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5 **Context dependence of female reproductive competition in**

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## **wild chacma baboons**

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25 **ABSTRACT**

26 Recent research reveals that female reproductive competition is common and may shape the  
27 social and reproductive strategies of female mammals. This study explores the determinants  
28 and intensity of female intrasexual conflicts in a wild promiscuous primate, the chacma  
29 baboon, *Papio ursinus*. We tested a suite of hypotheses to assess whether female–female  
30 aggression was primarily driven by instantaneous competition for food, mates or paternal  
31 care, or aimed at reducing future competition among offspring via reproductive  
32 suppression. Behavioural data were gathered from 53 females in two groups over two  
33 contrasting 2-year periods (2005–2006, 2013–2014): the first characterized by stability in the  
34 male dominance hierarchies, the second by instability induced by several immigration events  
35 and male take-overs. In both periods, we found that sexually receptive females received high  
36 levels of aggression from other sexually receptive females, consistent with competition over  
37 mating opportunities. In the unstable period, females exchanged higher rates of aggression  
38 than in the stable period, regardless of reproductive state, but lactating females received most  
39 aggression, consistent with higher competition over social access to male partners in response  
40 to increased infanticide risk. There was no evidence that aggression between females reflected  
41 either competition over food or reproductive suppression. These findings indicate that patterns  
42 of aggression between females fluctuate with sociodemographic factors affecting sexual and  
43 social access to males and reflect reproductive competition more closely than resource  
44 competition in this promiscuous primate society.

45

46 **KEYWORDS:** aggression, baboons, female–female competition, intrasexual selection,  
47 mating competition, paternal care

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49

## 50 INTRODUCTION

51 Female reproductive success has long been thought to be primarily limited by access to food  
52 resources in mammals, where females face high energetic demands during lactation and  
53 gestation (Emlen & Oring, 1977; Isbell, 1991; Koenig, 2002; Wrangham, 1980). However,  
54 recent research highlights intense reproductive competition between female mammals over  
55 access to high-quality mates or sperm, as well as over offspring care from fathers or helpers  
56 (Clutton-Brock, 2009; Clutton-Brock & Huchard, 2013; Rosvall, 2011; Stockley & Bro-  
57 Jørgensen, 2011). In the first case, mating competition among females may occur in some  
58 polygynous species where males vary in quality (reviewed in Jennions, 1997; Jennions &  
59 Petrie, 2000) or where they become sperm depleted (e.g. topi antelope, *Damaliscus lunatus*,  
60 Bro-Jørgensen, 2002, 2007; red deer, *Cervus elaphus*, Bebié & McElligott, 2006). In the  
61 second case, female reproductive competition to secure helpers (males or females) can be  
62 intense in socially monogamous species, such as in cooperative breeders where one female  
63 monopolizes most breeding attempts (e.g. meerkat, *Suricata suricatta*, Clutton-Brock et al.,  
64 2006; Damaraland mole-rat, *Cryptomys damarensis*, Bennett, Faulkes, & Molteno, 1996;  
65 common marmoset, *Callithrix jacchus*: Yamamoto, Arruda, Alencar, de Sousa, & Araújo,  
66 2009). Reproductive competition among females nevertheless remains understudied in  
67 polygynous species (including strictly polygynous and promiscuous species), where female  
68 reproductive skew is usually low (Clutton-Brock, 2007, 2009) and where males provide direct  
69 benefits in the form of paternal services to their genetic offspring (yellow baboon, *Papio*  
70 *cynocephalus*: Buchan, Alberts, Silk, & Altmann, 2003; chacma baboon, *Papio ursinus*:  
71 Huchard et al., 2010; rhesus macaque, *Macaca mulatta*: Kulik, Muniz, Mundry, & Widdig,  
72 2012), and occasionally unrelated juveniles (Barbary macaque, *Macaca sylvanus*: Ménard et  
73 al., 2001; olive baboon, *Papio anubis*: Smuts, 1985).

74           Importantly, the intensity and form of female–female competition may change over  
75 time depending on the females’ reproductive states, which are characterized by different  
76 needs and limiting resources (Gowaty, 2004; Huchard & Cowlshaw, 2011). Specifically,  
77 females are likely to compete over mates when sexually receptive, over food resources when  
78 pregnant or lactating, and over infant care when lactating (Huchard & Cowlshaw, 2011).  
79 Thus, reproductive synchrony between females is likely to intensify female reproductive  
80 competition, for instance in species with a short breeding season (e.g. Bro-Jørgensen 2002;  
81 Bro-Jørgensen 2007; Bebié & McElligott, 2006), but females may also compete with  
82 asynchronous females. Females that have already conceived might attempt to suppress or  
83 delay the conceptions of other females, to reduce competition for the resources necessary to  
84 raise offspring (Wasser & Barash, 1983; Young, 2009).

85           Reproductive suppression has been well documented in several cooperative breeders  
86 (e.g. Alpine marmot, *Marmota marmota*, Hackländer, Möstl, & Arnold, 2003; meerkat,  
87 Clutton-Brock et al., 2001; Young et al., 2006; mole-rat, Bennett, Faulkes, & Molteno, 1996;  
88 Faulkes, 1997). In such species, breeding females seem to suppress the reproduction of other  
89 group members either to reduce the number of births in a group and limit future competition  
90 for food (Clutton-Brock, Hodge, Flower, Spong, & Young, 2010; Young, Oosthuizen,  
91 Lutermann, & Bennett, 2010) and/or to maximize the number of helpers that will care for  
92 their offspring (Clutton-Brock & Huchard, 2013). Reproductive suppression is less well  
93 documented in noncooperative breeders, where it might similarly aim at reducing future group  
94 size and/or competition over paternal care (Clutton-Brock & Huchard, 2013). In yellow  
95 baboons and geladas, *Theropithecus gelada*, for instance, some early studies suggest that  
96 dominant females harass subordinate females that are sexually receptive and this could reduce  
97 their fertility (e.g. yellow baboons, Wasser & Starling, 1988, 1995; geladas, Dunbar, 1980;  
98 Dunbar & Dunbar, 1977). However, it remains unclear from these studies whether the lower

99 fertility of subordinate females is caused by harassment or by any other rank-related  
100 difference between females, and the reproductive suppression hypothesis thus deserves further  
101 investigation.

102         This study investigated the determinants and intensity of female–female aggression in  
103 relation to female reproductive state in wild chacma baboons, a promiscuous primate with a  
104 moderate female reproductive skew (Cheney et al., 2004; Johnson, 2003). Chacma baboons  
105 live in large, stable multimale–multifemale groups and breed year round (Alberts et al., 2005;  
106 Cheney et al., 2004). Females are philopatric and establish stable, linear dominance  
107 hierarchies in which daughters inherit their mother’s rank (Bergman, Beehner, Cheney, &  
108 Seyfarth, 2003; Seyfarth, 1976), while males usually disperse and fight fiercely to establish  
109 and maintain their social rank, which is associated with higher reproductive success (Bulger,  
110 1993; Weingrill, Lycett, Barrett, Hill, & Henzi, 2003). Female reproductive competition may  
111 take several forms in chacma baboons. First, cycling females may compete over access to  
112 sexual partners. Females display exaggerated sexual swellings (Huchard et al., 2009), are  
113 highly promiscuous, and sexually receptive females receive the highest rate of aggression  
114 from other females (Huchard & Cowlshaw, 2011), all of which suggest that mating  
115 competition may be intense. Second, lactating females may compete over access to male  
116 social partners, usually the genetic father of their offspring (Huchard et al., 2010; Moscovice  
117 et al., 2010), which provide infant protection services against infanticide by other males  
118 (Palombit, 2009; Palombit, Seyfarth, & Cheney, 1997). Where several lactating females are  
119 associated with the same male friend, the higher-ranking females attempt to exclude the  
120 lower-ranking females from associating with him (Palombit, Cheney, & Seyfarth, 2001).  
121 Because infanticide risk is highest during the first 6 months of an infant’s life (Palombit,  
122 2003), such competition over male friends is likely to be most intense at this time. Finally,  
123 females may attempt to suppress the reproduction of rivals either to reduce the number of

124 births and limit future competition for food and/or to stagger their births and avoid  
125 competition for access to fathers.

126         Our study was conducted in the Tsaobis baboon population. A previous study in this  
127 population found that most aggression was initiated by pregnant females but received by  
128 sexually receptive females (Huchard & Cowlshaw, 2011). These patterns could emerge from  
129 a variety of processes, including reproductive suppression by pregnant females and  
130 competition for mates between sexually receptive females, but identification of these  
131 processes requires analysis at the dyadic level which remains to be conducted. In addition,  
132 previous studies of aggression among female baboons have often failed to explore the role of  
133 food abundance or relatedness (Cheney, Silk, & Seyfarth, 2012; Huchard & Cowlshaw,  
134 2011; Wasser & Starling, 1988, 1995), which are likely to influence patterns of intrasexual  
135 aggression. Within- and between-year variation in the availability of food resources is likely  
136 to affect female–female aggression (Isbell, 1991; van Schaik, 1989; Wheeler, Scarry, &  
137 Koenig, 2013), and this may be particularly marked in desert and savannah environments that  
138 are highly seasonal and show high variability in rainfall between years (Anderson, 1982;  
139 Cowlshaw, 1997a; Henzi, Byrne, & Whiten, 1992). Female relatedness may also modulate  
140 intrasexual aggression since kin may be more or less aggressive towards one another solely  
141 because of their relatedness. In chacma baboons for instance, mother–daughter pairs show  
142 lower rates of conflict, while sisters exchange more aggression than nonkin (Silk et al., 2010).

143         In this study, we tested whether female–female aggression is primarily driven by  
144 instantaneous competition for food (Hypothesis 1, H1), mates (H2) or paternal care (H3), or  
145 by competition for future resources through reproductive suppression (H4). If females  
146 compete over food (H1), we expected aggression to peak among lactating and pregnant  
147 females (which face the highest energetic needs; Prediction 1a, P1a) and environmental  
148 factors to influence aggression (with higher levels when food is scarce; P1b). If females

149 compete for mating opportunities or sperm (H2), we expected aggression to be highest among  
150 sexually receptive females (P2a) and to increase with a more female-biased operational sex  
151 ratio (OSR; P2b). If females compete over paternal care (H3), we predicted that aggression  
152 would be highest among lactating females (P3a). If females attempt to cause reproductive  
153 suppression (H4), we predicted that pregnant and/or lactating females would target sexually  
154 receptive females (P4). To test these predictions, we examined variation in levels of female–  
155 female aggression received in relation to female reproductive state and further investigated  
156 dyadic patterns of agonistic interactions to investigate whether aggression received by a  
157 female varied according to her reproductive state and that of her aggressors. We investigated  
158 the determinants of female–female aggression in two periods characterized by contrasting  
159 sociodemographic dynamics (see Appendix Table A1). In the first period (2005–2006), there  
160 were few adult male immigrants and the male dominance hierarchy was stable. In the second  
161 period (2013–2014), the arrival of multiple male migrants led to intense male–male  
162 competition, repeated alpha-male take-overs and instability in the male hierarchy (Baniel,  
163 Cowlshaw, & Huchard, 2016), which are typically associated with high infanticide risk  
164 (Lukas & Huchard, 2014; Palombit, 1999; Zippel et al., 2017). We therefore expected females  
165 to compete more over paternal care in the second period (P3b). Finally, we also investigated  
166 whether the extent of reproductive synchrony at the group level (i.e. the proportion of females  
167 in the same reproductive state in a group at the same time, Ims 1990) influenced the  
168 aggression exchanged between females, as females in the same reproductive state are  
169 expected to compete with one another under hypotheses H1–H3. We also investigated the  
170 potential independent effects of dominance rank and kinship on these patterns.

171

## 172 **METHODS**

### 173 *Study animals*

174 Data were collected from two habituated groups (J and L) of wild chacma baboons living at  
175 Tsaobis Nature Park in Namibia (22°22'S, 15°44'E), over four different periods: June–  
176 December 2005, May 2006–January 2007, June–October 2013 and May–November 2014 (for  
177 details on the site and population, see Cowlshaw 1997b). Group composition is given in  
178 Table A2. All individuals were recognizable and followed at close distance on foot from dawn  
179 to dusk. Females were considered adult when they reached menarche (Altmann & Alberts,  
180 2003). Age of females (in years) was estimated for all but two individuals from a combination  
181 of known birth dates and dental patterns of tooth eruption and wear, examined during captures  
182 (Huchard et al., 2009). The reproductive state of each adult female was recorded as pregnant  
183 (P), lactating (L) if her youngest infant was less than 6 months old, swollen (SW) if she was  
184 sexually receptive with a perineal swelling, and cycling nonswollen (NSW) if she was neither  
185 swollen, pregnant or lactating. Pregnancy was assigned post hoc following the birth of an  
186 infant and encompassed the 6 months separating the conceptive cycle from an infant birth.  
187 Lactating females with an infant that was older than 6 months were excluded from all  
188 analyses, because infanticide risk is considerably lower after 6 months (Palombit et al., 1997).

189

### 190 *Behavioural data*

191 All sexually mature females were chosen as focal subjects. We conducted 1 h focal animal  
192 samples (Altmann, 1974) spread equally across the day (divided into four 3 h blocks) for each  
193 individual. The choice of focal animal was semirandomized to balance observations equally  
194 across individuals, time periods and reproductive states. The same individual was not sampled  
195 more than once per half day. We included only focal samples  $\geq 45$  min (mean focal  
196 length $\pm$ SD: 59.7 $\pm$ 3.5 min). A total of 3140 focal samples on 53 females were collected across  
197 the following reproductive states: cycling nonswollen ( $N=469$  observations of 36 females,  
198 range 1–40, mean $\pm$ SD: 13.0 $\pm$ 9.7 focal samples per individual), lactating (586, 41, 1–34,

199 14.3±8.9), pregnant (714, 47, 1–46, 15.2±9.7) and swollen (1371, 39, 2–109, 35.2±31.5).  
200 Some females were present during all four study periods (2005, 2006, 2013, 2014) while  
201 others were present during only one to three periods (either because they became sexually  
202 mature or died). During focal samples, all occurrences of agonistic interactions (attacks,  
203 chases, threats) and approach–avoid interactions (displacements, supplants; for definitions,  
204 see Huchard & Cowlshaw, 2011) were noted on a continuous basis, along with the identity of  
205 the receiver and initiator. We observed 1339 aggressive incidents received (54 attacks, 97  
206 chases, 78 threats, 540 displacements, 570 supplants). In addition, throughout the day, we  
207 collected ad libitum agonistic interactions, recording the identity of individuals and direction  
208 of interaction ( $N=2737$  aggressive events observed).

209 Female dominance ranks were established using both ad libitum and focal  
210 observations of agonistic interactions. We calculated female dominance hierarchies separately  
211 in each year using Matman 1.1.4 (Noldus Information Technology, Wageningen, the  
212 Netherlands). Female dominance hierarchies were always linear ( $N_{2005} = 412$  interactions,  
213  $N_{2006} = 576$  interactions,  $N_{2013} = 367$  interactions,  $N_{2014} = 1259$  interactions in group L;  $N_{2005} =$   
214  $184$  interactions,  $N_{2006} = 460$  interactions,  $N_{2013} = 590$  interactions,  $N_{2014} = 978$  interactions in  
215 group J; Landau's linearity index  $h$ :  $P < 0.05$  in all cases). In the following analysis, we used  
216 relative female rank to control for variation in group size. To calculate female relative rank,  
217 female absolute ranks were standardized to vary between 0 and 1, using the formula  $1 - ((1 -$   
218  $r)/(1 - n))$ , where  $r$  is the absolute rank of an individual (ranging from 1 to the group size,  $n$ ).

219

### 220 ***Group level reproductive synchrony***

221 To determine the extent of reproductive synchrony between females, we first calculated the  
222 Shannon–Weiner diversity index ( $H$ ) for each day and for each group,  $H = -\sum[(\pi_i) \times \ln(\pi_i)]$ ,  
223 where  $\pi_i$  is the proportion of females in each reproductive state category  $i$  (number of

224 nonswollen/swollen/pregnant/lactating females divided by the total number of females). We  
225 then used the equitability score,  $E = H/H_{\max}$ , where  $H_{\max}$  is the number of categories (equal to  
226 4), as our index of reproductive synchrony. Values close to zero indicate high reproductive  
227 synchrony (one or a subset of reproductive state(s) are predominant) and values close to one  
228 indicate low reproductive synchrony (the reproductive states are equally distributed).

229

### 230 *Pairwise relatedness between females*

231 All adult females were genotyped at 16 microsatellite loci from tissue samples, except for one  
232 adult female whose genotype is unknown. Pairwise coefficients of relatedness ( $r$ ) were  
233 calculated between all females using a triadic likelihood estimator of relatedness (Wang,  
234 2007), and ranged from 0.00 to 0.72 (median = 0.13; mean $\pm$ SD = 0.20 $\pm$ 0.19,  $N=981$  dyads for  
235 53 individuals). Full details regarding genotyping and relatedness calculations in our  
236 population can be found in Huchard et al. (2010).

237

### 238 *Environmental data*

239 Tsaobis Nature Park comprises steep rocky hills and is bordered to the north by the ephemeral  
240 Swakop River. The weather is hot and dry with seasonal rains that fall mostly between  
241 November and March. The Swakop River supports patches of riparian woodland dominated  
242 by large trees and bushes such as *Faidherbia albida*, *Prosopis glandulosa* and *Salvadora*  
243 *persica*, while the vegetation of the surrounding hills is much sparser, including small  
244 perennial bushes and annual herbs and grasses (Cowlshaw & Davies, 1997). We assessed  
245 food availability using the normalized difference vegetation index (NDVI; Pettorelli 2013), a  
246 satellite-based proxy of primary productivity (estimating ‘greenness’, with higher positive  
247 values representing more productive areas). NDVI has previously been shown to be a robust  
248 indicator of habitat quality for baboons (Zinner, Pelaez, & Torkler, 2001).

249 We downloaded NDVI data for the Tsaobis area over the 4 years of the study from the  
250 NASA Land Processes Distributed Active Archive Center (Reverb|ECHO service,  
251 <http://reverb.echo.nasa.gov/>) with a 250×250 m spatial resolution per 16-day period (MODIS  
252 13Q1 v006; Didan 2015). Based on GPS locations acquired every 30 min by observers with  
253 the groups (beginning when the group left the sleeping cliff in the morning until the group  
254 reached the sleeping cliff in the evening), we computed the utilization distribution (UD) of  
255 each study group for each of the 16-day NDVI periods, provided GPS locations were  
256 available for at least 5 days. These UD<sub>s</sub> were calculated using the BRB/MKDE method  
257 (Benhamou, 2011; Benhamou & Cornélis, 2010). In total, in J group we analysed 40 periods  
258 involving 12.3±3.5 (mean±SD) tracking days per period, and in L group we analysed 40  
259 periods involving 10.8±5.2 tracking days per period. We then combined our NDVI and UD  
260 maps to compute the UD-weighted mean NDVI value for each of the various 16-day NDVI  
261 periods, hereafter NDVI<sub>UDw</sub>. This NDVI<sub>UDw</sub> was computed by identifying each 250×250 cell  
262 that the baboons used in the 16-day period, weighting the NDVI score in that cell by the  
263 measure of intensity of utilization, and then taking the mean of these weighted cell scores. In  
264 this way, we estimated the mean level of ‘greenness’ the two groups experienced for each 16-  
265 day period. For the additional 17 periods where we had fewer than 5 days of GPS data  
266 (mainly at the start/end of field seasons and during mid-season breaks), we used the midrange  
267 of the NDVI<sub>UDw</sub> values from the previous and next 16-day periods (or the same values as  
268 these periods, if only one or the other was available). We were therefore able to include a total  
269 of 57 periods for both groups in our analysis.

270

271 *Statistical analysis*

272 *Overall pattern of aggression received*

273 We investigated patterns of aggression received from other females, according to the  
274 reproductive state of the focal female across the two contrasting periods. We ran a general  
275 linear mixed model (GLMM) with a Poisson error structure, using the number of aggressive  
276 interactions (including agonistic and approach-avoid interactions) received per hour as the  
277 response variable, and the individual focal sample as the unit of analysis. Random effects  
278 comprised female identity crossed with the date of focal sampling (as these variables may  
279 generate nonindependent estimates of the rates of aggression between females). Fixed effects  
280 comprised the following variables: the reproductive state of the focal female (four classes:  
281 nonswollen, swollen, pregnant, and lactating); the period of study (split as stable, 2005–2006  
282 or unstable, 2013–2014); an interaction term between female reproductive state and the period  
283 of study, to test whether the pattern of aggression received by females in each reproductive  
284 state differed between the two periods; the reproductive synchrony at the group level ( $E$ ); the  
285 food availability at the group level ( $NDVI_{Udw}$ ); the number of adult females in the group, to  
286 control for demographic changes since more females could result in more aggression; the  
287 dominance rank of the focal female, to control for the fact that aggression received is likely to  
288 be rank dependent, independently of the other fixed effects; the age of the focal female,  
289 because older females were previously found to receive more and initiate less aggression  
290 (Huchard & Cowlshaw, 2011); and group identity, to control for possible differences  
291 between social groups.

292

### 293 *Dyadic patterns of aggression received*

294 We examined dyadic patterns of agonistic interactions received by females according to their  
295 reproductive states and the reproductive states of their aggressors. We arranged the data set as  
296 follows. For each focal female in a given reproductive state, we created a list of all other  
297 females in a given reproductive state that were groupmates (e.g. for female A when swollen,

298 in a group including two other females, B and C, the dyads might comprise: A swollen→B  
299 swollen, A swollen→B pregnant, A swollen→C pregnant, A swollen→C lactating; while  
300 other combinations, such as A swollen→B lactating and A swollen→C nonswollen, were not  
301 observed). Dyads in a particular reproductive configuration were included only if they were  
302 observed for at least 5 h (i.e. only 53% of all possible dyads were included). We also created a  
303 variable ‘Aggression’ which summed all the aggressive interactions received by the focal  
304 female within each of these dyads. We then ran four GLMMs with a Poisson error structure  
305 for four subsets of the data set that were defined by whether the focal female (receiver of the  
306 dyad) was (1) nonswollen, (2) swollen, (3) pregnant or (4) lactating, using ‘Aggression’ as the  
307 response variable. The duration of focal observations available for a given dyad in a specific  
308 reproductive configuration, i.e. in a period during which the reproductive state of each  
309 interacting female did not change, was log transformed and included as an offset variable to  
310 control for the variation in observation time across dyads. Random effects comprised the  
311 crossed identity of the aggressor and receiver. Fixed effects comprised the following  
312 variables: the reproductive state of the aggressor (nonswollen, swollen, pregnant, lactating);  
313 the period of study (stable, 2005–2006 or unstable, 2013–2014); the interaction between the  
314 aggressor's reproductive state and the period of study, to test whether the pattern of aggression  
315 received by females in each reproductive state differed between periods; the rank difference  
316 between the aggressor and the focal receiver (positive if the aggressor is higher ranking than  
317 the receiver, and vice versa); the pairwise coefficient of relatedness between the focal receiver  
318 and the aggressor; the proportion of females in the same reproductive state as the focal  
319 receiver in the group (i.e. number of nonswollen/swollen/pregnant/lactating females,  
320 respectively, divided by the total number of adult females) to control for temporal variations  
321 in the number of females in each reproductive state; the total number of adult females in the  
322 group; and group identity.

323 For the model focusing on aggression received by swollen females, we added an extra fixed  
324 effect: the daily OSR to test prediction P2b. We calculated it as the number of swollen  
325 females divided by the number of adult males.

326

327 All GLMMs were run using the glmer function of the lme4 package (Bates, Maechler, Bolker,  
328 & Walker, 2014) in R version 3.4.1 (R Core Team, 2017). All quantitative variables were z-  
329 transformed to have a mean of zero and a standard deviation of one (by subtracting the mean  
330 from each value and dividing by the standard deviation) to facilitate model convergence. The  
331 significance of the fixed factors was tested using a likelihood ratio test, LRT (assuming an  
332 asymptotic chi-square distribution of the test statistic) and using the full model to avoid  
333 problems arising from stepwise model-selection procedures (Mundry & Nunn, 2009;  
334 Whittingham, Stephens, Bradbury, & Freckleton, 2006). We only tested two two-way  
335 interactions for which we had a clear prediction. Nonsignificant interactions were omitted  
336 from the full model to limit risks of over-parameterization. The significance of the fixed  
337 factors was assessed by computing their 95% Wald confidence intervals (using the  
338 confint.merMod function) and by checking that they did not cross zero. To test for significant  
339 differences between levels of multilevel categorical variables (e.g. 'reproductive state of  
340 aggressor'), we changed the reference category sequentially (Pinheiro & Bates, 2000). To  
341 validate models, we checked the distribution of residuals (i.e. plotted the residuals against the  
342 continuous predictors and checked that the residuals were normally distributed). Sample sizes  
343 are indicated in the table presenting the results of the corresponding model.

344

#### 345 *Ethical note*

346 Our research procedures were evaluated and approved by the Ethics  
347 Committee of the Zoological Society of London and the Ministry of Environment and

348 Tourism (MET), Namibia, and adhered to the ASAB/ABS Guidelines for the Treatment of  
349 Animals in Behavioural Research and Teaching. Our research was conducted under MET  
350 permit numbers 886/2005, 1039/2006, 1786/2013 and 1892/2014.

351

## 352 **RESULTS**

### 353 *Overall pattern of aggression received*

354 The pattern of aggressive interactions received by females was strongly dependent on their  
355 reproductive state and showed clear differences between periods of social stability and  
356 instability (indicated by a significant interaction between period and reproductive state, Table  
357 1, Fig. 1). We therefore ran the GLMM separately for each period (stable versus unstable) to  
358 explore the differences between different female reproductive states in more detail. When the  
359 social hierarchy was stable (2005–2006), most aggression was received by swollen and  
360 nonswollen females, while pregnant and lactating females received low levels of aggression  
361 (Table A3, Fig. 2a). When the social hierarchy was unstable (2013–2014), the pattern was  
362 almost reversed: swollen females received lower levels of aggression and lactating females  
363 the most aggression, in support of P3b (Table A3, Fig. 2b). Notably, the rate of agonistic  
364 interactions received by females was much higher in the unstable than in the stable period  
365 (pooled across all focal observations of all females in any reproductive state: mean±SD  
366  $0.33\pm 0.78$  aggressive incidents per hour in 2005–2006 versus  $0.52\pm 1.01$  in 2013–2014), but  
367 this may reflect the greater number of females present in the unstable period (Table A1).

368 Contrary to the feeding competition hypothesis (prediction P1b),  $NDVI_{UDw}$  did not  
369 influence the amount of aggression received by females (Table 1, Fig. 1). As expected,  
370 increasing reproductive synchrony was found to intensify levels of aggression received by  
371 females. Finally, the effects of dominance rank were consistent across periods, with higher-

372 ranking females receiving less aggression, while female age, the number of adult females in  
373 the group and group identity were not significant.

374

### 375 *Dyadic patterns of aggression received*

376 Aggression received by a female in a given reproductive state was found to vary according to  
377 the reproductive state of her aggressors (Tables 2, 3, A4 and A5). Here we consider swollen,  
378 lactating, pregnant and cycling nonswollen females in turn.

379 Swollen females were targeted by the same categories of aggressors across stable and  
380 unstable periods (chi-square analysis of deviance of the models with and without the  
381 interaction term between aggressor's reproductive state and period:  $\chi^2_3=1.51$ ,  $P=0.681$ ). In  
382 support of the mating competition hypothesis (prediction P2a), swollen females faced most  
383 aggression from other swollen females (Table 2, Fig. 3a); however, the effect of OSR on the  
384 level of aggression received by swollen females was nonsignificant which failed to support  
385 prediction P2b. Pregnant and lactating females did not target swollen females, which fails to  
386 support the reproductive suppression hypothesis (P4).

387 Patterns of aggression received by lactating females were also comparable across  
388 periods (chi-square analysis of deviance of the models with and without the interaction term  
389 between aggressor's reproductive state and period:  $\chi^2_3=5.46$ ,  $P=0.141$ ). Lactating females  
390 were not targeted by females of any particular reproductive state, which fails to support our  
391 predictions P1a and P3a, respectively focussing on feeding competition and competition for  
392 male paternal care (Table 3, Fig. 3b).

393 Finally, pregnant females were targeted more by nonswollen, pregnant and swollen  
394 females (Table A4, Fig. 3c), and this pattern was consistent across periods. Nonswollen  
395 females received aggression indiscriminately from females of all states across both periods  
396 (Table A5, Fig. 3d).

397           Across models, the relatedness between females and their aggressors did not influence  
398 the amount of aggression received, but the rank difference did: females consistently received  
399 more aggression when the rank difference was greater. The amount of aggression received  
400 was largely independent of the number of females in the group, except for swollen females,  
401 which received less aggression when more females were present. Similarly, the aggression  
402 faced by females in each reproductive state was largely independent of the proportion of  
403 females in the same state, except for nonswollen females, which received less aggression  
404 when there was a greater proportion of nonswollen females in the group. There were no  
405 differences between groups.

406

## 407 **DISCUSSION**

408 We investigated the pattern of aggression exchanged among females in relation to their  
409 reproductive state in a wild primate population where females breed year round (i.e. where all  
410 reproductive states coexist), to assess whether female–female aggression was primarily driven  
411 by instantaneous competition for food, mates and paternal care, or by competition for future  
412 resources (such as food or paternal care), through reproductive suppression. We examined  
413 these questions in two periods of contrasting social stability. The hypothesis, predictions and  
414 associated results are summarized in Table A6. Our findings highlight that the direction and  
415 intensity of aggression exchanged among females is mediated by their reproductive state and  
416 group level reproductive synchrony, and less so by food availability or relatedness between  
417 dyads. In particular, we found that swollen or lactating females received the most aggression,  
418 contingent on the period in question. This indicates that reproductive competition may play a  
419 central role in structuring female social relationships in this population, despite patterns of  
420 nonseasonal breeding and moderate female reproductive skew. We discuss below the fit of

421 our findings to our hypotheses regarding the determinants of female–female competition in  
422 baboons.

423

424 *Evidence of competition over mating opportunities*

425 Our findings largely support the mating competition hypothesis. Huchard and Cowlshaw  
426 (2011) previously established that sexually receptive females faced higher levels of  
427 aggression than other females in the stable period. However, as the reproductive state of the  
428 aggressors was unknown, it was difficult to disentangle whether this pattern represented  
429 mating competition between swollen females or an attempt from pregnant and lactating  
430 females to prevent conception (i.e. reproductive suppression). Here, we found that the  
431 aggression experienced by swollen females came mainly from other swollen females in both  
432 periods, providing further support for the mating competition hypothesis. Nevertheless, the  
433 OSR did not predict the intensity of female–female competition in either period. It is possible  
434 that the OSR, which assumes that all males are equally attractive to fertile females, represents  
435 a poor measure of male mating competition in species like chacma baboons where paternity  
436 analyses have revealed a pronounced reproductive skew towards high-ranking males  
437 (Huchard et al., 2010; Moscovice et al., 2010). Similarly, we calculated the OSR according to  
438 whether females were swollen or not, but fertility still varies markedly during the swollen  
439 period (according to proximity to ovulation), and this might have introduced some noise into  
440 the OSR measure.

441 Oestrous females may compete for sperm, good genes and/or future paternal care.  
442 Competition for sperm and fertilization insurance is not the most likely possibility, given that  
443 baboons are nonseasonal breeders (Clarke, Henzi, & Barrett, 2012) and that the OSR is  
444 usually male biased in groups. Females may show a preference for the dominant male, if his  
445 high rank reflects some aspect of his genetic quality or if he is able to provide the most

446 effective infant protection services. Since a single male baboon can only mate-guard one  
447 female at a time (Alberts, Altmann, & Wilson, 1996; Alberts, Watts, & Altmann, 2003), two  
448 synchronous females are likely to compete over his sexual access. In line with this, Cheney,  
449 Silk, and Seyfarth (2012) found a positive correlation between the dominance ranks of male  
450 and female consort partners, suggesting that high-ranking females might successfully  
451 outcompete other females. Competition over paternal care may appear more likely than for  
452 good genes, for several reasons. First, offspring from subordinate males suffer higher  
453 infanticide risk, suggesting that high-ranking males are more efficient at protecting their own  
454 offspring (Palombit, 2003), or that they represent a threat for the offspring of females that  
455 have mated with subordinate rivals (Huchard et al., 2010). Second, female baboons actively  
456 compete to monopolize paternal care for their offspring once it is born, indicating that  
457 paternal services are important to females (Palombit, Cheney, & Seyfarth, 2001; this study).  
458 Finally, the heritability of social dominance is moderate (Wilson et al., 2011; Wilson, Gelin,  
459 Perron, & Réale, 2009), and this is probably especially true in species where the turnover of  
460 dominant males is relatively fast, and where many males will access dominance at one point  
461 in their life, as is the case for baboons.

462 Wider evidence of female intrasexual competition over mating opportunities or  
463 partners is increasingly obvious in other promiscuous primates. Bailey, Eberly, and Packer  
464 (2015) found that female olive baboons experienced less aggression from unrelated females  
465 after the onset of their pregnancy sign (female baboons exhibit a deep reddening of the  
466 paracallosal skin approximately 3 weeks after conception: Altmann 1973), and proposed that  
467 pregnancy coloration may be a mechanism by which females advertise their change of  
468 reproductive status to escape mating competition with other females. In primates living in  
469 multimale–multifemale groups, exaggerated sexual signals such as sexual swellings and  
470 copulation calls are commonly found. Such signals, which have probably evolved in response

471 to male mate choice (Nunn, 1999; Zinner, Nunn, van Schaik, & Kappeler, 2004), largely  
472 imply that sexually receptive females face intense competition to be chosen (Clutton-Brock &  
473 Huchard, 2013; Fitzpatrick, Altmann, & Alberts, 2015; Huchard et al., 2009) and may  
474 compete to obtain the right quantity of male care for their offspring (Alberts & Fitzpatrick,  
475 2012). In chimpanzees, *Pan troglodytes*, females refrain from producing copulation calls if a  
476 high-ranking female is nearby, suggesting that they are trying to conceal their sexual activity  
477 in the presence of potential female harassers (Townsend, Deschner, & Zuberbuehler, 2008).

478

#### 479 *Some evidence of competition over male social partners*

480 Overall, we found mixed evidence in support of our hypothesis that females compete over  
481 paternal care: lactating females did not receive most aggression from other lactating females,  
482 but instead received comparable levels of aggression from females in all reproductive states in  
483 both periods. However, lactating females received much higher levels of aggression in the  
484 unstable period (Fig. 2b), when the number of immigrant males and of adult females was  
485 high. A previous study in our population has shown that male–female friendships start with  
486 infant conception and are maintained throughout pregnancy and lactation (Baniel et al., 2016).  
487 As a result, males are often engaged in friendships with multiple pregnant and lactating  
488 females and may be mate guarding a swollen female at the same time. All these females share  
489 the same goal of maintaining close proximity to the male to benefit from his services, but  
490 there is only limited space around him (Huchard & Cowlshaw, 2011). This may explain why  
491 lactating females are targeted by pregnant, lactating and swollen females, as well as why  
492 aggression increases with the number of females in the group. Moreover, while lactating and  
493 pregnant females may be less diligent about staying close to their offspring’s sire at times of  
494 social stability, they may compete more aggressively for access during periods of instability,  
495 when they are stressed by immigrant males (Engh et al., 2006) and the associated risks of

496 infanticide and feticide increase (Pereira, 1983; Zippel et al., 2017). Further analyses of  
497 female–female aggression that explicitly take patterns of male–female friendships into  
498 account will help to elucidate these patterns.

499

#### 500 *Lack of evidence for competition over food*

501 We found little support for the hypothesis that females compete mainly over food: aggression  
502 was not maximal among pregnant and lactating females, which experience the highest  
503 energetic demands, nor did it peak when food was scarce. The absence of support for the  
504 competition-for-food hypothesis is surprising, because savannah baboons often live in  
505 demanding environments where body condition varies with food abundance (e.g. Altmann,  
506 Scheller, Altmann, Muruthi, & Sapolsky, 1993; Bercovitch & Strum, 1993) and affects female  
507 reproductive success (Beehner, Nguyen, Wango, Alberts, & Altmann, 2006; Huchard et al.,  
508 2009). We can envisage three possible explanations, which are not mutually exclusive. First,  
509 it may be that our measure of food abundance, NDVI ‘greenness’, is a poor proxy during the  
510 dry season, when most of our data were collected. This is because the baboons then forage  
511 mostly in the woodland patches of the dry Swakop riverbed, which have perennial leaf cover  
512 by virtue of the groundwater supporting them. Second, it is also possible that the existence of  
513 strict dominance hierarchies among females efficiently regulates feeding competition (the  
514 rank difference between aggressor and receiver was a strong predictor of the likelihood of  
515 receiving aggression) but not mating competition, where the stakes are higher and male  
516 strategies intrude, with males exerting mate choice (Huchard & Cowlshaw, 2011; Isbell,  
517 1991). Third, females may also reduce aggression during foraging through social strategies.  
518 Previous studies in chacma baboons have shown that low-ranking females with strong social  
519 bonds to other females receive less agonism during foraging and are better tolerated at shared  
520 feeding sites (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; King, Isaac, & Cowlshaw,

521 2009; Marshall, Carter, Ashford, Rowcliffe, & Cowlshaw, 2015). However, this is unlikely to  
522 be the case with mating competition, where females cannot easily share a male partner.

523

#### 524 *Lack of evidence for reproductive suppression*

525 We found no support for reproductive suppression: swollen females received most of their  
526 aggression from other swollen females, and not from pregnant and lactating females. Previous  
527 studies in yellow baboons showing that regular attacks from dominant females towards  
528 cycling subordinate females could increase the number of cycles before conception (Wasser  
529 & Starling, 1988, 1995) did not take the dominance rank of the victim and the reproductive  
530 state of the aggressor into account, so their results remain difficult to interpret. It is possible  
531 however, that reproductive suppression takes other forms to that envisaged here. For example,  
532 pregnant and lactating females could also attack females in early pregnancy to induce  
533 miscarriage, or nonswollen females (before they become swollen) to suppress ovulation, or  
534 specifically target those females that attempt to have sex with their male friend (instead of any  
535 swollen female indiscriminately). Further analyses that explore female–female aggression in  
536 these time windows and contexts may help to evaluate these hypotheses.

537

#### 538 *Variation in intensity of reproductive competition*

539 This work highlights that the determinants and intensity of female–female competition change  
540 through time according to variation in sociodemographic factors. Female baboons exchanged  
541 higher rates of aggression (regardless of reproductive state) when more females were present  
542 in the group and in a period of greater social instability among males. In addition, the patterns  
543 of dyadic interactions were also altered across time periods. In 2005–2006, when few males  
544 were present in each group (see Table A1), aggression was maximal among swollen females;  
545 in 2013–2014, when the male hierarchy was unstable, lactating females were the main target

546 of female aggression, as a likely response to the higher competition for social access to  
547 protective male partners. In line with the idea that females compete for males, Cheney, Silk,  
548 and Seyfarth (2012) found that as the number of swollen females per adult male increased in  
549 the Moremi population of chacma baboons there were higher rates of female aggression, less  
550 stable female bonds and increased female mortality, suggesting an increase in female  
551 reproductive competition when males are in shorter supply. Overall, our results add to  
552 growing evidence that the direction and strength of sexual selection in females are largely  
553 context dependent, and that female reproductive strategies are flexible and adjusted to socio-  
554 environmental factors (Gowaty, 2004; Gowaty & Hubbell, 2005). It also stresses the need to  
555 study social and sexual behaviour over long periods of time and under different  
556 sociodemographic conditions (Clutton-Brock & Sheldon, 2010), since we could have drawn  
557 different conclusions on the drivers of female reproductive competition if focusing only on  
558 the 2005–2006 or 2013–2014 data sets.

559

## 560 *Conclusion*

561 Our study found that the intensity and determinants of aggression among females reflect  
562 reproductive competition more closely than resource competition in wild chacma baboons,  
563 and specifically sexual and social access to males. Mating competition between females  
564 appears important, even though baboons are promiscuous and breed throughout the year with  
565 few females being synchronously sexually receptive, so that access to sex by females should  
566 rarely be limiting. Females may, in fact, compete over male protection services at two distinct  
567 points in the reproductive cycle: before conception, when swollen females are competing for  
568 sexual access to mates that have the potential to become effective infant protectors, and after  
569 conception, when lactating females are competing for the social proximity of the offspring's  
570 father. Importantly, the intensity of reproductive competition also appears to vary with those

571 demographic factors (such as male immigration rates) and social factors (such as male rank  
572 stability) that affect male partner availability and infanticide risk.

573

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587

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855

856 **APPENDIX**

857 **Table 1.** Influence of the focal female reproductive state on the rate of agonistic interactions received from other females

Response variable	Fixed factors	Levels	Estimate	SE	95% confidence interval	LRT	df	P	
Rate of aggression received (no./h)	Reproductive state <sup>a</sup>	Nonswollen	0.37	0.25	[-0.13; 0.87]				
		Swollen	0.53	0.18	<b>[0.17; 0.89]</b>				
		Lactating	-0.11	0.21	[-0.53; 0.31]				
	Period <sup>b</sup>	unstable	0.86	0.27	<b>[0.34; 1.39]</b>				
		Reproductive state <sup>a</sup> *Period <sup>b</sup>	Nonswollen: unstable	-0.15	0.28	[-0.70; 0.40]	48.59	3	<b>&lt;0.001</b>
			Swollen: unstable	-0.64	0.21	<b>[-1.06; -0.22]</b>			
	Lactating: unstable		0.87	0.24	<b>[0.40; 1.34]</b>				
	Reproductive synchrony		-0.21	0.10	<b>[-0.41; -0.02]</b>	4.57	1	<b>0.033</b>	
	NDVI <sub>UDw</sub>		0.02	0.14	[-0.26; 0.30]	0.02	1	0.896	
	No. of adult females		-0.35	0.19	[-0.72; 0.02]	3.30	1	0.069	
Dominance rank		-1.31	0.14	<b>[-1.59; -1.03]</b>	52.13	1	<b>&lt;0.001</b>		
Age		-0.24	0.12	[-0.48; 0.01]	3.08	1	0.079		
Group <sup>c</sup>	L		0.04	0.16	[-0.27; 0.35]	0.07	1	0.797	

858

859 Parameters and tests are based on 2919 observations (including 1250 incidents of aggression received) distributed among 50 females and were  
 860 analysed using a GLMM controlling for the date of focal observation and focal female identity. Likelihood ratio tests (LRTs) are used to test for  
 861 the significance of each variable (but are not given if the fixed effect is involved in an interaction), while the confidence intervals are used to test  
 862 for the significance of each level of the qualitative variables. The 95% confidence intervals and *P* values of statistically significant results are  
 863 highlighted in bold.

864 <sup>a</sup> Reference category: pregnant.

865 <sup>b</sup> Reference category: stable.

866 <sup>c</sup> Reference category: J.

867 **Table 2.** Influence of the reproductive state of the aggressor on the occurrence of agonistic interactions received by swollen females

868

Response variable	Fixed factors	Levels	Estimate	SE	95% confidence interval	LRT	df	P
No. of aggressive acts received by swollen females <sup>a</sup>	Reproductive state aggressor	Nonswollen (ref: pregnant)	-0.08	0.19	[-0.46; 0.29]	32.54	3	< <b>0.001</b>
		Swollen (ref: pregnant)	0.65	0.18	<b>[0.31; 1.00]</b>			
		Lactating (ref: pregnant)	-0.22	0.17	[-0.56; 0.11]			
		Swollen (ref: nonswollen)	0.74	0.15	<b>[0.44; 1.03]</b>			
		Swollen (ref: lactating)	0.87	0.2	<b>[0.48; 1.27]</b>			
		Lactating (ref: nonswollen)	-0.14	0.21	[-0.55; 0.28]			
	Relatedness aggressor–receiver		-0.26	0.14	[-0.53; 0.00]	3.81	1	0.051
	Rank difference aggressor–receiver		2.02	0.27	<b>[1.50; 2.54]</b>	48.13	1	< <b>0.001</b>
	OSR		0.64	0.37	[-0.09; 1.37]	2.83	1	0.092
	Proportion swollen in group		-0.83	0.51	[-1.83; 0.17]	2.50	1	0.114
No. of adult females		-1.07	0.33	<b>[-1.71; -0.42]</b>	9.99	1	<b>0.002</b>	
Period <sup>b</sup>	Unstable	0.31	0.43	[-0.54; 1.15]	0.49	1	0.483	
Group <sup>c</sup>	L	0.28	0.42	[-0.55; 1.11]	0.43	1	0.512	

869

870 Parameters and tests are based on 1345 focal observations (including 417 incidents of aggression received) distributed among 52 aggressors and

871 36 receivers. The GLMM was performed controlling for aggressor and receiver identity. Likelihood ratio tests (LRTs) are used to test for the

872 significance of each variable, while the confidence intervals are used to test for the significance of each level of the qualitative variables. The

873 95% confidence intervals and *P* values of statistically significant results are highlighted in bold.

874 <sup>a</sup>The duration (h) of observation of each dyad was fitted as an offset fixed factor, to control for variation in observation time across dyads.

875 <sup>b</sup>Reference category: stable.

876 <sup>c</sup>Reference category: J.

877 **Table 3.** Influence of the reproductive state of the aggressor on the occurrence of agonistic interactions received by *lactating* females.

878

Response variable	Fixed factors	Levels	Estimate	SE	95% confidence interval	LRT	df	P
No. of aggressive acts received by lactating females <sup>a</sup>	Reproductive state aggressor	Nonswollen (ref: pregnant)	-0.09	0.28	[-0.64; 0.47]	2.46	3	0.482
		Swollen (ref: pregnant)	0.31	0.24	[-0.16; 0.78]			
		Lactating (ref: pregnant)	-0.08	0.25	[-0.57; 0.40]			
		Swollen (ref: nonswollen)	0.40	0.30	[-0.19; 0.98]			
		Swollen (ref: lactating)	0.40	0.30	[-0.19; 0.98]			
		Lactating (ref: nonswollen)	0.00	0.30	[-0.59; 0.60]			
	Relatedness aggressor-receiver		0.05	0.17	[-0.29; 0.39]	0.10	1	0.756
	Rank difference aggressor-receiver		2.98	0.42	<b>[2.16; 3.79]</b>	51.25	1	<b>&lt;0.001</b>
	Proportion lactating in group		-0.09	0.35	[-0.77; 0.60]	0.06	1	0.801
	No. of adult females		0.13	0.44	[-0.73; 0.99]	0.09	1	0.764
Period <sup>b</sup>	unstable	0.64	0.56	[-0.46; 1.74]	1.29	1	0.256	
Group <sup>c</sup>	L	0.30	0.53	[-0.75; 1.34]	0.32	1	0.574	

879

880 Parameters and tests are based on 571 focal observations (including 231 incidents of aggression received) distributed among 52 aggressors and  
 881 35 receivers. The GLMM was performed controlling for aggressor and receiver identity. Likelihood ratio tests (LRTs) are used to test for the  
 882 significance of each variable, while the confidence intervals are used to test for the significance of each level of the qualitative variables. The  
 883 95% confidence intervals and *P* values of statistically significant results are highlighted in bold.

884 <sup>a</sup> The duration(h) of observation of each dyad was fitted as an offset fixed factor, to control for variation in observation time across dyads.

885 <sup>b</sup> Reference category: stable.

886 <sup>c</sup> Reference category: J.

887 **Table A1.** Sociodemographic parameters of J and L groups in the stable period (2005–2006) and the unstable period (2013–2014).

888

	Stable period (2005–2006)	Unstable period (2013–2014)
No. of adult males	5.4 ± 1.9	8.7 ± 1.3
<b>No. of immigrant males</b>	<b>?<sup>a</sup>–3 (J, L)</b>	<b>5-7 (J, L)</b>
<b>No. alpha male take-overs<sup>b</sup></b>	<b>0-1 (L, J)</b>	<b>11-16 (J, L)</b>
No. of adult females	12.9 ± 3.7	17.8 ± 0.8
Sex ratio	1 male for 2.54 females	1 male for 2.10 females
No. of nonswollen females	1.8 ± 1.2	3.1 ± 2.1
<b>No. of swollen females</b>	<b>1.3 ± 1.3</b>	<b>2.6 ± 1.8</b>
No. of pregnant females	3.6 ± 2.4	6.5 ± 2.3
No. of lactating females	2.7 ± 2.5	2.6 ± 1.4
Operational sex ratio	0.36 ± 0.26	0.30 ± 0.20
Reproductive synchrony	0.74 ± 0.11	0.83 ± 0.12

889

890 The demographic parameters are present as a daily mean ± SD (including all days where the groups were followed). Those sociodemographic  
891 parameters that differ by ≥100% are highlighted in bold.

892 <sup>a</sup> J group was habituated in 2005 onward, so the group composition was unknown in 2004 and consequently the number of new immigrant males  
893 in 2005 is unknown. However, no new male immigrated in J group from 2005 to 2006.

894 <sup>b</sup> Number of changes in the identity of the alpha male per time step, based on Elo-rating scores.

895 **Table A2:** Demography of J and L groups in 2005, 2006, 2013 and 2014

896

Year	Number of adult males		Number of adult females		Number of juveniles <sup>a</sup>	
	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

897

898 Demography varies due to emigrations, immigrations, births, deaths, and transitions to adulthood.

899 <sup>a</sup>Subadult males (i.e. between 4 and 8 years old) are counted as juveniles in this study.

900 **Table A3.** Influence of the focal female reproductive state on the rate of agonistic interactions received from other females in the stable period  
 901 (2005–2006) and in the unstable period (2013–2014)

Response variable	Fixed factors	Levels	Stable period						Unstable period					
			Estimate	SE	95% confidence interval	LRT	df	P	Estimate	SE	95% confidence interval	LRT	df	P
Rate of aggression received (number/h)	Reproductive state	Nonswollen (ref: pregnant)	0.56	0.28	<b>[0.01; 1.12]</b>	16.81	3	< <b>0.001</b>	0.26	0.12	<b>[0.02; 0.50]</b>	50.72	3	< <b>0.001</b>
		Swollen (ref: pregnant)	0.58	0.21	<b>[0.18; 0.99]</b>				-0.09	0.12	[-0.31; 0.14]			
		Lactating (ref: pregnant)	-0.16	0.23	[-0.61; 0.28]				0.70	0.11	<b>[0.49; 0.92]</b>			
		Swollen (ref: nonswollen)	0.02	0.22	[-0.4; 0.44]				-0.35	0.11	<b>[-0.57; -0.12]</b>			
		Swollen (ref: lactating)	0.75	0.20	<b>[0.35; 1.15]</b>				-0.79	0.12	<b>[-1.03; -0.55]</b>			
		Lactating (ref: nonswollen)	-0.73	0.28	<b>[-1.27; -0.18]</b>				0.44	0.13	<b>[0.19; 0.69]</b>			
	Reproductive synchrony		-0.27	0.16	[-0.59; 0.05]	2.63	1	0.105	-0.21	0.13	[-0.46; 0.04]	2.57	1	0.109
	NDVI <sub>UDW</sub>		-0.26	0.34	[-0.94; 0.41]	0.59	1	0.442	0.02	0.16	[-0.29; 0.33]	0.01	1	0.913
	No. of adult females		1.78	1.04	[-0.26; 3.83]	2.92	1	0.088	-1.85	0.57	<b>[-2.98; -0.73]</b>	10.07	1	<b>0.002</b>
	Dominance rank		-1.84	0.30	<b>[-2.44; -1.25]</b>	30.93	1	< <b>0.001</b>	-1.22	0.16	<b>[-1.52; -0.91]</b>	39.01	1	< <b>0.001</b>
	Age		0.41	0.33	[-0.23; 1.05]	1.73	1	0.188	-0.44	0.15	<b>[-0.73; -0.16]</b>	8.53	1	<b>0.003</b>
	Group <sup>a</sup>	L	1.78	1.05	[-0.27; 3.83]	2.89	1	0.089	0.18	0.17	[-0.16; 0.52]	1.03	1	0.311

902 Parameters and tests are based on 1428 observations (including 471 incidents of aggression received) distributed among 24 females in the stable  
 903 period and on 1491 observations (including 779 incidents of aggression received) distributed among 39 females in the unstable period; they were  
 904 analysed using a GLMM controlling for the date of focal observation and focal female identity. Likelihood ratio tests (LRTs) are used to test for  
 905 the significance of each variable, while the confidence intervals are used to test for the significance of each level of the qualitative variables. The  
 906 95% confidence intervals and *P* values of statistically significant results are highlighted in bold.

907 <sup>a</sup> Reference category: J.

909 **Table A4.** Influence of the reproductive state of the aggressor on the occurrence of agonistic interactions received by pregnant females

910

Response variable	Fixed factors	Levels	Estimate	SE	95% confidence interval	LRT	df	P
No. of aggressive acts received by pregnant females <sup>a</sup>	Reproductive state aggressor	Non-swollen (ref: pregnant)	0.19	0.26	[-0.32; 0.69]	7.04	3	0.071
		Swollen (ref: pregnant)	-0.07	0.29	[-0.64; 0.50]			
		Lactating (ref: pregnant)	-0.61	0.27	<b>[-1.14; -0.09]</b>			
		Swollen (ref: nonswollen)	-0.26	0.30	[-0.85; 0.33]			
		Swollen (ref: lactating)	0.54	0.37	[-0.18; 1.26]			
		Lactating (ref: nonswollen)	-0.8	0.32	<b>[-1.43; -0.17]</b>			
	Relatedness aggressor-receiver		-0.10	0.18	[-0.46; 0.26]	0.23	1	0.633
	Rank difference aggressor-receiver		2.16	0.44	<b>[1.29; 3.03]</b>	35.87	1	<b>&lt;0.001</b>
	Proportion pregnant in group		0.49	0.37	[-0.23; 1.21]	1.73	1	0.189
	No. of adult females		0.16	0.5	[-0.81; 1.14]	0.04	1	0.845
Period <sup>b</sup>	Unstable		-0.25	0.57	[-1.37; 0.87]	0.08	1	0.784
Group <sup>c</sup>	L		0.05	0.52	[-0.96; 1.07]	0.02	1	0.893

911

912 Parameters and tests are based on 676 focal observations (including 182 incidents of aggression received) distributed among 52 aggressors and  
 913 39 receivers. The GLMM was performed controlling for aggressor and receiver identity. Likelihood ratio tests (LRTs) are used to test for the  
 914 significance of each variable, while the confidence intervals are used to test for the significance of each level of the qualitative variables. The  
 915 95% confidence intervals and *P* values of statistically significant results are highlighted in bold.

916 <sup>a</sup> The time (h) of observation of each dyad was fitted as an offset fixed factor, to control for variation in observation time across dyads.

917 <sup>b</sup> Reference category: stable.

918 <sup>c</sup> Reference category: J.

919 **Table A5.** Influence of the reproductive state of the aggressor on the occurrence of agonistic interactions received by cycling nonswollen females

Response variable	Fixed factors	Levels	Estimate	SE	95% confidence interval	LRT	df	P
No. of aggressive acts received by nonswollen females <sup>a</sup>	Reproductive state aggressor	Nonswollen (ref: pregnant)	-0.11	0.31	[-0.72; 0.50]	0.66	3	0.883
		Swollen (ref: pregnant)	-0.07	0.35	[-0.76; 0.61]			
		Lactating (ref: pregnant)	0.15	0.26	[-0.36; 0.65]			
		Swollen (ref: nonswollen)	0.04	0.42	[-0.78; 0.86]			
		Swollen (ref: lactating)	0.87	0.20	[0.48; 1.27]			
		Lactating (ref: nonswollen)	0.26	0.35	[-0.43; 0.95]			
	Relatedness aggressor–receiver		0.11	0.21	[-0.30; 0.52]	0.27	1	0.603
	Rank difference aggressor–receiver		1.78	0.32	<b>[1.16; 2.40]</b>	28.34	1	<b>&lt;0.001</b>
	Proportion nonswollen in group		-1.23	0.45	<b>[-2.11; -0.35]</b>	8.14	1	<b>0.004</b>
	No. of adult females		-0.17	0.53	[-1.20; 0.87]	0.10	1	0.756
Period <sup>b</sup>	Unstable	0.15	0.55	[-0.92; 1.22]	0.07	1	0.786	
Group <sup>c</sup>	L	0.93	0.52	[-0.08; 1.94]	3.24	1	0.072	

920

921 Parameters and tests are based on 434 focal observations (including 123 incidents of aggression received) distributed among 51 aggressors and  
 922 30 receivers. The GLMM was performed controlling for aggressor and receiver identity. Likelihood ratio tests (LRTs) are used to test for the  
 923 significance of each variable, while the confidence intervals are used to test for the significance of each level of the qualitative variables. The  
 924 95% confidence intervals and *P* values of statistically significant results are highlighted in bold.

925 <sup>a</sup> The duration(h) of observation of each dyad was fitted as an offset fixed factor, to control for variation in observation time across dyads.

926 <sup>b</sup> Reference category: stable.

927 <sup>c</sup> Reference category: J.

928 **Table A6.** Summary of hypotheses, predictions and results, according to the two sets of analyses

929

930

	Hypothesis				Results of tests
	Food	Mates	Paternal care	Reproductive suppression	
931					
932	<b>Overall patterns by reproductive state</b>				Tables 1, A3, Figs 1, 2
933	Swollen females received most aggression	-	+ <sup>s</sup> [yes]	-	+ <sup>s</sup> [yes]
934	Lactating females received most aggression	-	-	+ <sup>u</sup> [yes]	-
935	Pregnant and lactating females received most aggression	+ <sup>u</sup> [no]	-	-	-
936	Aggression higher when food is scarce	+ <sup>u</sup> [no]	-	-	-
937	Aggression higher when females are in synchrony	+ <sup>b</sup> [yes]	+ <sup>b</sup> [yes]	+ <sup>b</sup> [yes]	-
938	<b>Dyadic patterns by reproductive state</b>				Tables 2, 3, A4, A5, Fig. 3
939	Aggression higher among pregnant and lactating females	+ <sup>u</sup> [no]	-	-	-
940	Aggression higher among lactating females	-	-	+ <sup>u</sup> [no]	-
941	Aggression higher among swollen females	-	+ <sup>b</sup> [yes]	-	-
942	Aggression higher when the OSR is higher	-	+ <sup>u</sup> [no]	-	-
943	Pregnant and lactating females target swollen females	-	-	-	+ <sup>u</sup> [no]

941 A + and- indicate whether the stated pattern is predicted under that hypothesis or not, and the outcome is given in brackets as either supported  
 942 [yes] or unsupported [no]. Where supported, a superscript indicates whether the pattern is observed in the stable period [s], unstable period [u] or  
 943 both [b]. OSR: operational sex ratio.

944 **Figure legend**

945

946 **Figure 1:** Representation of the estimates of fixed effects and 95% confidence intervals (CI)  
947 of the GLMM modelling the rate of aggressive interactions received (a) in the stable period  
948 (2005–2006) and (b) in the unstable period (2013–2014). The vertical dashed line represents  
949 zero (fixed effects are not significant when their CI cross this line). The fixed effects for  
950 reproductive state are shown relative to pregnant females. NSW: cycling nonswollen; SW:  
951 swollen; L: lactating.

952

953 **Figure 2:** Distribution of the rate of aggressive interactions received (a) in the stable period  
954 (2005–2006) and (b) in the unstable period (2013–2014) by females in different reproductive  
955 states: cycling nonswollen (NSW), swollen (SW), pregnant (P) and lactating (L). Box plots  
956 are drawn from the raw individual means per year. The bottom and top of the box,  
957 respectively, represent the 25th and 75th quartiles and the bold horizontal line the median.  
958 Whiskers show the interquartile range. Open squares indicate the mean of the distribution.  
959 The significance of the comparisons between reproductive states is evaluated by changing  
960 contrasts in each GLMM (see Table A3). Note that, because the raw data do not control for  
961 any other fixed or random effects, the statistical tests give the most reliable indication of  
962 where true differences lie. \* $P < 0.05$ .

963

964 **Figure 3:** Distribution of the rate of aggressive interactions received by (a) swollen, (b)  
965 lactating, (c) pregnant and (d) cycling nonswollen females from females in different  
966 reproductive states: cycling nonswollen (NSW), swollen (SW), pregnant (P) and lactating (L).  
967 Box plots are drawn from the raw individual means per year. The bottom and top of the box,  
968 respectively, represent the 25th and 75th quartiles and the bold horizontal line the median.  
969 Whiskers show the interquartile range. Open squares indicate the mean of the distribution.  
970 The significance of the comparisons between reproductive states is evaluated by changing  
971 contrasts in each GLMM. Note that, because the raw data do not control for any other fixed or  
972 random effects, the statistical tests give the most reliable indication of where true differences  
973 lie. \* $P < 0.05$ .

974

Figure 1.

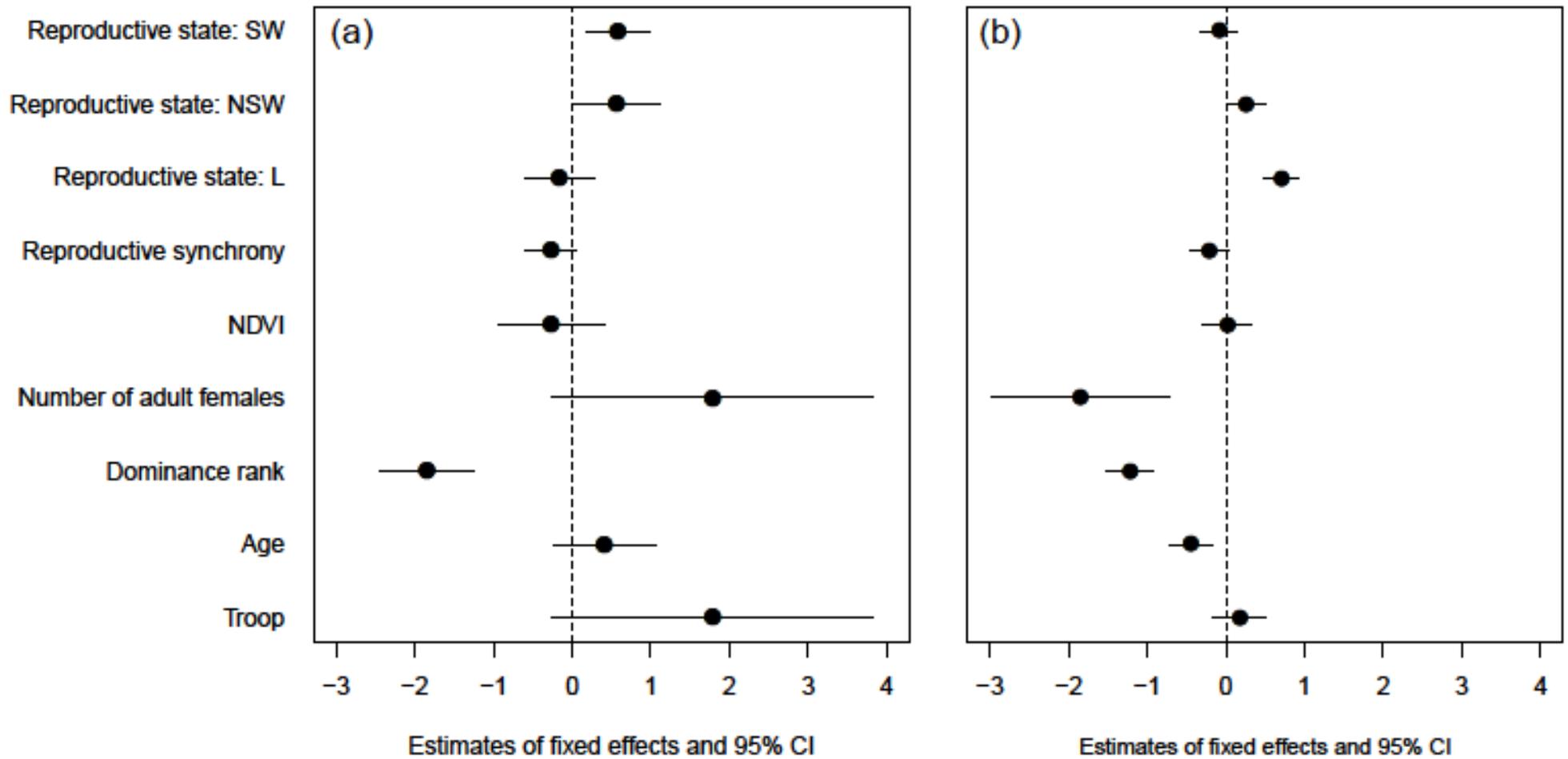


Figure 2.

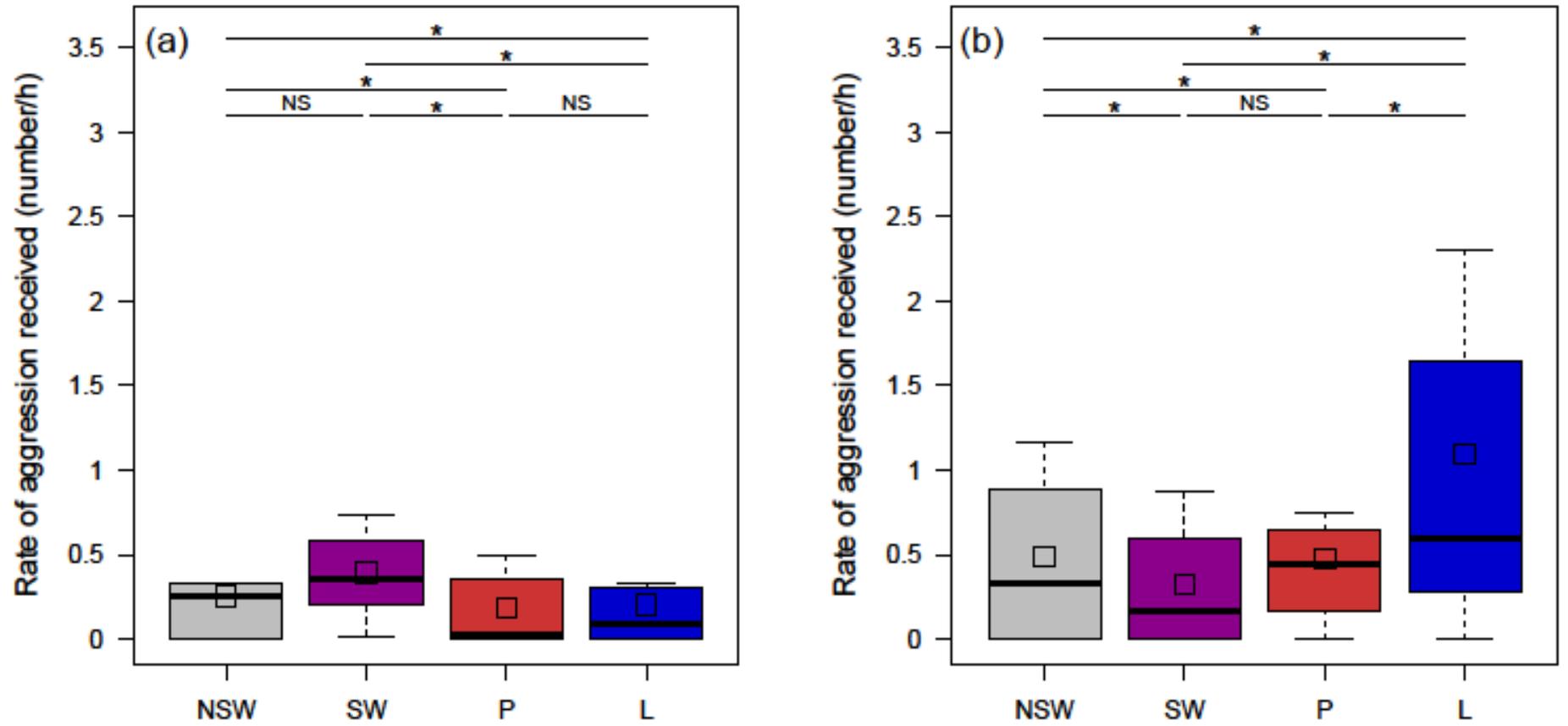


Figure 3.

