely to be aggressive
276 towards oestrous females that were mate-guarded by their male friend (mean dyadic rate \pm sd:
277 0.07 \pm 0.35 time/h), than towards unguarded females (0.03 \pm 0.18) or females guarded by
278 another male (0.01 \pm 0.13) (Table 1, Figure 1a), even when controlling for the fact that females
279 sharing the same male spend more time in close proximity. Furthermore, pregnant and
280 lactating females that had conceived more recently were more likely to be aggressive towards
281 oestrous females (P2) (Table 1, Figure 1b), though this effect of reproductive synchrony was
282 not greater when the oestrous female was mate-guarded by their male friend than when
283 unguarded or guarded by another male (interaction between reproductive synchrony and male
284 sharing status: $\chi^2_2=1.45, p=0.485$).

285

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

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

296

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

299 Oestrous females received twice as much aggression from the female friends of their mate-
300 guarding male in non-conceptive cycles (mean \pm sd amount of aggression received: 0.13 \pm 0.19,
301 $N=31$ cycles) than in conceptive cycles (0.07 \pm 0.13 time/h, $N=20$ cycles). The probability of
302 conception of an oestrous female thus decreased when she faced more aggression from the
303 female friends of her mate (P5), but remained unaffected by aggression received from other
304 female group-mates (Table 3, Figure 2d). Females were also more likely to conceive with
305 high-ranking males. The observed association between lower aggression and a greater
306 likelihood of conception might also arise if mate-guarding males more actively protected
307 oestrous females during aggressive interactions with other females during conceptive cycles.
308 However, we assessed the occurrence of male protection of oestrous females (in 2013-14),
309 and male support was involved in only 9 of 144 aggressive incidences initiated by a pregnant

310 or lactating female towards an oestrous female (including 6 from the mate-guarding male and
311 3 from other males). Moreover, only one of these cases occurred during a conceptive cycle.
312 Males therefore rarely intervened in conflicts among females, regardless of their fertility.

313

314 **4. Discussion**

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

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

353 The exact mechanisms linking female harassment and reproductive suppression in
354 baboons remain unknown. Reproductive suppression could be mediated by direct mating
355 interference, given that pregnant and lactating females attack oestrous females more
356 frequently when they show higher levels of sexual activity. Such aggression may inhibit the
357 sexual activity of oestrous females, particularly subordinates. However, copulations still occur
358 at a high frequency during mate-guarding episodes, suggesting that mating interference alone
359 is unlikely to explain the observed decline in fertility, and that physiological stress may play a

360 critical role. High rates of aggression and elevated levels of cortisol have been found to
361 disrupt ovulation and the secretion of sex hormones in several captive primates [24,44] and to
362 cause implantation failure in hamsters [45]. This interpretation is also consistent with our
363 finding that pregnant and lactating females harass oestrous females not just at the time of
364 ovulation but throughout the oestrus cycle.

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

376

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

382

383 **Data accessibility.** Data are available through the public depository GitHub at:

384 <https://github.com/AliceBaniel/Reproductive-suppression-chacma-baboon>

385

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

388

389 **Competing interests.** We have no competing interests.

390

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402

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

533

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]				

534

^aReference category: J group

535

^bReference category: 2005

536

537

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

544

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]				

545

^a Reference category: not mate-guarded by the male

546

^b Reference category: J group

547

^c Reference category: 2005

548

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

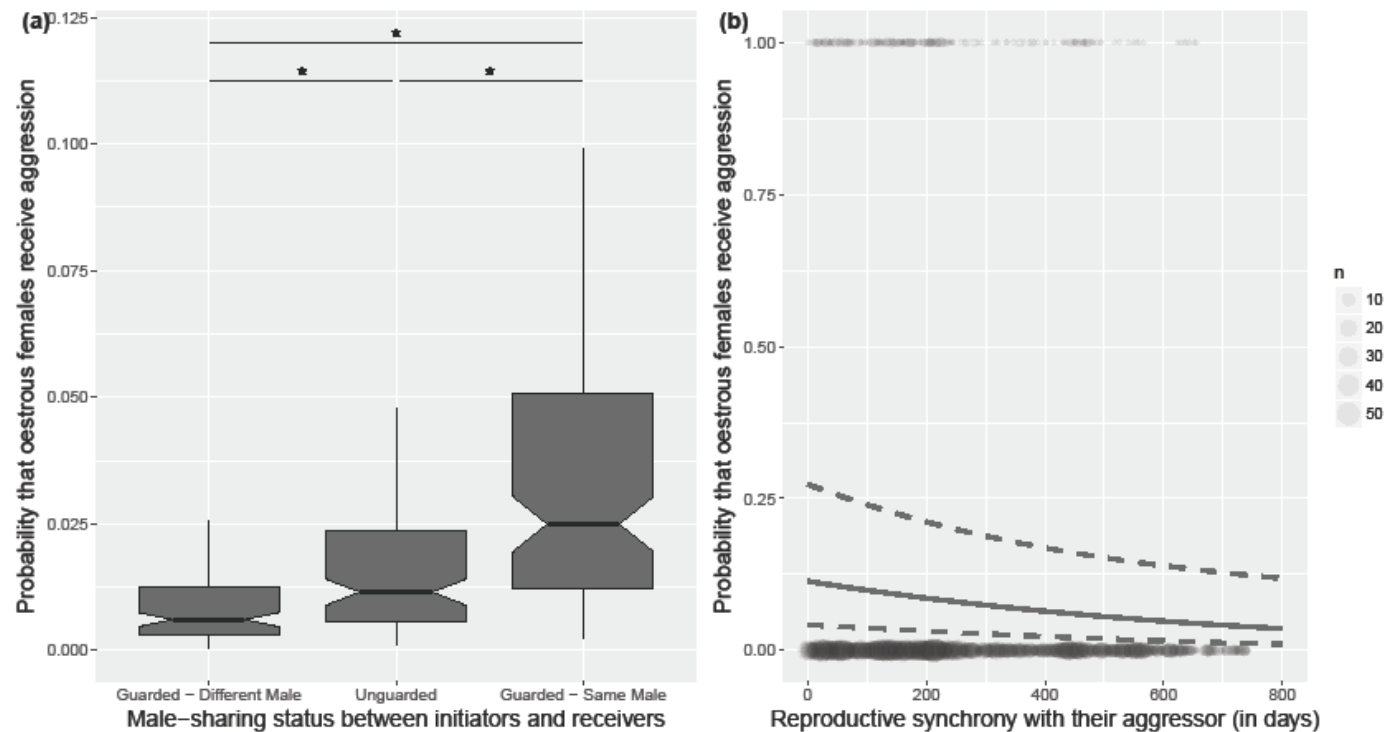
554

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

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

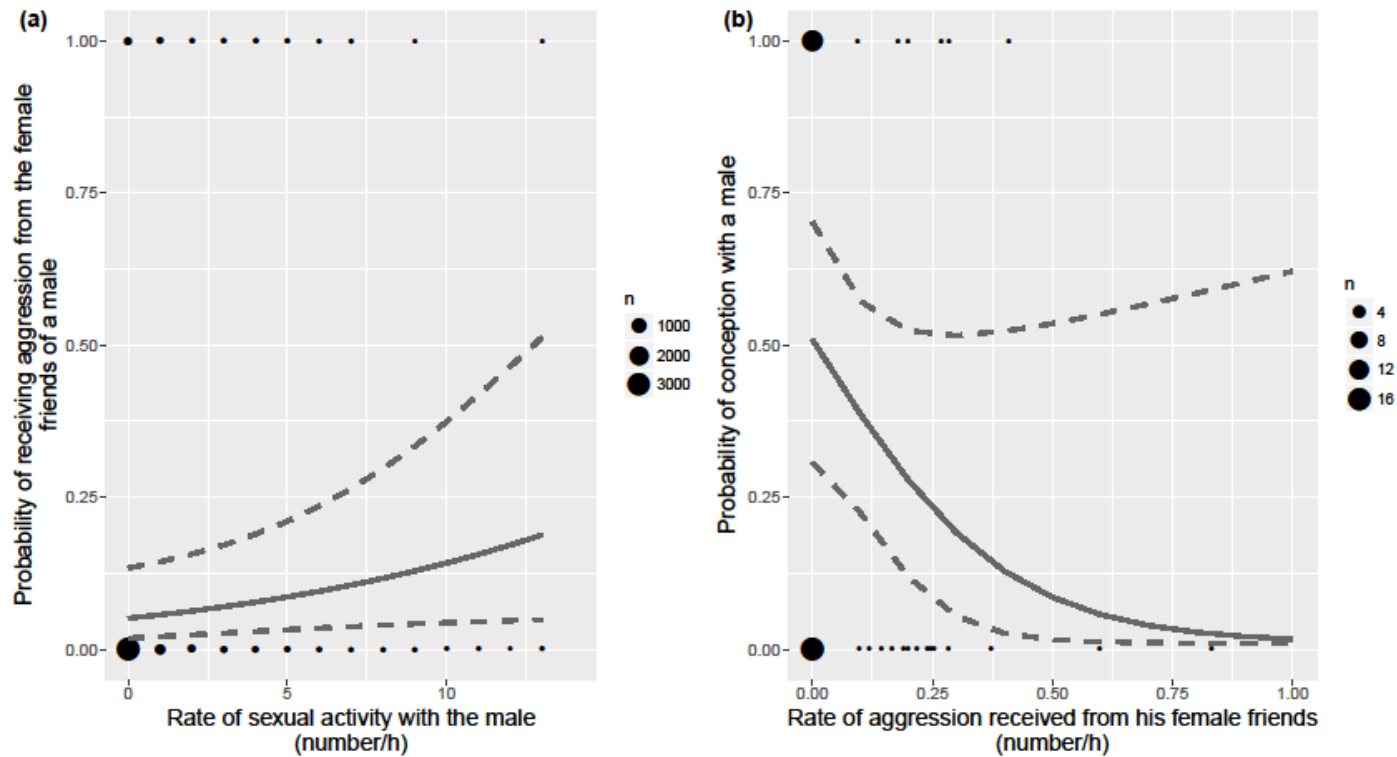
557

558 **Figure 1:** Predicted probability that oestrous females receive aggression from pregnant and lactating females, according to (a) their male sharing
 559 status and (b) their reproductive synchrony. In (a), boxplots are drawn from the distribution of the predicted probabilities, while varying the rank
 560 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
 561 proximity of 0.21 minutes), in J troop in 2014 for categorical variables. Comparisons between the different levels of the variable “male sharing
 562 status” are denoted by "*" if statistically significant. In (b) the solid line is the model prediction, and the dotted lines represent the 95%
 563 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
 564 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
 565 the dyad, and their size is proportional to the number of occurrences in the dataset.



566

567 **Figure 2:** Predicted probability that oestrous females (a) receive aggression from the female friends of a male, according to their sexual activity
 568 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
 569 lines represent the model predictions and the dotted lines the 95% confidence interval. In (a) the prediction line is drawn holding all other fixed
 570 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
 571 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
 572 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
 573 of aggression from other females (0.28 aggressive act/hour). The black dots represent the raw data: whether aggression was exchanged (1) or not
 574 (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.



575

Electronic Supplementary Material Files

576

577

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

579

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

580

581

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

582

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

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

589

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

590 **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.

591

592

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)

593

594

* 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.

595

596

597 **Appendix 1. Dominance ranks of males and females**

598 Individual dominance ranks were assessed through focal and *ad libitum* observations of
599 approach-avoid interactions (*supplants*, when one animal actively displaces another to take its
600 place; *displacements*, when one animal passes close to another and makes it move away) and
601 agonistic interactions (*attacks*, any agonistic physical contacts including hits, bites, or
602 grabbing movements; *chases*, when one animal chases another for a distance of at least 3 m;
603 and *threats*, including staring, head bobbing, and ground sweeping while oriented toward the
604 targeted individual). Female dominance hierarchies were calculated separately in each year
605 using Matman 1.1.4 (Noldus Information Technology 2003) and were always linear ($N_{2005} =$
606 412 interactions, $N_{2006} = 576$, $N_{2013} = 367$, $N_{2014} = 1259$ in group L; $N_{2005} = 184$, $N_{2006} = 460$,
607 $N_{2013} = 590$, $N_{2014} = 978$ in group J, Landau's linearity index h : $p < 0.05$ in all cases). In the
608 analyses, we used relative female rank to control for variation in group size, where absolute
609 ranks were standardised to vary between 0-1 using the formula: $1 - ((1-r)/(1-n))$, where r is the
610 absolute rank of an individual (ranging from 1 to the group size, n). In contrast to females, the
611 male hierarchies were much less stable within a year [1], so male ranks were established using
612 an Elo-rating procedure implemented in the R package EloRating (version 0.43) [2].
613 Compared to matrices of dyadic interactions where ranks are calculated over a given time
614 period, an Elo-rating procedure continuously updates rankings according to the temporal
615 sequence of interactions, and is better adapted to situations of unstable social dominance
616 [2,3]. This gives a score for each individual on each day of observation. We derived a daily
617 standardised rank by scaling the Elo-rating score of each individual proportionally between 0
618 (corresponding to the minimal score and thus the lowest ranking male) and 1 (corresponding
619 to the maximal score and the highest ranking male).

620

621 **Appendix 2. Details on the identification of heterosexual friendships**

622 The male friend of each pregnant and lactating female was identified using a combination of
623 spatial proximity and grooming allocation indices, following an established method [1]. First,
624 we calculated dyadic proximity and grooming scores between all pregnant or lactating
625 females and resident males. The grooming allocation index was calculated as the number of
626 grooming bouts that a female gives to a male divided by the total number of grooming bouts
627 given by that female to any male of the group. The dyadic spatial proximity index was
628 calculated as the number of scans where the male was the female's nearest neighbour divided
629 by the total number of scans collected for that female. Second, for each behavioural index
630 (grooming and spatial proximity), we investigated if one or two males had an outstandingly

631 high score compared to other males, hereafter referred as the “preferred male(s)”: we ranked
632 males from the highest to the lowest score, then calculated the ratio of the highest index
633 divided by the second highest index and the ratio of the second highest index divided by the
634 third highest index. If the first ratio was higher than two (i.e. the male with the highest index
635 had twice as many interactions with the female than the second male), we assigned only one
636 preferred male - the one with the highest score - to the female. If the second ratio was also
637 higher than two, we assigned two preferred males - the ones with first and second highest
638 indices - to the female. Otherwise, we considered that the female had no preferred male for
639 this reproductive state. Thus, pregnant/lactating females could have one, two or no preferred
640 male(s) if no male had a highly differentiated score compared to the others. Then, we
641 compared the preferred male(s) designated by each behavioural index and considered as
642 "male friend" the male that was preferred according to both grooming and proximity indices.

643

644 **Appendix 3. Details on the GLMM procedure**

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

661

662 **Appendix 4. Calculation of male mating skew**

663 The extent of female competition over male care is influenced by how matings (and thus
664 paternity) are distributed across males. If there is a high reproductive skew among males, then

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

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

682
683

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

690 B index values that stand close to one indicate a high reproductive skew, while values
691 that stand close to zero indicate a low skew, with zero indicating a random distribution.
692 Negative values indicate a more even distribution of paternity than would be expected by
693 chance. We found a value of 0.63 in L troop and 0.70 in J troop, indicating an important
694 mating skew among males. These values are larger than those previously found in savanna
695 baboons (i.e. *P. ursinus*: 0.05, *P. anubis*: 0.12) [11]. This might be due to the fact that we are

696 using mate-guarding success during peri-ovulatory periods instead of the number of
697 copulations obtained throughout the fertile phase (which is less biased toward high ranking
698 males).

699

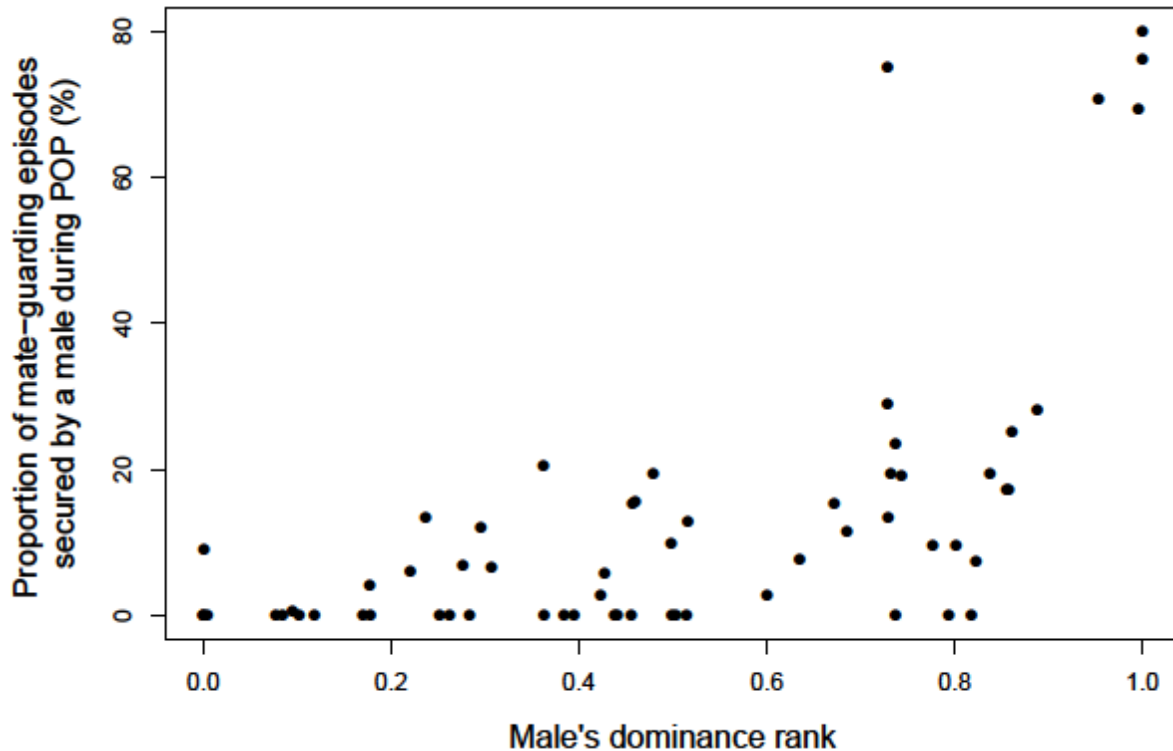
700 **Appendix 5. Calculation of the correlation between male mating success and rank**

701 To further assess the extent of male mating skew among males during our study period, we
702 measured the correlation between the proportion of mate-guarding episodes captured by a
703 male during the POP periods and his dominance rank. Similarly, we calculated (1) the number
704 of mate-guarding episodes captured by each male, like M_{POP} , but per group and per year, (2)
705 the corresponding total number of POP_{MG} days where each male was present per group and
706 per year and (3) the mean dominance rank of each male over the POP_{MG} days in a given year
707 (using the daily estimate of male rank - see Appendix 1). We then ran a linear mixed model
708 using the male M_{POP} scores as the response variable. Fixed effects comprised mean male
709 dominance rank, the number of POP_{MG} days where the male was present (to control for
710 variation in the time spent by each male in the group), year and group. We also included one
711 random effect, the identity of the male (to control for male pseudoreplication across years).
712 We found that the proportion of all mate-guarding episodes secured by a male during the
713 fertile window (POP) of any female was strongly correlated with his dominance rank:
714 $\beta \pm SE = 13.44 \pm 2.23$, 95% CI=[9.02;17.74], $\chi^2_1 = 29.26$, $p < 0.001$, $N = 62$ male-year-group
715 combinations, see Figure S1), indicating a high male mating skew. The conditional coefficient
716 of determination (representing the variance explained by the entire model, including both
717 fixed and random effects) is 0.76 and the marginal coefficient of determination (representing
718 the variance explained by the fixed effects only) is 0.57. On average across the 8
719 combinations of year and troop, males with the highest rank position across the POP_{MG} days
720 monopolize 48.20% (min=17.26%, max=80.00%) of the possible mate-guarding events.

721

722

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



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