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Original Article

Female–female aggression around mating: an extra cost of sociality in a multimale primate society

Elise Huchard[a,b] **and Guy Cowlishaw**[c]
[a]Department of Behavioral Ecology and Sociobiology, German Primate Center, Kellnerweg 4, 37077 Göttingen, Germany, [b]Courant Research Centre "Evolution of Social Behavior," Georg-August-University, Kellnerweg 6, 37077 Göttingen, Germany, and [c]Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK

Multimale–multifemale groups, where both sexes mate promiscuously and the operational sex ratio is male biased, represent a classical mammalian society. Theory predicts low mating competition between females in such societies, but this is inconsistent with the frequent occurrence of female sexual signals. This study explores the determinants of female competition under such conditions by testing 3 hypotheses relating to patterns of aggression over the reproductive cycle in wild chacma baboons (*Papio ursinus*). Primarily, we expect the frequency of aggression to be highest among 1) lactating and pregnant females, who experience the greatest energetic demands, if females compete mainly over food, 2) lactating females, if females compete mainly over paternal care of infants, or 3) sexually active (swollen) females, if females compete mainly over mates. Data were collected from 27 females in 2 groups over 18 months and analyzed using mixed models. Our results provide most support for the mating competition hypothesis: aggression increases with the number of swollen females in a group, swollen females receive the most aggression, and mate-guarded swollen females receive more aggression than when unguarded. However, our analyses further indicate that such aggression rather than arising from direct mating competition, most likely reflects reproductive suppression and/or an increased exposure of swollen females to incidental aggression. These findings reveal the importance of sex in shaping social relationships among females in large primate groups where they were traditionally considered to be determined primarily by access to resources. Aggression associated with access to mates represents an extra cost of sociality to females. *Key words:* aggression, baboons, female–female competition, intrasexual selection, reproductive strategies, sociality. *[Behav Ecol]*

INTRODUCTION

Our understanding of sexual selection is based on the paradigm that decreased investment in gametes and parental care by males increases the relative numbers of sexually active males to receptive females (the operational sex ratio, or OSR), and in turn the intensity of intrasexual competition and variance in male breeding success (Bateman 1948; Trivers 1972; Emlen and Oring 1977). However, research over the years has revealed many inconsistencies in the relationships between parental investment, reproductive competition, and morpho-behavioral sex differences that suggest additional complexities in this traditional scheme (Gowaty 2004; Kokko et al. 2006; Clutton-Brock 2007). Unfortunately, these studies have also revealed a striking weakness in our knowledge of how sexual selection operates in females. In an attempt to fill this gap, more recent work has clarified some of the selective pressures underpinning the evolution of female secondary sexual characters, namely male choosiness and female intrasexual competition over reproductive resources (Clutton-Brock 2009; Watson and Simmons 2010). Such mechanisms can occur even in species with "classical" sex roles (i.e., where females face the highest costs of reproduction, OSRs are biased toward males, and males are the principal competitors). This research, by highlighting the potential flexibility of sex roles, has stressed the need to broaden our traditional views of sexual selection (Clutton-Brock 2007, 2009; Gowaty and Hubbell 2009).

Female intrasexual competition over reproduction appears to occur where the resources necessary for successful reproduction are limited (Clutton-Brock 2007, 2009; Stockley and Bro-Jorgensen 2011), specifically 1) the food or breeding territories necessary for successful pregnancy and weaning, 2) infant care from mates or helpers, and 3) good-quality mates or sperm. In the first case, competition for access to resources frequently translates into intense female competition for social rank, which is often related to female ability to produce or rear offspring in group-living species (birds: Bertram 1992; mammals: Fedigan 1983; and insects: Reeve 1991). In the second case, female–female competition for infant care is classically observed in cooperative breeders, where infant survival is conditional on the intensity of care received from helpers. There, a single female can monopolize reproduction in each group through a combination of physiological suppression (meerkats: Clutton-Brock et al. 2001; marmosets: French 1997), infanticide (meerkats: Clutton-Brock et al. 1998; common marmosets: Saltzman et al. 2009), or eviction of potential competitors from the group (meerkats: Clutton-Brock et al. 1998). As a result, fewer females than males may breed as dominants, variance in breeding success may be higher in

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Address correspondence to E. Huchard. E-mail: ehuchard@gmail.com.

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females than males, and females may be more aggressive to each other than are males (Clutton-Brock et al. 2006). In the case of female competition for good-quality mates or sperm, most studies have focused on mating systems where the OSR is less biased than normal (i.e., leks, harems, or strong breeding seasonality). In some polygynous ungulates where males initially compete intensely for access to females, estrous females can subsequently compete aggressively for the attentions of favored males (e.g., topi, *Damaliscus lunatus*: Bro-Jørgensen 2002, 2007). Similarly, in langurs (*Presbytis entellus*), females can interfere as frequently as males to disrupt copulations (Sommer 1989), whereas higher conflict rates among female ring-tailed lemurs (*Lemur catta*) during the mating season might reflect competition over sperm (von Engelhardt et al. 2000).

The diversity of resources that can influence female reproductive success also implies that females experience different types of competition at different points in their reproductive cycle. Specifically, they are expected to compete over mates when they come into estrus, over food resources when they are gestating and lactating, and over infant care when they are lactating. Quantifying the fluctuations in intrasexual competition induced by changes in female reproductive state might therefore help to identify the bottlenecks in female reproduction (Gowaty 2004; Gowaty and Hubbell 2005), and thus draw a more comprehensive picture of the determinants of female intrasexual competition across socioecological contexts and mating systems. Gaining such a general understanding will nevertheless also be conditional on gathering data from an unbiased range of taxa: in particular, we should not focus exclusively on those systems with unusually female-biased OSRs to investigate the occurrence of female mating competition.

This study explores the intensity and potential determinants of female intrasexual competition in a species with conventional sex roles, through an examination of the frequency of agonistic interactions exchanged among females in relation to their reproductive state. We focus on chacma baboons (*Papio ursinus*), which represent a typical mammalian model: Females face high costs of reproduction with long periods of gestation and lactation, whereas males compete intensely over sex, leading to dimorphism in both body and canine size (Plavcan 2001). Nevertheless, females may still experience strong competition for food, infant care, and mates. Chacma baboons live in multimale–multifemale groups that can often exceed the optimal size for their environment (because groups will not fission before their size is sufficient to ensure both daughter groups will be large enough for protection from predators) (Dunbar 1996; Henzi et al. 1997), potentially enhancing feeding competition, especially where food resources are highly monopolizable. Infanticide by males can also be frequent in chacma baboons (Palombit 2003), which can lead to female competition for the services of protective males (Palombit 2001). Finally, despite the fact that baboons exhibit a male-biased OSR and are nonseasonal breeders such that females are rarely synchronously receptive (Huchard et al. 2009), females display large sexual swellings (Huchard et al. 2009), emit copulation calls when mating (O'Connell and Cowlishaw 1994), and mate promiscuously (Palombit 2003; Clarke et al. 2009; Huchard et al. 2010). These patterns are indicative of female–female mating competition, consistent with the observation that maximally swollen females are often monopolized by dominant males in mate-guarding episodes lasting several days (Huchard et al. 2009), during which time the guarding males concentrate on their "chosen" partners and typically ignore other receptive females.

We test 3 hypotheses. First, if female reproduction is mainly limited by access to food resources during gestation and lactation (hypothesis 1), we predict that (1a) rates of female–female aggression will increase with the number of pregnant or lactating females in the group and (1b) rates of aggression (both initiated and received) will be maximal among these females because they face the highest energetic demands. Second, if females compete mainly over male infant protection services (hypothesis 2), we predict that (2a) rates of female–female aggression will increase with the number of lactating females in the group, (2b) the intensity of intrasexual competition will be maximal among lactating females, and (2c) females forming heterosexual bonds with alpha males will face higher rates of intrasexual aggression than those forming friendships with other males or that have no male friend (because females are likely to compete more strongly for high-quality partners and/or those that are most capable of protecting their offspring against potential infanticidal males). Finally, if females compete mainly over mating opportunities or sperm (hypothesis 3), we predict that (3a) rates of female–female aggression will increase with the number of sexually receptive females in the group, (3b) the intensity of intrasexual competition will be maximal among sexually receptive females (reflecting direct competition for male access), and (3c) mate-guarded females will face higher rates of intrasexual aggression than nonguarded females (because they "monopolise" mates, at least from a competing female's perspective).

MATERIALS AND METHODS

Study animals and sample collection

Data were collected from a wild population of chacma baboons at Tsaobis Leopard Park in central Namibia (for details of the site and population, see, e.g., Cowlishaw 1999). Two habituated groups, L and J, form the main focus of study. These comprised, in October 2006, 9 adult or subadult males, 16 adult females, and 32 juveniles for the larger group (Group J) and 7 adult or subadult males, 9 females, and 16 juveniles for the smaller group (Group L). All subjects were fully habituated to observers on foot, and adults were individually identifiable.

The reproductive state of each female was recorded as pregnant (P), lactating (L) if her youngest infant was less than 6 months old, swollen (S) if she was sexually receptive and presented a perineal swelling, and cycling (C) if she was not swollen, not pregnant and not lactating. Pregnancy could, in most cases (16/18 females), be determined a posteriori as the 6 months preceding an infant's birth. Two females aborted over the course of the study, and their pregnancy was defined as the period separating the end of their conceptive cycle from their abortion. Abortion was directly observed in one case (a dead fetus). In the second case, it was deduced from a cessation of cycling (>40 days) without evidence of menstruation (i.e., vaginal bleeding followed by sexual swelling within a week) (Beehner et al. 2006) but followed by a redness of the paracallosal skin (a signal of pregnancy in baboons), which was suddenly interrupted when the female resumed cycling after 3.5 months.

Age was estimated through dentition, examined during group captures. Groups J and L were captured in October and November 2006, respectively (Huchard et al. 2010). Twenty-five of 27 sexually mature females were captured. Tooth eruption schedules for baboons were used to assign age up to the eruption of the molars (Kahumbu and Eley 1991), whereas age beyond this point was estimated on the basis of molar wear (Huchard et al. 2009).

Behavioral data

All sexually mature females ($N = 27$ in total) from both study groups were followed during 2 consecutive field seasons, running from May–December 2005 and from April 2006–January 2007. Two young females were included in this sample during the course of the study period (when they started cycling, respectively in November 2005 and April 2006), whereas two females disappeared shortly before the end of the study period (September 2006). Behavioral data were collected on foot, during full-day follows, using 1-h focal animal sampling periods (Altmann 1974) spread equally across the day (split into four 3-h time blocks) for each individual. Observations interrupted during the first 50 min were excluded from the analysis, such that the mean length of focals was 58.8 min (standard deviation [SD] = 3.7). The choice of a focal female was randomized (although nonindependent from her reproductive state), and the same individual was sampled no more than once per half day to ensure the independence of each focal observation. A total of 1782 focal observations were included in the analysis (number of observations per female: range: 18–142, mean ± standard error [SE]: 66.0 ± 1.3 h) distributed across the following reproductive states: cycling ($N = 352$ observations of 27 females, range: 1–22, mean ± SE: 13.0 ± 6.2 h per individual), lactating ($N = 351$ observations of 20 females, range: 8–33, mean ± SE: 17.5 ± 0.3 h per individual), pregnant ($N = 129$ observations of 18 females, range: 1–18, mean ± SE: 8.2 ± 0.3 h per individual), and swollen ($N = 950$ observations of 18 females, range: 8–110, mean ± SE: 52.8 ± 1.7 h). Among swollen females, 14 were observed when involved in mate-guarding episodes ($N = 288$ observations, range: 3–53, mean ± SE: 20.6 ± 1.16 h per female).

All occurrences of agonistic interactions involving the focal female were recorded together with the identity of the receiver and initiator of each interaction. Agonistic interactions were categorized as threats (including staring, head bobbing, and ground sweeping while oriented toward the targeted individual), displacements (when one animal passes close to another and makes it move away), supplants (when one animal actively displaces another to take its place), chases (when one animal chases another for a distance of at least 3 m), and attacks (when physical contact is made by an individual, usually after a chase). A total of 1027 interactions received (including 87 threats, 285 displacements, 428 supplants, 161 chases, and 66 attacks) and 413 interactions initiated (including 59 threats, 90 displacements, 146 supplants, 64 chases, and 54 attacks) were observed during the female focals.

Adult dominance ranks were established using ad libitum and focal observations of agonistic and approach–avoid interactions (Huchard et al. 2010). The dominance hierarchy was always linear ($N = 1190$ interactions in Group L, $N = 1173$ in Group J, Landau's linearity index h: $P < 0.05$ in both cases), with adult males outranking adult females. Dominance rank was described as proportional rank, expressed from 0 to 1 (i.e., absolute rank/number of same sex animals in group) to control for differences in group size. Male ranks remained stable, except for minor changes due to the emigration of 4 (nonalpha) males in J Group, but this did not affect the hierarchy among the remaining males. Male ranks were analyzed as a binary variable (the alpha male: 1; all other males: 0) and thus unaffected by such fluctuations.

Heterosexual friendships between lactating females and males were identified using quantitative indices of proximity (within 1 and 5 m) and confirmed by patterns of grooming (for further details, see Huchard et al. 2010). In 18 of the 21 mother–infant pairs monitored, the mothers established friendships with 1 or 2 resident males. Four females had more than one friend. In 3 cases, females possessed 2 friends simultaneously. In the last case, one female gave birth twice during the study and associated with 1–2 friends each time. Following Palombit et al. (1997), her consecutive friendships were analyzed separately because they were separated by more than a year. Seventeen females (with 18 infants) of all dominance ranks and ages formed 21 friendships with 7 different males. The alpha males were involved in 10 of 21 (48%) friendships.

Mate guarding, defined as periods of sexual activity and close persistent following of a female by a male that involves exclusion of other males from access to the female (Alberts et al. 1996), was monitored through focal observations, which were carried out on a daily basis for swollen females (Huchard et al. 2009). Any changes in patterns of consortship were recorded *ad libitum* if they occurred outside focal sampling (visibility conditions are excellent at Tsaobis). Mate guarding was coded as a binary variable (guarded: 1; unguarded: 0).

Statistical analysis

We first investigated the influence of the number of females that were simultaneously in the same reproductive state in the social group (cycling, swollen, pregnant, and lactating) on the rate of agonistic interactions exchanged with other females (number per hour, both initiated and received). Although the results from these different models cannot be considered independent because the number of females in a given reproductive state is not independent from the number of females in another reproductive state (pairwise Pearson's correlations between the number of females in each state: $P < 0.05$, $n = 349$ days, in all cases, except for the pregnant-versus-lactating-females comparison, where $P = 0.19$), the absolute value of the correlation coefficient was low in every case ($\rho < 0.34$). We also present a further model testing for the effect of the number of lactating plus pregnant females (as an index of the intensity of the competition for food resources) on the rate of agonistic interactions. Because group membership, female identity and date of focal sampling were all expected to generate nonindependent estimates of the rate of agonistic interactions exchanged among females, we used a mixed model approach, where the random factors comprised female identity nested in group identity, crossed with the date of focal sampling. We used general linear mixed models (GLMMs, using the lmer function in R) because our response variable (number of agonistic interactions exchanged per hour) was poisson distributed.

We then investigated the influence of a female's reproductive state on the rate of agonistic interactions that she exchanged with other females (number per hour, both initiated and received). Reproductive state (4 classes: cycling, swollen, pregnant, and lactating) was fitted as a fixed factor together with female social rank and age, which were considered as potentially influential effects. The structure of the random effects was the same as in our first model. Unless specified, all models presented hereafter include these 2 control variables (rank and age) as fixed effects and the same random effects. The influence of reproductive state was investigated in relation to 2 different response variables, namely the rate of aggression received by the focal female (from other sexually mature females) and initiated by the focal female (toward other sexually mature females).

We subsequently restricted the dataset to lactating females only to investigate the potential influence of the rank of male friends on the rate of agonistic interactions received. The variable "male rank" was thus included as a fixed factor (in addition to the control variables mentioned above) in the GLMM explaining the rate of agonistic interactions received.

Three females had 2 male friends including the alpha male; they contributed only one data point in our model and were considered as forming friendships with the alpha male (because the alpha male was considered a valuable and limited resource, a friendship with him could increase the aggression faced by a female even if she had another male friend).

Further, we used the dataset including only sexually receptive females to investigate the potential influence of mate guarding on the rate (number per hour) of agonistic interactions exchanged (either initiated or received) with other sexually receptive females. We thus ran a second set of 2 GLMMs with the same structure of random effects and the same control variables (female rank, age) as fixed factors, plus the mate-guarding variable.

The significance of the fixed variables was always tested using the full model (i.e., inferences were drawn with all predictors present) to avoid the potential problems associated with stepwise model selection procedures (Whittingham et al. 2006; Mundry and Nunn 2009). The significance of the fixed quantitative factors was evaluated according to the principle of marginality, testing each term after all others (i.e., comparing 2 models differing only in the presence of the tested fixed effect) (Pinheiro and Bates 2000). We used likelihood-ratio tests to evaluate the significance of a categorical variable with more than 2 classes (in this case, female reproductive state), whereas *z*-tests were used to evaluate the significance of quantitative variables or of a given class of a categorical variable. All statistical analyses were run using software R 2.11.1 (R Development Core Team 2008).

RESULTS

Focal females initiated an average of 0.23 (range: 0–7, median: 0, SD = 0.63) and received an average of 0.58 (range: 0–10, median: 0, SD = 1.10) aggressive interactions per hour. Patterns of variation in the mean rate of aggressive interactions exchanged were substantial, especially in aggression received, both within and between individuals: the mean individual rate per hour (±SD) of interactions initiated ranged from 0.04 ± 0.20 (median: 0) to 0.75 ± 1.21 (median: 0), and the mean individual rate of interactions received ranged from 0.02 ± 0.14 (median: 0) to 1.11 ±1.64 (median: 1).

Fluctuations of female–female aggression in relation to the intensity of competition

The rate of aggression exchanged among females was positively influenced by the number of sexually receptive females, and to a lesser extent the number of cyling females, in the group. Conversely, aggression levels decreased with an increasing number of lactating females or pregnant females within each group (Figure 1, Table 1).

Fluctuations of female–female aggression across the reproductive cycle

Female reproductive state had a strong influence on the rate of aggression received (GLMM, $X^2_3 = 23.48$, $P < 10^{-4}$, Table 2, Figure 2a) and, to a lesser extent, on the rate of aggression initiated (GLMM, $X^2_3 = 11.71$, $P < 0.01$). Swollen females faced the highest rate of aggression (although not significantly different from that experienced by cycling nonswollen females). In contrast, most aggression was initiated by pregnant and cycling females. Social rank also, unsurprisingly, correlated with the rate of aggression faced by females (Table 2), and this effect remained constant throughout our analyses (see below).

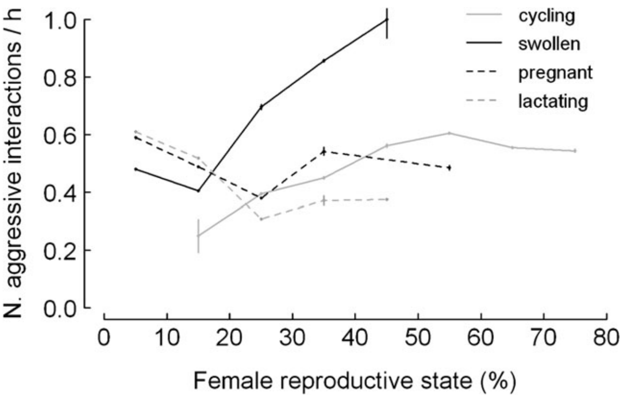

Figure 1
Relationship between the rate (number per hour) of aggressive interactions exchanged among females and the mean proportion of females in a given reproductive state. For the purposes of this figure, the number of agonistic interactions recorded per focal observation was averaged across the percentage of females in the same reproductive state in a given group (recorded on a daily basis) using the following categories: 0–10%, 10–20%, 20–30%, 30–40%, 40–50%, 50–60%, 60–70%, and >70%. Categories with less than 10 observations were excluded. Error bars indicate the standard error of the mean.

Heterosexual friendships and the intensity of female–female aggression

Focusing solely on lactating females, we further tested whether females involved in heterosexual friendships with alpha males received higher rates of aggression than females that had lower ranked friends or no friends. However, this was not the case ($N = 69$ interactions distributed across 350 focal observations of 20 females, $X^2_1 = 0.23$, $P = 0.63$) when controlling for female rank (z value $= -2.92$, $P < 0.01$) and age (z value $= 0.91$, $P = 0.36$).

Mate-guarding episodes and the intensity of female–female aggression

The rates of aggression received by mate-guarded females sharply increased compared with nonguarded females (Figure 3, Table 3). However, there was no effect of mate-guarding episodes on the rates of aggression initiated by swollen females targeting other females (Table 3), indicating that the high rate of aggression faced by mate-guarded females is not a direct consequence of the aggression they initiate.

Table 1
Influence of the number of females in a given reproductive state per group on the rate of aggression exchanged by 27 focal females

Fixed factor	Estimate	SE	*z* value	*P* value
Number of swollen females per group	0.13	0.03	3.75	$<10^{-3}$
Number of lactating females per group	−0.08	0.03	−3.08	<0.01
Number of pregnant females per group	−0.09	0.03	−3.27	0.001
Number of cycling females per group	0.05	0.02	2.09	0.04
Number of lactating plus pregnant females per group	−0.08	0.02	−4.44	$<10^{-3}$

Parameters and tests are based on 1782 observations and 912 interactions and performed using GLMMs controlling for focal sampling date, group, and female identity (fitted as random factors).

Table 2

Influence of focal female's reproductive state on the rate of aggressive interactions exchanged

Response variable	Fixed factor		Estimate	SE	*z* value	*P* value
Interactions received ($N = 614$)	Social rank		−2.42	0.32	−7.55	<0.001
	Age		0.04	0.02	1.76	0.08
	Reproductive state[a]	Lactating	−0.66	0.17	−3.88	<0.001
		Pregnant	−0.79	0.24	−3.26	<0.01
		Cycling	−0.16	0.15	−1.12	0.26
Interactions initiated ($N = 298$)	Social rank		1.95	0.30	6.39	<0.001
	Age		−0.06	0.02	−2.35	0.02
	Reproductive state[a]	Lactating	−0.35	0.21	−1.71	0.09
		Pregnant	0.51	0.24	2.10	0.04
		Cycling	0.17	0.19	0.90	0.37

Parameters and tests are based on 1782 observations distributed among 25 females and performed using a GLMM controlling for focal sampling date and focal female identity nested in group identity (fitted as random factors).

[a] Reference category: swollen.

Hypotheses and tests

These results are summarized in relation to the hypotheses and predictions under exploration in Table 4.

DISCUSSION

Our study, investigating patterns of variation in the intensity of female–female competition in a species with conventional sex roles, highlights a dramatic relationship between the reproductive state and the amount of aggression faced by females. First, the frequency of aggression exchanged among females increased with the number of sexually receptive females in the group. Second, although sexually receptive females received most aggression, lactating females received least aggression. Finally, mate-guarded females faced twice as much aggression as nonguarded females. What can such patterns tell us regarding the determinants of intrasexual competition among female baboons, and what are the wider implications for our understanding of sexual selection among females in species with conventional sex roles?

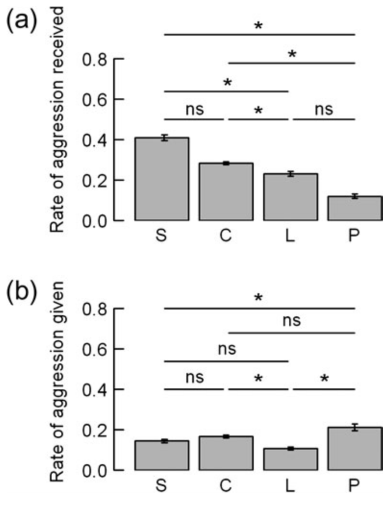

Figure 2
Comparison of the mean rate (number per hour) of aggressive interactions exchanged among females in different reproductive states: cycling but nonswollen ("C"), swollen ("S"), pregnant ("P"), and lactating ("L"). (a) Interactions received. (b) Interactions initiated. Error bars indicate the standard error of the sample mean, which is averaged across individual means. Although means and standard errors are directly inferred from the raw data, the significance of the comparisons are evaluated using GLMMs correcting for female rank, age, and group membership, and noted "ns" if nonsignificant, and "*" if significant.

The hypotheses under test

Our first hypothesis, that females mainly compete over the food resources necessary to undergo successful gestation and lactation, reflects the classic interpretation of ecological resources as the limiting factor on female reproductive success (Crook 1970; Clutton-Brock and Harvey 1976; Emlen and Oring 1977). Although we found that pregnant females did initiate most aggression, in partial support of this hypothesis, the rest of our predictions were not supported (Table 4). In particular, our data showed that an increasing number of pregnant or lactating females in a group decreased the frequency of female–female aggression. Additionally, lactating females initiated and faced the lowest amounts of aggression despite the peak energetic costs of reproduction during lactation (rather than gestation) (Speakman 2008). Thus, variation in aggression among females does not appear to be driven by energetic needs as they covary with the female cycle. Such results might reflect the possibility that access to food is less limited in our study population than in others. However, these desert-dwelling baboons live in a demanding environment where the physical condition of females significantly affects their reproductive success (Huchard et al. 2009), suggesting that access to food resources does limit

Table 3

Influence of mate guarding on the rate of aggressive interactions exchanged by a focal female

Response variable	Fixed factor	Estimate	SE	*z* value	*P* value
Interactions received ($N = 404$)	Social rank	−2.41	0.33	−7.24	<0.001
	Age	0.03	0.02	1.40	0.16
	Mate guarding[a]	0.48	0.14	3.39	<0.001
Interactions initiated (N = 150)	Social rank	2.16	0.62	3.46	<0.001
	Age	−0.07	0.05	−1.36	0.17
	Mate guarding[a]	−0.32	0.23	−1.39	0.16

Parameters and tests are based on 910 observations distributed among 18 swollen females and performed using a GLMM controlling for focal sampling date and focal female identity nested in group identity (fitted as random factors).

[a] Reference category: non mate-guarded.

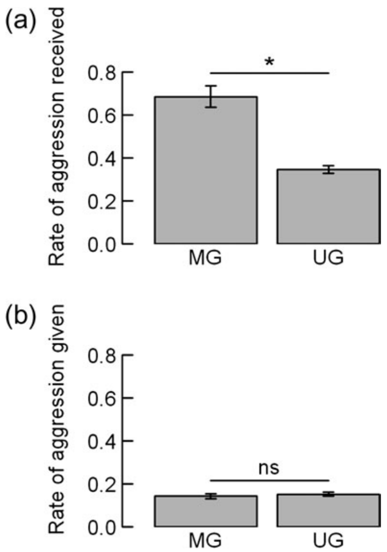

Figure 3
Comparison of the mean rate (number per hour) of aggressive interactions exchanged among sexually receptive females that are mate guarded (“MG”) or unguarded (“UG”). (a) Interactions received. (b) Interactions initiated. Error bars indicate the standard error of the sample mean, which is averaged across individual means. Although means and standard errors are directly inferred from the raw data, the significance of the comparisons are evaluated using GLMMs correcting for female rank, age, and group membership, and noted “ns” if nonsignificant, and “*” if significant.

reproduction. This might stand at odds with the lack of support for these predictions, and we return to this point later.

The finding that lactating females showed the lowest initiation rates for aggression (and also rarely received aggression) also fails to support our second hypothesis, that females compete for male care (infant protection services). Contrary to both hypotheses but consistent with previous observations in baboons (Seyfarth 1976; Wasser and Starling 1988), we found that lactating females rather seemed to reduce their agonistic interactions, presumably to protect their infant from the risk of injury during aggressive encounters. Females can regulate the amounts of aggression they initiate, and probably, to a certain extent, the aggression they receive. Yet, the levels of aggression received remain largely dependent on others and cannot be fully explained by the receiver’s behavior. In this case, the recent finding that young mothers might seek assistance from male friends to avoid harassment from other females (Lemasson et al. 2008; Nguyen et al. 2009), in conjunction with the natural attraction of females toward newborns (Seyfarth 1976; Silk et al. 2003), might together help to explain why lactating females receive relatively little aggression.

Our third hypothesis, that females compete mainly over mating opportunities or sperm, received more support. In support of prediction 3a, we found that the number of swollen females in a group, and so the reproductive synchrony of the group, is a major predictor of aggression exchanged (both initiated and received) among females. In partial support of prediction 3b, we also found that swollen females faced the highest rates of aggression. Finally, prediction 3c was fully supported: Swollen females experience more aggression when mate guarded. However, according to prediction 3b, we also expected sexually receptive females to initiate the most aggression, which was not the case. Rather, pregnant females were the most aggressive. These results are consistent with an earlier study in yellow baboons (Wasser and Starling 1988), which also reported a positive effect of reproductive synchrony on female–female aggression, and that sexually receptive females faced the most aggression, whereas pregnant females initiated most aggression. Although these findings suggest a primary role for mating competition in driving patterns of female–female aggression, they also highlight 2 important paradoxes: 1) if food is a limiting resource for baboons, and female social relationships primarily arise from the causes and consequences of feeding competition (Sterck et al. 1997; Koenig 2002), why should mating competition play a more important role than energetic needs in patterns of female–female aggression? and 2) why should females who are not sexually receptive direct so much aggression toward swollen females? There are 2 possible explanations of our findings that can resolve both paradoxes.

Interpretation 1: reproductive suppression

One possible explanation of our findings is that the patterns of aggression reflect socially mediated reproductive suppression, where aggression directed toward adult conspecific females decreases the target’s reproductive success (recently reviewed by Stockley and Bro-Jorgensen 2011). Thus, other females, through harassing sexually receptive females, attempt to delay the conception of future competitors to limit future feeding competition (Wasser and Barash 1983; Wasser and Starling 1988, 1995). According to this interpretation, estrous females are the primary targets of aggression because females in the follicular phase of their menstrual cycle are in the physiologically most suppressable state (Wasser 1983), whereas pregnant females derive the most benefit from initiating aggression because they are about to give birth. Such an interpretation could also explain an additional finding of our study, namely why older females initiate less aggression (Table 2), if females of lower reproductive value have less to gain by suppressing the reproduction of others. However, it remains unclear whether the elevated aggression faced by swollen females actually reduces their reproductive success. Indeed, the effects of elevated aggression on female reproduction reported by Wasser and Starling (1988, 1995) cannot be disentangled from the broader effects of dominance: Because those females facing higher rates of aggression were inevitably subordinates, other aspects of low rank might have been equally or more important. Indeed, there is good evidence that low-ranking females eat less (olive baboons: Barton and Whiten 1993) and that reduced food intake lowers reproductive success (yellow baboons: Altmann and Alberts 2003). Although evidence for reproductive suppression is traditionally drawn from a suite of behavioral and physiological phenomena that have never been reported in baboons, including female-mediated hormonal suppression (French 1997; Clutton-Brock et al. 2001), infanticide and harassment directed toward offspring (Clutton-Brock et al. 1998; Creel S and Creel NM 2001), and the eviction of potential competitors from the group (Clutton-Brock et al. 1998; Creel S and Creel NM 2001), recent reviews highlight the prevalence of more discrete forms of reproductive suppression resembling the patterns described here (Clutton-Brock 2009; Stockley and Bro-Jorgensen 2011), which may be relatively common in matrilocal mammals living in stable groups (Dunbar RIM and Dunbar EP 1977; Wasser and Starling 1988; Hackländer et al. 2003).

Interpretation 2: incidental aggression

Our second interpretation does not provide a single explanation of both paradoxes but rather involves independent

Table 4
Summary of the predictions tested, with associated results

Number	Hypotheses and predictions	Outcome
1	If females mainly compete over food during gestation and lactation, we expect that:	
(1a)	The intensity of intrasexual competition (aggression among females) increases with an increasing number of pregnant or lactating females in the social group	No
(1b)	The intensity of intrasexual competition is maximal among both lactating and pregnant females	No[a]
2	If females mainly compete over male protection for newborn offspring, we expect that:	
(2a)	The intensity of intrasexual competition increases with an increasing number of lactating females in the social group	No
(2b)	The intensity of intrasexual competition is maximal among lactating females	No
(2c)	Females forming heterosexual bonds with alpha males face higher rates of intersexual aggression than those forming friendships with other males or those without friendships	No
3	If females mainly compete over mating opportunities or sperm, we expect that:	
(3a)	The intensity of intrasexual competition increases with an increasing number of swollen females in the social group	Yes
(3b)	The intensity of intrasexual competition is maximal among swollen females	Yes[b]
(3c)	Mate-guarded females face higher rates of intrasexual aggression than nonguarded females	Yes

[a] Pregnant and lactating females do not consistently initiate or receive more aggression than swollen or cycling females; although pregnant females do initiate high rates of aggression, the reverse pattern is seen in lactating females and both show the lowest levels of received aggression.

[b] Swollen females receive more aggression than pregnant or lactating females but not cycling females; although cycling and swollen females initiate similar rates of aggression, these are not consistently higher than the initiation rates of pregnant or lactating females.

arguments to resolve each in turn. In the first case (why should mating competition play a more prominent role than feeding competition in driving female–female aggression?), it may be that conflicts over food resources can be more efficiently resolved than conflicts over mates through existing rank relationships in the dominance hierarchy. Indeed, feeding competition has probably been the major determinant in shaping female dominance hierarchies, at least where females are philopatric, such as in baboons (Wrangham 1980; van Schaik 1989; Isbell 1991). Such hierarchies regulate competition over access to monopolizable food resources, preventing the recurrence—and associated costs—of open conflicts over food. In contrast, female access to sex is more complicated. Unlike feeding competition, it does not occur on a routine daily basis, when it does occur the stakes are proportionally higher, and the resource in question is not divisible with allies. Additionally, and most importantly, it is not purely a female matter because it is complicated by male sexual strategies. As such, female dominance hierarchies are unlikely to be as efficient at regulating access to sex—and thus limiting the occurrence of open conflicts over access to mates. This in turn might explain why our observed rates of female–female conflicts are better predicted by female sexual receptivity than energetic needs. This interpretation is also consistent with Koenig's (2002) observation that, although traditional socioecological models have been relatively successful at predicting essential patterns of social organization and structure across species, patterns of aggression in female primates are still not well predicted by feeding competition regimes. Koenig further proposed that other factors beyond the traditional focus of feeding competition may be important, including male strategies and demographic constraints. Our results corroborate this view and emphasize the potential role of sexual competition in female social relationships.

Recognition of the importance of the dominance hierarchy in resolving competition without aggression leads on to the resolution of our second paradox (why should swollen females receive so much aggression from nonswollen females?). The patterns of aggression observed in our study are likely to reflect a variety of constraints and opportunities, which may partially obscure underlying patterns of competition. The pregnant and cycling (nonswollen) females, who share the highest rates of initiating aggression, are also those who experience the fewest constraints on their aggressive behavior: In comparison with swollen and lactating females, they are neither preoccupied with mating nor concerned over infant safety. Consequently, their rates of initiation may simply reflect the constraint-free baseline levels of aggression that females adopt to reinforce the dominance hierarchy (cf. Johnson 1989). This might also explain why younger females, who need to establish their dominance rank in the social group, initiate more aggression than older females (Silk 2002).

This explanation does not, however, explain why swollen females are so heavily targeted. From a mechanistic perspective, the high levels of aggression faced by females when swollen might arise from associated changes in their mobility and spatial position in the group. Although dominant individuals are typically found in the center and subordinates on the periphery of the group (Ron et al. 1996), swollen females, even though subordinate, disrupt this pattern by increasing their mobility and moving toward the center of the group to seek copulations with high-ranking males. This exposes such females to higher rates of aggression than they would otherwise encounter. Moreover, during consortships, although mate-guarding males typically follow their mate wherever she goes (Alberts et al. 1996), they are often escorted by a number of high-ranking females, invariably long-term associates of the male, who "harass" the guarded female by displacing, supplanting, or threatening her (Huchard E, unpublished observation). The disruptive behavior of swollen females in baboon groups is reflected in a recent study of behavioral synchrony in the same population, which showed that the extent of activity synchronization in a group decreases with the number of swollen females (King and Cowlishaw 2009). Thus, although swollen females experience the highest levels of aggression, the observed patterns of agonistic interaction suggest that such aggression may be an incidental product of mating behavior rather than indicative of mating competition.

The costs of aggression

Whether or not reproductive suppression, incidental aggression, or a combination of these processes is responsible for the patterns observed, it remains the case that sexually receptive and mate-guarded females face higher rates of aggression and thus pay a social cost in order to mate. Moreover, although a female's access to sex is not fully ruled by its dominance rank, such costs will prove higher for subordinate females, who consistently face more aggression than others. This effect is clearly shown by the significance of dominance rank in all the models we conducted. In contrast to males, for whom patterns of aggression surrounding access to mating opportunities through social hierarchies have been extensively studied (e.g., Cowlishaw and Dunbar 1991) and are well described by the priority-of-access model (Altmann 1962; Alberts et al. 2003), the idea of corresponding patterns in females has been less often envisaged. This opens a new dimension to the study of the reproductive consequences of social hierarchies in female primates and other taxa living in comparable social systems, which have so far been more focused on the outcomes (i.e., reproductive success) than on the mechanisms, at least in terms of access to mating opportunities. Although the male-biased OSR clearly limits the intensity of such effects relative to the experiences of males, subordinate females may still suffer significant costs that could contribute to their common tendency to exhibit a relatively poor reproductive performance (e.g., Smuts and Nicolson 1989; Altmann and Alberts 2003; Wasser et al. 2004) and shorter lifespan (Silk et al. 2010).

CONCLUSIONS

In contrast to male–male competition, female–female conflicts over reproduction have been overlooked (Clutton-Brock 2009). However, recent reviews suggest that female competition is widespread and can be expressed through a variety of forms that are typically less obvious than male–male competition, as female mammals compete for both resources and mates in order to secure reproductive benefits (Stockley and Bro-Jorgensen 2011). Our results, showing that sexual receptivity and mate guarding dramatically increase the rates of aggression faced by female baboons, extend the present empirical record in 2 ways. First, our findings show that sexual activity is a primary determinant of female–female aggression and thus female social relationships, even though it might not reflect mating competition. Second, and perhaps most importantly, our results show that access to mates incurs high levels of aggression that represent one further cost of sociality to females, especially subordinate females, which has so far been largely underestimated in multimale–multifemale groups where both sexes mate promiscuously, a typical model of mammalian societies.

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