Context dependence of female reproductive competition in wild chacma baboons

Alice Baniel[1,2,3,§], Guy Cowlishaw[3], Elise Huchard[2]

[1] Institute for Advanced Study in Toulouse, Toulouse, France

[2] Institut des Sciences de l'Evolution de Montpellier, UMR 5554, CNRS, Université de Montpellier, Montpellier, France

[3] Institute of Zoology, Zoological Society of London, London, U.K.

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[§]Correspondence: A. Baniel, Institute for Advanced Study in Toulouse, 21 allée de Brienne, 31015 Cedex 6, Toulouse, France.
E-mail address: alice.baniel@gmail.com

ABSTRACT

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

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

INTRODUCTION

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

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

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

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

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

In this study, we tested whether female–female aggression is primarily driven by instantaneous competition for food (Hypothesis 1, H1), mates (H2) or paternal care (H3), or by competition for future resources through reproductive suppression (H4). If females compete over food (H1), we expected aggression to peak among lactating and pregnant females (which face the highest energetic needs; Prediction 1a, P1a) and environmental factors to influence aggression (with higher levels when food is scarce; P1b). If females compete for mating opportunities or sperm (H2), we expected aggression to be highest among sexually receptive females (P2a) and to increase with a more female-biased operational sex ratio (OSR; P2b). If females compete over paternal care (H3), we predicted that aggression would be highest among lactating females (P3a). If females attempt to cause reproductive suppression (H4), we predicted that pregnant and/or lactating females would target sexually receptive females (P4). To test these predictions, we examined variation in levels of female–female aggression received in relation to female reproductive state and further investigated dyadic patterns of agonistic interactions to investigate whether aggression received by a female varied according to her reproductive state and that of her aggressors. We investigated the determinants of female–female aggression in two periods characterized by contrasting sociodemographic dynamics (see Appendix Table A1). In the first period (2005–2006), there were few adult male immigrants and the male dominance hierarchy was stable. In the second period (2013–2014), the arrival of multiple male migrants led to intense male–male competition, repeated alpha-male take-overs and instability in the male hierarchy (Baniel, Cowlishaw, & Huchard, 2016), which are typically associated with high infanticide risk (Lukas & Huchard, 2014; Palombit, 1999; Zipple et al., 2017). We therefore expected females to compete more over paternal care in the second period (P3b). Finally, we also investigated whether the extent of reproductive synchrony at the group level (i.e. the proportion of females in the same reproductive state in a group at the same time, Ims 1990) influenced the aggression exchanged between females, as females in the same reproductive state are expected to compete with one another under hypotheses H1–H3. We also investigated the potential independent effects of dominance rank and kinship on these patterns.

METHODS

Study animals

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

Behavioural data

All sexually mature females were chosen as focal subjects. We conducted 1 h focal animal samples (Altmann, 1974) spread equally across the day (divided into four 3 h blocks) for each individual. The choice of focal animal was semirandomized to balance observations equally across individuals, time periods and reproductive states. The same individual was not sampled more than once per half day. We included only focal samples ≥ 45 min (mean focal length±SD: 59.7±3.5 min). A total of 3140 focal samples on 53 females were collected across the following reproductive states: cycling nonswollen (*N*=469 observations of 36 females, range 1–40, mean±SD: 13.0±9.7 focal samples per individual), lactating (586, 41, 1–34, 14.3±8.9), pregnant (714, 47, 1–46, 15.2±9.7) and swollen (1371, 39, 2–109, 35.2±31.5). Some females were present during all four study periods (2005, 2006, 2013, 2014) while others were present during only one to three periods (either because they became sexually mature or died). During focal samples, all occurrences of agonistic interactions (attacks, chases, threats) and approach–avoid interactions (displacements, supplants; for definitions, see Huchard & Cowlishaw, 2011) were noted on a continuous basis, along with the identity of the receiver and initiator. We observed 1339 aggressive incidents received (54 attacks, 97 chases, 78 threats, 540 displacements, 570 supplants). In addition, throughout the day, we collected ad libitum agonistic interactions, recording the identity of individuals and direction of interaction (N=2737 aggressive events observed).

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

Group level reproductive synchrony

To determine the extent of reproductive synchrony between females, we first calculated the Shannon–Weiner diversity index (H) for each day and for each group, $H = -\Sigma[(pi) \times \ln(pi)]$, where pi is the proportion of females in each reproductive state category i (number of nonswollen/swollen/pregnant/lactating females divided by the total number of females). We then used the equitability score, $E = H/H_{\max}$, where $H_{\max}$ is the number of categories (equal to 4), as our index of reproductive synchrony. Values close to zero indicate high reproductive synchrony (one or a subset of reproductive state(s) are predominant) and values close to one indicate low reproductive synchrony (the reproductive states are equally distributed).

Pairwise relatedness between females

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

Environmental data

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

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

Statistical analysis

Overall pattern of aggression received

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

Dyadic patterns of aggression received

We examined dyadic patterns of agonistic interactions received by females according to their reproductive states and the reproductive states of their aggressors. We arranged the data set as follows. For each focal female in a given reproductive state, we created a list of all other females in a given reproductive state that were groupmates (e.g. for female A when swollen, in a group including two other females, B and C, the dyads might comprise: A swollen→B swollen, A swollen→B pregnant, A swollen→C pregnant, A swollen→C lactating; while other combinations, such as A swollen→B lactating and A swollen→C nonswollen, were not observed). Dyads in a particular reproductive configuration were included only if they were observed for at least 5 h (i.e. only 53% of all possible dyads were included). We also created a variable 'Aggression' which summed all the aggressive interactions received by the focal female within each of these dyads. We then ran four GLMMs with a Poisson error structure for four subsets of the data set that were defined by whether the focal female (receiver of the dyad) was (1) nonswollen, (2) swollen, (3) pregnant or (4) lactating, using 'Aggression' as the response variable. The duration of focal observations available for a given dyad in a specific reproductive configuration, i.e. in a period during which the reproductive state of each interacting female did not change, was log transformed and included as an offset variable to control for the variation in observation time across dyads. Random effects comprised the crossed identity of the aggressor and receiver. Fixed effects comprised the following variables: the reproductive state of the aggressor (nonswollen, swollen, pregnant, lactating); the period of study (stable, 2005–2006 or unstable, 2013–2014); the interaction between the aggressor's reproductive state and the period of study, to test whether the pattern of aggression received by females in each reproductive state differed between periods; the rank difference between the aggressor and the focal receiver (positive if the aggressor is higher ranking than the receiver, and vice versa); the pairwise coefficient of relatedness between the focal receiver and the aggressor; the proportion of females in the same reproductive state as the focal receiver in the group (i.e. number of nonswollen/swollen/pregnant/lactating females, respectively, divided by the total number of adult females) to control for temporal variations in the number of females in each reproductive state; the total number of adult females in the group; and group identity.

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

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

Ethical note

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

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

RESULTS

Overall pattern of aggression received

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

Contrary to the feeding competition hypothesis (prediction P1b), $\mathrm{NDVI}_{\mathrm{UDw}}$ did not influence the amount of aggression received by females (Table 1, Fig. 1). As expected, increasing reproductive synchrony was found to intensify levels of aggression received by females. Finally, the effects of dominance rank were consistent across periods, with higher-ranking females receiving less aggression, while female age, the number of adult females in the group and group identity were not significant.

Dyadic patterns of aggression received

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

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

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

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

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

DISCUSSION

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

Evidence of competition over mating opportunities

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

Oestrous females may compete for sperm, good genes and/or future paternal care. Competition for sperm and fertilization insurance is not the most likely possibility, given that baboons are nonseasonal breeders (Clarke, Henzi, & Barrett, 2012) and that the OSR is usually male biased in groups. Females may show a preference for the dominant male, if his high rank reflects some aspect of his genetic quality or if he is able to provide the most effective infant protection services. Since a single male baboon can only mate-guard one female at a time (Alberts, Altmann, & Wilson, 1996; Alberts, Watts, & Altmann, 2003), two synchronous females are likely to compete over his sexual access. In line with this, Cheney, Silk, and Seyfarth (2012) found a positive correlation between the dominance ranks of male and female consort partners, suggesting that high-ranking females might successfully outcompete other females. Competition over paternal care may appear more likely than for good genes, for several reasons. First, offspring from subordinate males suffer higher infanticide risk, suggesting that high-ranking males are more efficient at protecting their own offspring (Palombit, 2003), or that they represent a threat for the offspring of females that have mated with subordinate rivals (Huchard et al., 2010). Second, female baboons actively compete to monopolize paternal care for their offspring once it is born, indicating that paternal services are important to females (Palombit, Cheney, & Seyfarth, 2001; this study). Finally, the heritability of social dominance is moderate (Wilson et al., 2011; Wilson, Gelin, Perron, & Réale, 2009), and this is probably especially true in species where the turnover of dominant males is relatively fast, and where many males will access dominance at one point in their life, as is the case for baboons.

Wider evidence of female intrasexual competition over mating opportunities or partners is increasingly obvious in other promiscuous primates. Bailey, Eberly, and Packer (2015) found that female olive baboons experienced less aggression from unrelated females after the onset of their pregnancy sign (female baboons exhibit a deep reddening of the paracallosal skin approximately 3 weeks after conception: Altmann 1973), and proposed that pregnancy coloration may be a mechanism by which females advertise their change of reproductive status to escape mating competition with other females. In primates living in multimale–multifemale groups, exaggerated sexual signals such as sexual swellings and copulation calls are commonly found. Such signals, which have probably evolved in response to male mate choice (Nunn, 1999; Zinner, Nunn, van Schaik, & Kappeler, 2004), largely imply that sexually receptive females face intense competition to be chosen (Clutton-Brock & Huchard, 2013; Fitzpatrick, Altmann, & Alberts, 2015; Huchard et al., 2009) and may compete to obtain the right quantity of male care for their offspring (Alberts & Fitzpatrick, 2012). In chimpanzees, *Pan troglodytes*, females refrain from producing copulation calls if a high-ranking female is nearby, suggesting that they are trying to conceal their sexual activity in the presence of potential female harassers (Townsend, Deschner, & Zuberbuehler, 2008).

Some evidence of competition over male social partners

Overall, we found mixed evidence in support of our hypothesis that females compete over paternal care: lactating females did not receive most aggression from other lactating females, but instead received comparable levels of aggression from females in all reproductive states in both periods. However, lactating females received much higher levels of aggression in the unstable period (Fig. 2b), when the number of immigrant males and of adult females was high. A previous study in our population has shown that male–female friendships start with infant conception and are maintained throughout pregnancy and lactation (Baniel et al., 2016). As a result, males are often engaged in friendships with multiple pregnant and lactating females and may be mate guarding a swollen female at the same time. All these females share the same goal of maintaining close proximity to the male to benefit from his services, but there is only limited space around him (Huchard & Cowlishaw, 2011). This may explain why lactating females are targeted by pregnant, lactating and swollen females, as well as why aggression increases with the number of females in the group. Moreover, while lactating and pregnant females may be less diligent about staying close to their offspring's sire at times of social stability, they may compete more aggressively for access during periods of instability, when they are stressed by immigrant males (Engh et al., 2006) and the associated risks of infanticide and feticide increase (Pereira, 1983; Zipple et al., 2017). Further analyses of female–female aggression that explicitly take patterns of male–female friendships into account will help to elucidate these patterns.

Lack of evidence for competition over food

We found little support for the hypothesis that females compete mainly over food: aggression was not maximal among pregnant and lactating females, which experience the highest energetic demands, nor did it peak when food was scarce. The absence of support for the competition-for-food hypothesis is surprising, because savannah baboons often live in demanding environments where body condition varies with food abundance (e.g. Altmann, Scheller, Altmann, Muruthi, & Sapolsky, 1993; Bercovitch & Strum, 1993) and affects female reproductive success (Beehner, Nguyen, Wango, Alberts, & Altmann, 2006; Huchard et al., 2009). We can envisage three possible explanations, which are not mutually exclusive. First, it may be that our measure of food abundance, NDVI ‘greenness’, is a poor proxy during the dry season, when most of our data were collected. This is because the baboons then forage mostly in the woodland patches of the dry Swakop riverbed, which have perennial leaf cover by virtue of the groundwater supporting them. Second, it is also possible that the existence of strict dominance hierarchies among females efficiently regulates feeding competition (the rank difference between aggressor and receiver was a strong predictor of the likelihood of receiving aggression) but not mating competition, where the stakes are higher and male strategies intrude, with males exerting mate choice (Huchard & Cowlishaw, 2011; Isbell, 1991). Third, females may also reduce aggression during foraging through social strategies. Previous studies in chacma baboons have shown that low-ranking females with strong social bonds to other females receive less agonism during foraging and are better tolerated at shared feeding sites (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; King, Isaac, & Cowlishaw, 2009; Marshall, Carter, Ashford, Rowcliffe, & Cowlishaw, 2015). However, this is unlikely to be the case with mating competition, where females cannot easily share a male partner.

Lack of evidence for reproductive suppression

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

Variation in intensity of reproductive competition

This work highlights that the determinants and intensity of female–female competition change through time according to variation in sociodemographic factors. Female baboons exchanged higher rates of aggression (regardless of reproductive state) when more females were present in the group and in a period of greater social instability among males. In addition, the patterns of dyadic interactions were also altered across time periods. In 2005–2006, when few males were present in each group (see Table A1), aggression was maximal among swollen females; in 2013–2014, when the male hierarchy was unstable, lactating females were the main target of female aggression, as a likely response to the higher competition for social access to protective male partners. In line with the idea that females compete for males, Cheney, Silk, and Seyfarth (2012) found that as the number of swollen females per adult male increased in the Moremi population of chacma baboons there were higher rates of female aggression, less stable female bonds and increased female mortality, suggesting an increase in female reproductive competition when males are in shorter supply. Overall, our results add to growing evidence that the direction and strength of sexual selection in females are largely context dependent, and that female reproductive strategies are flexible and adjusted to socio-environmental factors (Gowaty, 2004; Gowaty & Hubbell, 2005). It also stresses the need to study social and sexual behaviour over long periods of time and under different sociodemographic conditions (Clutton-Brock & Sheldon, 2010), since we could have drawn different conclusions on the drivers of female reproductive competition if focusing only on the 2005–2006 or 2013–2014 data sets.

Conclusion

Our study found that the intensity and determinants of aggression among females reflect reproductive competition more closely than resource competition in wild chacma baboons, and specifically sexual and social access to males. Mating competition between females appears important, even though baboons are promiscuous and breed throughout the year with few females being synchronously sexually receptive, so that access to sex by females should rarely be limiting. Females may, in fact, compete over male protection services at two distinct points in the reproductive cycle: before conception, when swollen females are competing for sexual access to mates that have the potential to become effective infant protectors, and after conception, when lactating females are competing for the social proximity of the offspring's father. Importantly, the intensity of reproductive competition also appears to vary with those demographic factors (such as male immigration rates) and social factors (such as male rank stability) that affect male partner availability and infanticide risk.

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APPENDIX

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[a]	Nonswollen	0.37	0.25	[-0.13; 0.87]			
		Swollen	0.53	0.18	**[0.17; 0.89]**			
		Lactating	-0.11	0.21	[-0.53; 0.31]			
	Period[b]	unstable	0.86	0.27	**[0.34; 1.39]**			
	Reproductive state[a]*Period[b]	Nonswollen: unstable	-0.15	0.28	[-0.70; 0.40]	48.59	3	**<0.001**
		Swollen: unstable	-0.64	0.21	**[-1.06; -0.22]**			
		Lactating: unstable	0.87	0.24	**[0.40; 1.34]**			
	Reproductive synchrony		-0.21	0.10	**[-0.41; -0.02]**	4.57	1	**0.033**
	NDVI_{UDw}		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	**[-1.59; -1.03]**	52.13	1	**<0.001**
	Age		-0.24	0.12	[-0.48; 0.01]	3.08	1	0.079
	Group[c]	L	0.04	0.16	[-0.27; 0.35]	0.07	1	0.797

Parameters and tests are based on 2919 observations (including 1250 incidents of aggression received) distributed among 50 females and were analysed using a GLMM controlling for the date of focal observation and focal female identity. Likelihood ratio tests (LRTs) are used to test for 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 for the significance of each level of the qualitative variables. The 95% confidence intervals and *P* values of statistically significant results are highlighted in bold.

[a] Reference category: pregnant.

[b] Reference category: stable.

[c] Reference category: J.

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

Response variable	Fixed factors	Levels	Estimate	SE	95% confidence interval	LRT	*df*	*P*
No. of aggressive acts received by swollen females[a]	Reproductive state aggressor	Nonswollen (ref: pregnant)	-0.08	0.19	[-0.46; 0.29]	32.54	3	**<0.001**
		Swollen (ref: pregnant)	0.65	0.18	**[0.31; 1.00]**			
		Lactating (ref: pregnant)	-0.22	0.17	[-0.56; 0.11]			
		Swollen (ref: nonswollen)	0.74	0.15	**[0.44; 1.03]**			
		Swollen (ref: lactating)	0.87	0.2	**[0.48; 1.27]**			
		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	**[1.50; 2.54]**	48.13	1	**<0.001**
	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	**[-1.71; -0.42]**	9.99	1	**0.002**
	Period[b]	Unstable	0.31	0.43	[-0.54; 1.15]	0.49	1	0.483
	Group[c]	L	0.28	0.42	[-0.55; 1.11]	0.43	1	0.512

Parameters and tests are based on 1345 focal observations (including 417 incidents of aggression received) distributed among 52 aggressors and 36 receivers. The GLMM was performed controlling for aggressor and receiver identity. Likelihood ratio tests (LRTs) are used to test for the significance of each variable, while the confidence intervals are used to test for the significance of each level of the qualitative variables. The 95% confidence intervals and *P* values of statistically significant results are highlighted in bold.

[a] The duration (h) of observation of each dyad was fitted as an offset fixed factor, to control for variation in observation time across dyads.

[b] Reference category: stable.

[c] Reference category: J.

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

Response variable	Fixed factors	Levels	Estimate	SE	95% confidence interval	LRT	*df*	*P*
No. of aggressive acts received by lactating females[a]	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	**[2.16; 3.79]**	51.25	1	**<0.001**
	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[b]	unstable	0.64	0.56	[-0.46; 1.74]	1.29	1	0.256
	Group[c]	L	0.30	0.53	[-0.75; 1.34]	0.32	1	0.574

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

[a] The duration(h) of observation of each dyad was fitted as an offset fixed factor, to control for variation in observation time across dyads.

[b] Reference category: stable.

[c] Reference category: J.

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

	Stable period (2005–2006)	Unstable period (2013–2014)
No. of adult males	5.4 ± 1.9	8.7 ± 1.3
No. of immigrant males	**?[a]–3 (J, L)**	**5-7 (J, L)**
No. alpha male take-overs[b]	**0-1 (L, J)**	**11-16 (J, L)**
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
No. of swollen females	**1.3 ± 1.3**	**2.6 ± 1.8**
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

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

[a] J group was habituated in 2005 onward, so the group composition was unknown in 2004 and consequently the number of new immigrant males in 2005 is unknown. However, no new male immigrated in J group from 2005 to 2006.

[b] Number of changes in the identity of the alpha male per time step, based on Elo-rating scores.

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

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

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

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

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

			Stable period						Unstable period					
Response variable	Fixed factors	Levels	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	**[0.01; 1.12]**	16.81	3	**<0.001**	0.26	0.12	**[0.02; 0.50]**	50.72	3	**<0.001**
		Swollen (ref: pregnant)	0.58	0.21	**[0.18; 0.99]**				-0.09	0.12	[-0.31; 0.14]			
		Lactating (ref: pregnant)	-0.16	0.23	[-0.61; 0.28]				0.70	0.11	**[0.49; 0.92]**			
		Swollen (ref: nonswollen)	0.02	0.22	[-0.4; 0.44]				-0.35	0.11	**[-0.57; -0.12]**			
		Swollen (ref: lactating)	0.75	0.20	**[0.35; 1.15]**				-0.79	0.12	**[-1.03; -0.55]**			
		Lactating (ref: nonswollen)	-0.73	0.28	**[-1.27; -0.18]**				0.44	0.13	**[0.19; 0.69]**			
	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
	$NDVI_{UDw}$		-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	**[-2.98; -0.73]**	10.07	1	**0.002**
	Dominance rank		-1.84	0.30	**[-2.44; -1.25]**	30.93	1	**<0.001**	-1.22	0.16	**[-1.52; -0.91]**	39.01	1	**<0.001**
	Age		0.41	0.33	[-0.23; 1.05]	1.73	1	0.188	-0.44	0.15	**[-0.73; -0.16]**	8.53	1	**0.003**
	Group[a]	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

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

[a] Reference category: J.

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

Response variable	Fixed factors	Levels	Estimate	SE	95% confidence interval	LRT	*df*	*P*
No. of aggressive acts received by pregnant females[a]	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	**[-1.14; -0.09]**			
		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	**[-1.43; -0.17]**			
	Relatedness aggressor-receiver		-0.10	0.18	[-0.46; 0.26]	0.23	1	0.633
	Rank difference aggressor-receiver		2.16	0.44	**[1.29; 3.03]**	35.87	1	**<0.001**
	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[b]	Unstable	-0.25	0.57	[-1.37; 0.87]	0.08	1	0.784
	Group[c]	L	0.05	0.52	[-0.96; 1.07]	0.02	1	0.893

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

[a] The time (h) of observation of each dyad was fitted as an offset fixed factor, to control for variation in observation time across dyads.

[b] Reference category: stable.

[c] Reference category: J.

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[a]	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	**[1.16; 2.40]**	28.34	1	**<0.001**
	Proportion nonswollen in group		-1.23	0.45	**[-2.11; -0.35]**	8.14	1	**0.004**
	No. of adult females		-0.17	0.53	[-1.20; 0.87]	0.10	1	0.756
	Period[b]	Unstable	0.15	0.55	[-0.92; 1.22]	0.07	1	0.786
	Group[c]	L	0.93	0.52	[-0.08; 1.94]	3.24	1	0.072

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

[a] The duration(h) of observation of each dyad was fitted as an offset fixed factor, to control for variation in observation time across dyads.

[b] Reference category: stable.

[c] Reference category: J.

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

	Hypothesis				Results of tests
	Food	Mates	Paternal care	Reproductive suppression	
Overall patterns by reproductive state					Tables 1, A3, Figs 1, 2
Swollen females received most aggression	-	+[yes^{s}]	-	+[yes^{s}]	
Lactating females received most aggression	-	-	+[yes^{u}]	-	
Pregnant and lactating females received most aggression	+[no]	-	-	-	
Aggression higher when food is scarce	+[no]	-	-	-	
Aggression higher when females are in synchrony	+[yes^{b}]	+[yes^{b}]	+[yes^{b}]	-	
Dyadic patterns by reproductive state					Tables 2, 3, A4, A5, Fig. 3
Aggression higher among pregnant and lactating females	+[no]	-	-	-	
Aggression higher among lactating females	-	-	+[no]	-	
Aggression higher among swollen females	-	+[yes^{b}]	-	-	
Aggression higher when the OSR is higher	-	+[no]	-	-	
Pregnant and lactating females target swollen females	-	-	-	+[no]	

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

Figure legend

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

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

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

Figure 1.

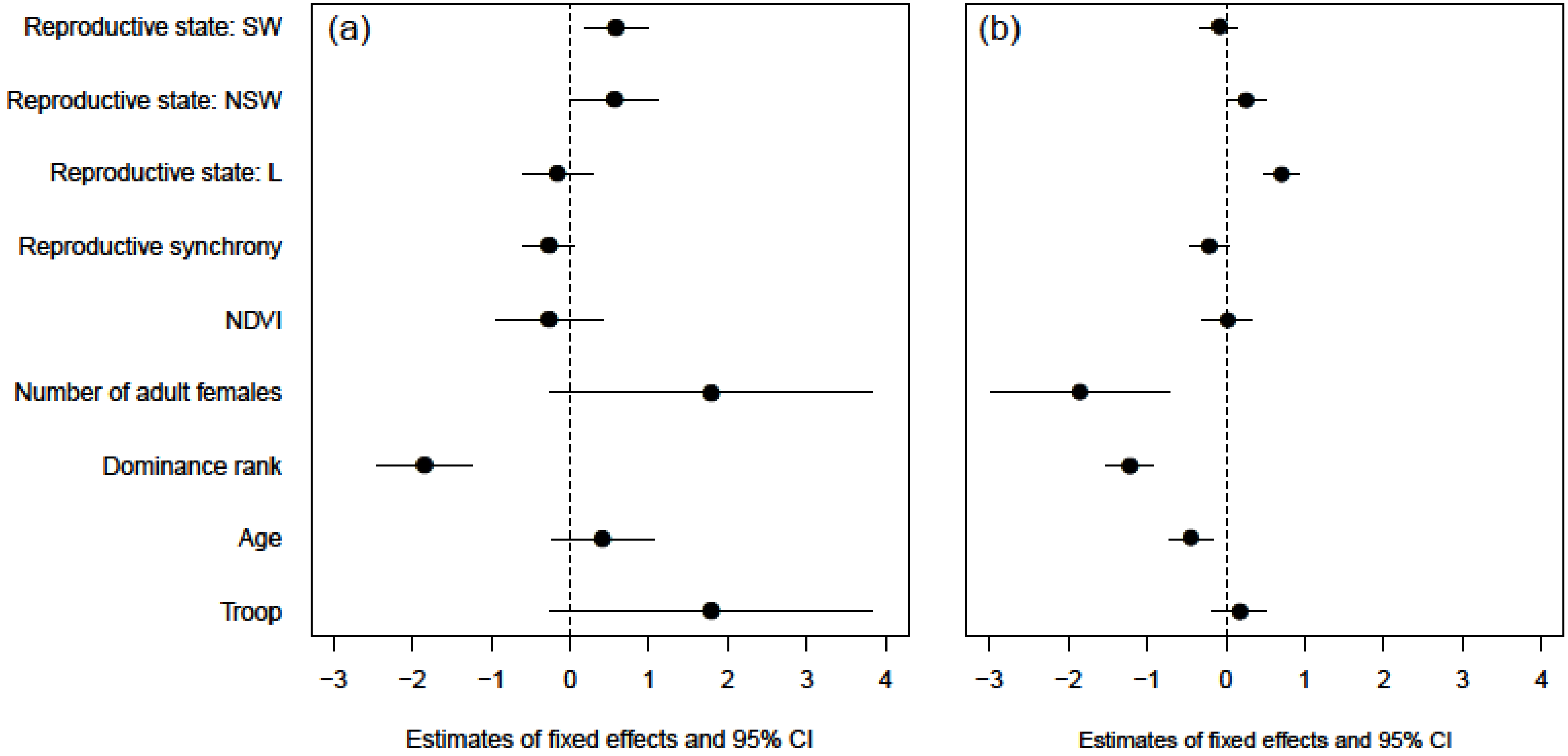

(a)
(b)
Reproductive state: SW
Reproductive state: NSW
Reproductive state: L
Reproductive synchrony
NDVI
Number of adult females
Dominance rank
Age
Troop
−3
−2
−1
0
1
2
3
4
Estimates of fixed effects and 95% CI
Estimates of fixed effects and 95% CI

Figure 2.

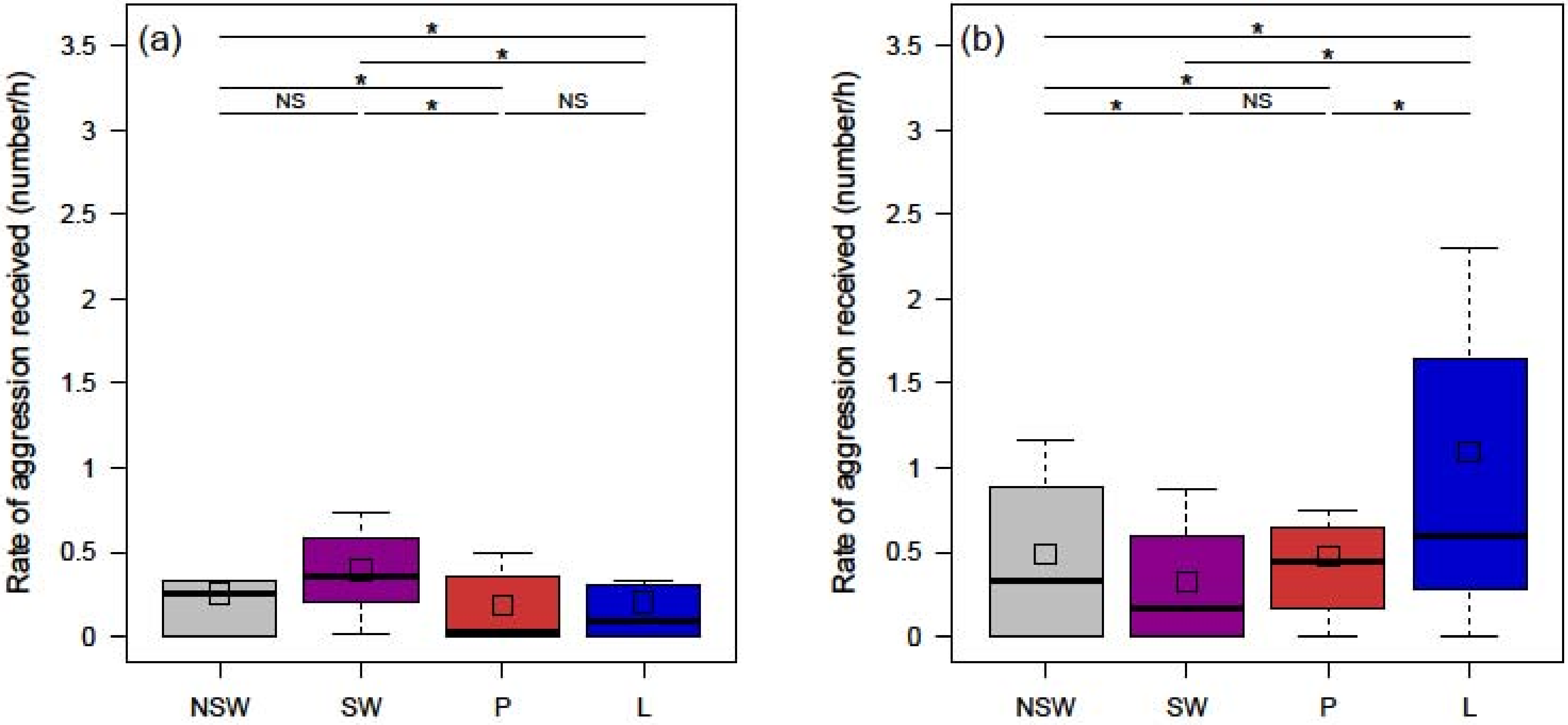
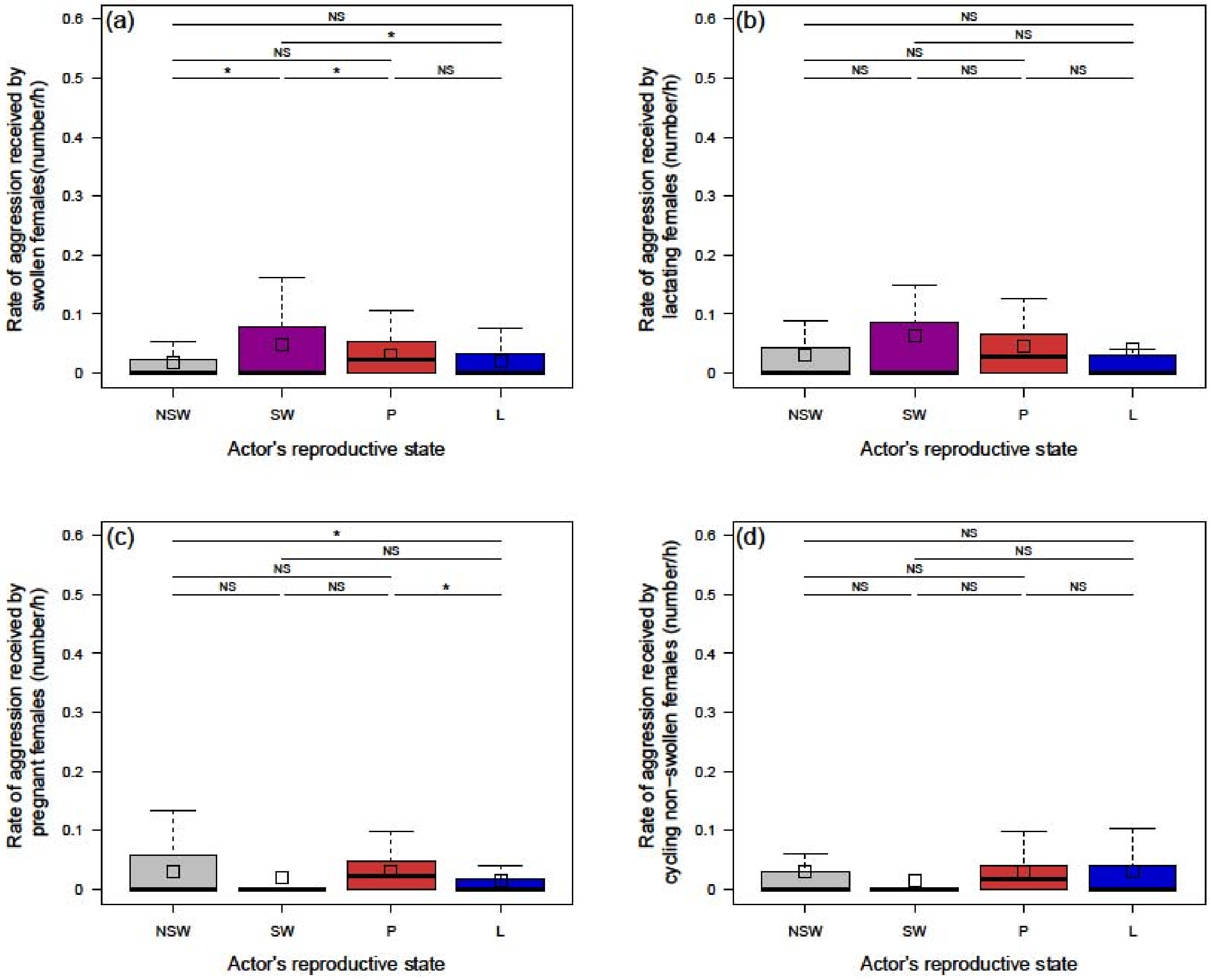

(a)
(b)
Rate of aggression received (number/h)
0
0.5
1
1.5
2
2.5
3
3.5
NSW
SW
P
L
NS
*

Figure 3.


(a)
Rate of aggression received by swollen females(number/h)
0.6
0.5
0.4
0.3
0.2
0.1
0
NS
*
NS
*
*
NS
NSW
SW
P
L
Actor's reproductive state
(b)
Rate of aggression received by lactating females (number/h)
0.6
0.5
0.4
0.3
0.2
0.1
0
NS
NS
NS
NS
NS
NS
NSW
SW
P
L
Actor's reproductive state
(c)
Rate of aggression received by pregnant females (number/h)
0.6
0.5
0.4
0.3
0.2
0.1
0
*
NS
NS
NS
NS
*
NSW
SW
P
L
Actor's reproductive state
(d)
Rate of aggression received by cycling non−swollen females (number/h)
0.6
0.5
0.4
0.3
0.2
0.1
0
NS
NS
NS
NS
NS
NS
NSW
SW
P
L
Actor's reproductive state