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Evidence for intrasexual selection in wild female baboons

Dorothy L. Cheney [a,*], Joan B. Silk [b], Robert M. Seyfarth [c]

[a] Department of Biology, University of Pennsylvania, Philadelphia, PA, U.S.A.
[b] Department of Anthropology, University of California, Los Angeles, CA, U.S.A.
[c] Department of Psychology, University of Pennsylvania, Philadelphia, PA, U.S.A.

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Because female reproductive success in social mammals is determined largely by parental rather than mating effort, intrasexual competition among females has typically been assumed to occur primarily over food. Recently, however, renewed attention has been paid to the importance of other sources of variation in female fitness, with a concomitant focus on a broader definition of intrasexual selection that encompasses both competition for resources and competition for mates and social partners. We present behavioural and demographic data gathered over 15 years on a group of wild chacma baboons, *Papio hamadryas ursinus*, which show that females incur several costs when living in groups with many females and comparatively few males: increased intrasexual aggression, less stable bonds with female partners and increased mortality. Female–female aggression was higher in years when the adult sex ratio was more highly skewed towards females, with low-ranking females exhibiting particularly high rates of aggression towards other females. Females' social bonds with other females also became less stable in years when the group contained many females. Finally, female mortality rates were highest in years when the group contained comparatively more females and fewer males. The negative correlation between the number of males and female mortality suggests that the increase in mortality was due to increased predation rather than food competition. Results indicate that intrasexual competition for social partners, mates, paternal investment, and perhaps also male protection occurs even in species where females exhibit low reproductive skew.

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Discussions about the costs and benefits of female sociality in mammals have tended to emphasize selective pressures related to food competition. Because female reproductive success is determined largely by parental effort and nutritional condition (Trivers 1972), female sociality is thought to reflect a trade-off between benefits associated with enhanced between-group competition and reduced predation risk and costs associated with increased within-group food competition (Emlen & Oring 1977; Wrangham 1980; van Schaik 1983; Janson & van Schaik 1988; Sterck et al. 1997; Koenig 2002; Majolo et al. 2008). As the number of females in a group increases, within-group competition is expected to intensify, leading groups to become less cohesive and even to fission.

Recently, however, renewed attention has been paid to the importance of other sources of variation in female fitness, with a concomitant focus on a broader definition of intrasexual selection that encompasses variation in access not just to food but also to mates and same-sex social partners (Carranza 2009; Clutton-Brock 2009; Clutton-Brock & McAuliffe 2009; Stockley & Bro-Jorgensen 2011; Rosvall 2011). For example, female chacma baboons, *Papio hamadryas ursinus*, that are able to maintain strong bonds with other females experience higher longevity and offspring survival than females with weaker bonds, and these benefits are largely independent of dominance rank (Silk et al. 2003, 2009, 2010b). Similar correlations between strong same-sex bonds and female reproductive success have been documented in horses, *Equus equus* (Cameron et al. 2009); bottlenose dolphins, *Tursiops truncatus* (Frère et al. 2010), house mice, *Mus musculus* (Weidt et al. 2008), rats, *Rattus norvegicus* (Yee et al. 2008), and humans (e.g. Holt-Lunstad et al. 2010). Just as increasing numbers of females may intensify resource competition, however, so may they constrain females' ability to maintain all of their possible social relationships. Literature surveys suggest that, as the number of females in a group increases, the relative proportion of grooming that females are able to devote to each group member decreases, thereby decreasing group cohesion (Dunbar 1991; Henzi et al. 1997; Lehmann et al. 2007).

In many species, females also compete actively for access to mates and paternal investment (reviewed in: Carranza 2009; Clutton-Brock 2009; Clutton-Brock & McAuliffe 2009; Stockley & Bro-Jorgensen 2011; Rosvall 2011). Such competition is particularly

* Correspondence: D. L. Cheney, Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, U.S.A.
E-mail address: cheney@sas.upenn.edu (D. L. Cheney).

intense in socially monogamous species with high degrees of paternal investment (e.g. many birds; West-Eberhard 1983; Kraaijeveld et al. 2007; Rosvall 2011) and cooperatively breeding species with high reproductive skew (e.g. meerkats, *Suricata suricatta*, Clutton-Brock et al. 2006; Alpine marmots, *Marmota marmota*: Hacklander et al. 2003). However, female mate competition also occurs in species with low reproductive skew, and strongly biased sex ratios heighten such competition (e.g. antelope: Milner-Gulland et al. 2003; ponies, *Equus caballus*: Rutberg & Greenberg 1990; Bro-Jorgensen 2007; house mice: Rusu & Krackow 2004; gorillas, *Gorilla gorilla*: Watts 1990; chimpanzees, *Pan troglodytes*: Niemeyer & Anderson 1983; bonobos, *Pan paniscus*: Hohmann & Fruth 2003; baboons, *Papio hamadryas* spp.: Seyfarth 1978; Dunbar & Sharman 1983; reviewed in: Stockley & Bro-Jorgensen 2011; Rosvall 2011).

In one study of chacma baboons, rates of female–female aggression increased as the proportion of sexually receptive females in the group increased, with pregnant females showing the highest rates of aggression (Huchard & Cowlishaw 2011). One interpretation of this behaviour is that food competition favours females who attempt to suppress the reproduction of rivals (see also Wasser & Starling 1988). However, such aggression may also reflect competition for paternal investment in offspring. Lactating female chacma baboons compete to form 'friendships' with resident adult males (Palombit et al. 2001) that may function to deter infanticide (Palombit et al. 1997; Weingrill 2000; Clarke et al. 2009). Competition for male friends may exacerbate mate competition because lactating females form friendships preferentially with their primary consort partner, who is often their infants' father (Moscovice et al. 2010). Increased competition for mates and the paternal investment they provide may represent another cost of increasing female numbers, and this will be exacerbated when the adult sex ratio is heavily skewed towards females.

While most groups of mammals show adult female-biased sex ratios, it remains unclear whether this skew benefits or harms females. Most species of polygynous mammals are sexually dimorphic, with the result that males are dominant to females and can exclude them from desirable resources. Females living in groups with many males and a more evenly balanced sex ratio may therefore incur costs associated with decreased access to food. Conversely, if males contribute to parental care, or if predation rates are high, large numbers of males may enhance female and offspring survival. There is some indication that, as predation risk increases, primate groups experience a disproportionate increase in the number of males over what would be predicted by the number of females (Hill & Lee 1998). If the presence of many males deters predation, females may experience lower mortality rates when there are more males present and the group's sex ratio is more evenly balanced. The degree to which variation in sex ratios influences female fitness, however, has seldom been considered.

In this paper, we use behavioural and demographic data collected over a 15-year period on a group of wild chacma baboons to examine how variation in the relative numbers of males and females affects female intrasexual competition, the strength of female bonds and female mortality.

METHODS

Study Group and Demographic Analysis

Research was conducted during 1992–2007 on a group of wild chacma baboons in the Moremi Game Reserve in the Okavango Delta of Botswana (Cheney et al. 2004; Cheney & Seyfarth 2007). All research was conducted using noninvasive methods approved by the Animal Care and Use Committee of the University of

Pennsylvania (Protocol no. 19001). The group had been observed since 1978 and was fully habituated to humans on foot. Information about maternal kinship was available for all individuals, and paternal relatedness was known for some. During 1992–2007, group size (i.e. individuals > 1 year) ranged from 55 to 76. The primary causes of mortality in this population are infanticide and predation by leopards, lions and other predators. Predation is estimated to account for more than 96% of juvenile and adult deaths (Busse 1982; Cheney et al. 2004; Cheney & Seyfarth 2007).

As in other species of cercopithecine primates, female baboons remain in their natal groups throughout their lives and assume dominance ranks similar to their mothers' (Melnick & Pearl 1987; Cheney & Seyfarth 2007). Adult female dominance ranks were calculated monthly based on the direction of approach–retreat interactions. For most of the study, the female dominance hierarchy remained stable.

Females in this population reach puberty at 4–5 years of age and usually give birth for the first time when they are 6–8 years of age. All females that reached 4 years of age ($N = 64$) were included in the demographic analyses. By the age of 4 years, males begin to dominate adult females (Engh et al. 2009). However, males do not enter the adult male dominance hierarchy or reach adult size until about 9 years of age, when they usually emigrate from their natal group.

Because they do not emigrate, females and juveniles that disappeared were assumed to be dead. In many cases, mortality could be ascribed to confirmed or strongly suspected predation (Cheney et al. 2004; Cheney & Seyfarth 2007). We did not attempt to calculate mortality rates for males because males that disappeared may have emigrated.

The annual number of individuals in each age/sex class was calculated as of 1 January each year. All analyses were restricted to individuals aged more than 4 years. The annual number of females 4 years or older varied from 24 to 36. The annual number of males 4 years or older varied from 16 to 25. The annual number of resident immigrant and natal males older than 9 years varied from 6 to 12. When calculating the adult sex ratio, we included females aged more than 4 years, fully grown immigrant males and natal males aged at least 9 years. Thus, subadult males (aged 4–8) were included in the 'number of males', but not in the 'adult sex ratio', category. The annual adult male:female ratio ranged from 1:2.5 to 1:4.5. Because group size was positively correlated with the number of females (two-tailed Spearman rank correlation: $r_S = 0.74$, $N = 15$ years, $P < 0.01$), the number of adult males ($r_S = 0.65$, $P < 0.02$) and the number of males ($r_S = 0.38$, $P < 0.20$) and, in particular, because we wanted to examine separately the effects of female and male numbers on behaviour and mortality, group size was not included as a predictor variable in statistical tests.

Behavioural and Statistical Analyses

Data on affiliative and aggressive behaviour were gathered using focal animal sampling (Altmann 1974) during 1992–1993 and 2001–2007 (7 years). Behavioural analyses were restricted to females aged at least 5 years because younger individuals were not consistently sampled in all years. Aggressive behaviour included headbobs, lunges, chases and bites. Because high-ranking females have more available targets for aggression than do low-ranking females, each female's annual rate of aggression was corrected for the number of females that ranked below her.

To examine whether cycling and pregnant females experienced more aggression than lactating females (Wasser & Starling 1988; Huchard & Cowlishaw 2011), we compared the frequency of each female's actual aggression given and received in each of three reproductive states (cycling, lactating and pregnant) with the amount that would have been expected given the proportion of

time that she spent in that state. This analysis was restricted to data gathered during 2003–2005, the 3 years for which we had the most accurate and continuous information about females' reproductive states. Females that were observed in only one reproductive state were not included in this analysis.

We were also interested in determining whether the consistency of females' preferences for their top partners varied in relation to the number of females in the group. To assess changes in the consistency of females' preferences from one year to the next, we modified the procedures used in Silk et al. (2010b, 2012).). First, we identified each female's top three partners (as measured by rate of approaches, groom presents, grooming initiations and grooming duration; see Silk et al. 2010b) in each year. Then, for females that were present during at least 2 years, we assessed the consistency of females' preferences from one year to the next using the following formula:

$$\frac{NS - U}{NS - S - X}$$

where N is the number of years in which partner choice was evaluated, S is the number of top partners being evaluated, U is the number of different top partners that the female had in those 2 years, and X is the number of top partners in the first year that died in the second year. (No female ever lost all three partners from one year to the next.) Here, $N = 2$ and $S = 3$, so the formula simplifies to $(6 - U/3 - X)$. Importantly, this index controls for changes in females' top partners that were due to deaths. Thus, females with low values were those that switched partners from one year to the next even though the previous year's partners were still present in the group. The value of the partner preference index (PPI) varied from 1, for females that had the same partners from one year to the next, to 0, for females that had a completely different set of partners in each year. PPI values were scored across 6 years (2001–2007).

In statistical tests, females were classified according to their dominance rank (calculated as the proportion of other females dominated) and the presence or absence of close kin (mothers, adult daughters, or adult maternal sisters) that were present in each year.

Statistical analyses were conducted with R statistical software (version 2.9.0, R Foundation for Statistical Computing, Vienna, Austria, R Development Core Team 2009). We used linear mixed models (LMM) for analyses in which individuals were sampled repeatedly and did not contribute equally to the data set. LMMs were calculated using the function 'lmer' of the R package 'lme4' (R package version 0.999375–31). We used a linear model (LM) for the analysis of annual mortality rates across the 15 complete years of observation (1993–2007). To begin analyses, we first examined a full model that used a single dependent measure and all possible predictors and their interactions. If the overall result was significant, we eliminated nonsignificant predictors and ran a second model that included all significant predictors and any possible interactions. Where we found a significant interaction between two effects, we split the data set and carried out post hoc comparisons to explore the nature of the interaction in more detail. In some simple analyses where individuals were not sampled repeatedly and contributed equally to the data set, we used a binomial test, chi-square test or a Spearman rank correlation coefficient. All correlations were corrected for ties, and all reported probability values are two tailed.

RESULTS

Female–Female Aggression

To examine which factors best predicted annual rates of female–female aggression, we first ran an LMM with each female's annual corrected rate of aggression towards other females as the dependent variable and number of females, number of males, sex ratio, female dominance rank, and their interactions as predictor variables. Female identity was entered as a random factor. Only sex ratio and dominance rank were significant predictors. There were no significant interactions (Table 1).

To examine more closely the role of these significant predictors, we next ran a LMM using only sex ratio, rank and their interaction as predictor variables. There was a significant interaction between sex ratio and rank, indicating that rates of female–female aggression were higher in years when the sex ratio was more skewed towards females, and that, as the sex ratio became more skewed, low-ranking females showed a relatively greater increase in rates of aggression towards other females than did high-ranking females (Table 1, Fig. 1).

Although baboons are not seasonal breeders, two or more females may be in oestrus simultaneously (Bulger 1993), and when that happens they cannot all form consortships with the alpha male. Information on the identity and rank of each female's primary consort partner was available for 22 conceptive cycles from 2004 to 2007 (Moscovice et al. 2010). There was a significant positive correlation between the dominance ranks of male and female consort partners ($r_S = 0.77$, $P < 0.01$), suggesting either that high-ranking females were able to exclude lower-ranking females from access to dominant partners and/or that high-ranking males preferred to mate with high-ranking females.

Mate competition also appears to have been associated with rare mob attacks on other females. As in other female cercopithecines, most aggressive interactions among female baboons are dyadic, and coalitions seldom involve more than two females (Wittig et al. 2007). The years from 2000 to 2005, however, comprised a period when the sex ratio was more skewed than average (1:4 versus 1:3 in other years) and female aggression rates were also higher than average (0.344/female/h versus 0.168/female/h). This period was also characterized by unusual mob attacks by females on other females and rare challenges to the female dominance hierarchy (described by Engh et al. 2006, 2009; Cheney & Seyfarth 2007). Most unusually for cercopithecine primates, the instigators often ranked lower than their opponents, and they typically targeted oestrous females that were in consort with an adult male (81% of 31 mob attacks) The attacks eventually led several adult and adolescent females to fall below their matriline's rank, while eight adolescent females rose above their matriline's rank (Engh et al. 2006, 2009).

With the exception of rare mob attacks, however, cycling females did not generally receive more aggression than would have been expected given the length of time that they spent in that reproductive state (binomial test: $N = 22$, 63.6% more, 36.4% less,

Table 1
Results of linear mixed models with each female's annual corrected rate of aggression towards other females as the dependent variable ($N = 195$) and number of females, number of males, sex ratio and female dominance rank as predictor variables (all continuous measures)

Female–female aggression†	Estimate	SE	t
Predictors			
No. of females aged >4 years	−0.009	0.019	−0.460
No. of males aged >4 years	0.056	0.068	0.822
Sex ratio	0.821	0.270	3.044**
Rank	−0.634	0.260	−2.440*
Significant predictors only			
Sex ratio	1.118	0.243	4.596**
Dominance rank	3.010	1.570	1.917
Sex ratio × rank	−0.998	0.425	−2.349*

*$P < 0.05$; **$P < 0.01$.
† Female identity ($N = 57$) was entered as a random factor.
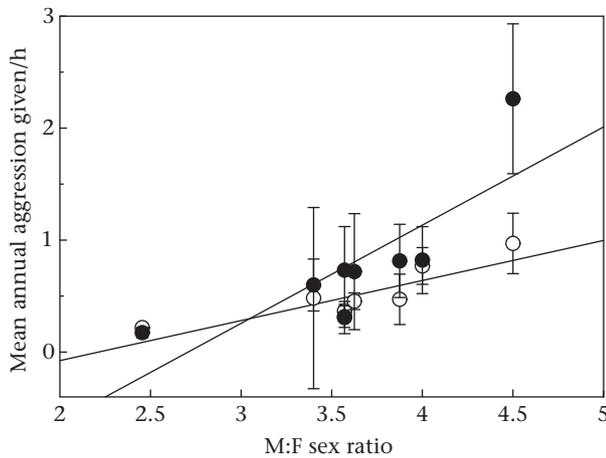
Figure 1. Mean annual rate of females' corrected rates of aggression towards other females in chacma baboons compared with the annual male:female ratio. Black circles: mean rates of aggression by females in the bottom half of the female dominance hierarchy; open circles: mean rates of aggression by females in the top half of the dominance hierarchy. Mean values are presented for illustrative purposes only. All statistical analyses were based on continuous measures. Lines represent the linear model that minimizes the sum of the squares of the residuals.

$P = 0.286$; cf. Huchard & Cowlishaw 2011). Also in contrast to Huchard & Cowlishaw's study (2011), we did not find that lactating females as a group received less aggression than expected ($N = 24$, more $= 33.3\%$, less $= 66.7\%$, $P = 0.152$), or that pregnant females gave more aggression ($N = 24$, 50% more, 50% less, $P > 0.999$).

Although there was little variation from year to year in the proportion of multiparous females that were cycling, pregnant or lactating, there was considerable annual variation in the proportion of females that were nulliparous (i.e. either cycling before their first conception or experiencing their first pregnancy: range 21–43%). An LMM revealed that female aggression rates were significantly higher in years when the group contained a higher proportion of nulliparous females ($r = 0.24$, $t = 3.49$, $N = 15$, $P < 0.001$).

Consistency of Social Bonds among Females

To examine the relationship between group composition and the consistency of females' partner preferences, we first ran an LMM with each female's partner preference index (PPI) as the dependent variable and number of females, number of males, adult sex ratio, female dominance rank, presence or absence of kin (a categorical variable) and their interactions as predictors. Female identity was entered as a random factor (Table 2).

Because this model suggested that dominance rank was unimportant, we deleted this predictor and ran a second model with number of females, number of males, adult sex ratio and the presence of kin as predictors. All were significant; there were no significant interactions (Table 2). Additional post hoc LMMs in which PPI was the dependent variable and each of the significant predictor variables was tested alone revealed a significant negative correlation only between PPI and the number of females ($t = -2.505$, $N = 148$, $P < 0.05$; number of males: $t = -0.374$, NS; sex ratio: $t = -0.821$, NS; presence of kin: $t = 1.474$, NS). Thus, as the number of females in the group increased, females were less likely to retain their top social partners from one year to the next (Fig. 2).

Mortality

To examine the factors associated with female mortality, we ran an LM with annual female mortality rate as the dependent variable

Table 2
Results of linear mixed models with each female's partner preference index (PPI) as the dependent variable ($N = 148$) and number of females, number of males, adult sex ratio, female dominance rank (included/excluded) (all continuous variables) and presence or absence of kin (a categorical variable) as predictors

Female PPI†	Estimate	SE	t
Predictors with dominance rank			
No. of females aged >4 years	−0.018	0.006	−3.011**
No. of males aged >4 years	−0.148	0.056	−2.663*
Adult sex ratio	−0.451	0.169	−2.676*
Dominance rank	0.037	0.089	0.412
Presence of kin	0.122	0.062	1.988
Predictors without dominance rank			
No. of females aged >4 years	−0.019	0.006	−3.065**
No. of males aged >4 years	−0.149	0.056	−2.684*
Sex ratio	−0.454	0.168	−2.695*
Presence of kin	0.133	0.056	2.391*

*$P < 0.05$; **$P < 0.01$.
† Female identity ($N = 44$) was entered as a random factor.

and the number of females, number of males, adult sex ratio and their interactions as predictors. This analysis revealed that annual mortality rates were significantly negatively correlated with the number of males ($t = -2.947$, $N = 15$, $P < 0.05$) and significantly positively correlated with the number of females ($t = 2.509$, $P < 0.05$) (Fig. 3).

There was some indication that, with the exception of very old females (>20 years), females in the top third of the dominance hierarchy experienced lower mortality rates than females in the bottom two-thirds of the hierarchy. Only 18% of the 33 females (aged < 20 years) that died between 1993 and 2007 ranked in the top third of the dominance hierarchy (one-sample chi-square test: $\chi^2_1 = 4.55$, $P = 0.066$). By contrast, 48% of females in the bottom third of the dominance hierarchy died during this time. Similarly, of the eight lactating females with young infants that died during this time, only one (13%) ranked in the top third of the dominance hierarchy.

Finally, there was no relationship between annual infant mortality and the number of females ($t = -0.015$, NS) or the number of males ($t = -0.383$, NS) in the group.

DISCUSSION

Taken together, our results suggest that female baboons incur several, probably independent, costs when living in groups with
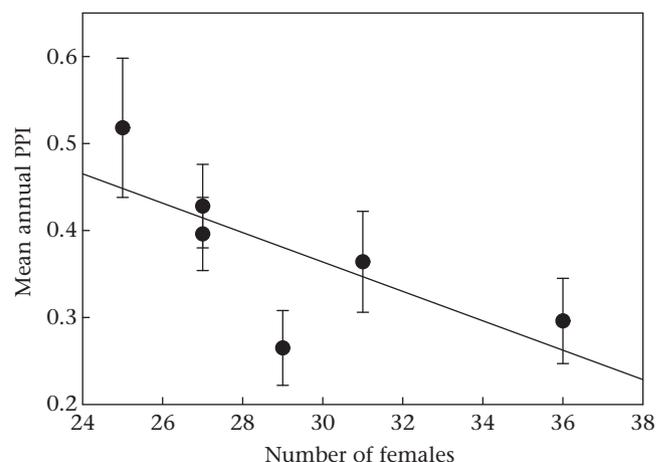
Figure 2. Females' mean annual partner preference indices (PPI) in chacma baboons compared with the annual number of females in the group. Legend as in Fig. 1.
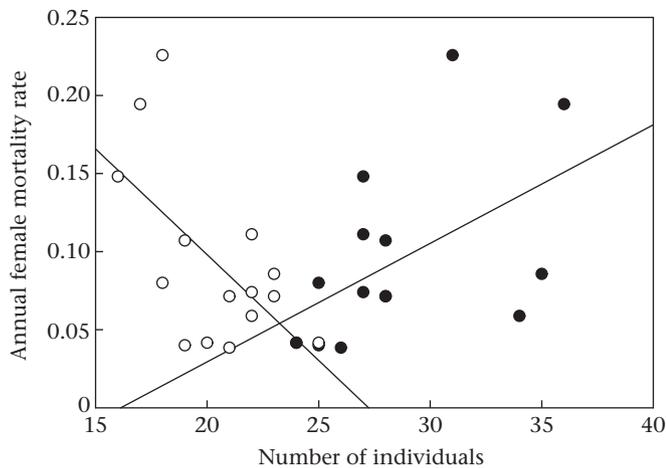
Figure 3. Mean annual female mortality rate in chacma baboons compared with annual number of males (open circles) and females (black circles) in the group. Legend as in [Fig. 1](#).

many females and few males: increased intrasexual aggression, less stable bonds with female partners and increased mortality rates. These costs appear to be unrelated to food competition.

Our results are consistent with previous research (Huchard & Cowlishaw 2011) suggesting that female baboons actively compete for access to males, and that they may do so because of the paternal investment they can potentially provide. Rates of female aggression, and in particular rates of aggression by low-ranking females, increased as the sex ratio became more skewed towards females, suggesting that when males were in relatively short supply there was more competition among females, and that this cost was borne primarily by low-ranking females.

Female–female competition for males may be particularly intense among chacma baboons because of the threat of infanticide by immigrant males (Palombit et al. 1997; Weingrill 2000; Clarke et al. 2009). Lactating females compete to establish friendships with males (Palombit et al. 2001), and individuals that are unable to do so show elevated glucocorticoid levels when a new male enters the group (Beehner et al. 2005; Engh et al. 2006). Females form friendships preferentially with former consort partners, who are often their infants' fathers (Moscovice et al. 2010). The fact that dominant females can displace subordinate females from male friends, and in some cases prevent them from forming friendships entirely, suggests that paternal investment is a limited commodity that cannot be shared across a large number of females. Thus, any females that become pregnant within the same year may pose a competitive threat that potentially affects infant survival. As a result, it may be advantageous for females in all reproductive states to attempt to prevent other females from mating and forming friendships with males.

Rates of female aggression were higher in years when the group included a larger proportion of nulliparous females. Access to mates and, subsequently, male friends may be especially important for young females, which often experience higher infant mortality rates (Nicolson 1987; Cheney et al. 2004). Older mothers tend to form weaker friendships than younger mothers and in some cases even prefer associating with male and female matrilineal kin, especially when they have subadult sons (Palombit et al. 2001). For all of these reasons, nulliparous females may be more likely than older females to mount challenges to the dominance hierarchy and attack other cycling females (for similar observations on rhesus macaques, *Macaca mulatta*, and yellow baboons, *P. h. cynocephalus*, see also Samuels & Hendrickson 1983; Samuels et al. 1987).

An additional cost of living with large numbers of females may be a reduction in the consistency of social bonds. The partner preference index (PPI) can be regarded as a psychological measure of females' ability or motivation to retain preferred female partners from one year to the next when those partners are still present in the group. Results indicate that females' partner consistency decreased as the number of females in the group increased. Whether this decrease resulted from increased competition for partners, the need to interact with more partners (Lehmann et al. 2007), or some combination of these and other factors remains to be determined. Previous analyses on the same social group have indicated that females with strong, consistent bonds experience lower mortality and higher offspring survival than those with weaker bonds (Silk et al. 2010a, b). Thus, to the extent that the presence of many females causes females' partner preferences to become less stable, large numbers of females may represent a fitness cost independent of those associated with increased competition for food, mates and male friends.

Finally, female mortality rates were significantly higher in years when the group contained high numbers of females and low numbers of males, suggesting that reduced survival may constitute a third cost of living in such groups. It seems unlikely that the increase in female mortality was due primarily to heightened food competition, because female mortality rates were negatively correlated with the number of males. If food competition had played an important role, this correlation would have been positive. Instead, it seems possible that females living in groups with relatively few males and relatively large numbers of females are at increased risk of predation, the primary cause of adult and juvenile mortality in this population (Cheney et al. 2004). Primate groups that confront high rates of predation typically include more males than would be expected given the number of females (Hill & Lee 1998). The presence of many males may reduce predation risk not only through early detection but also though active defence, because male baboons frequently attack and even injure predators such as leopards, *Panthera pardus*, and hyaenas, *Crocuta crocuta* (Cowlishaw 1994; Cheney et al. 2004). As a result, any decrease in the number of males relative to females may put females at increased predation risk; such groups may even attract predators. More data on dispersal patterns and group cohesion (e.g. King & Cowlishaw 2009) will be needed to investigate these questions.

High-ranking females may be buffered to some degree from these risks. High-ranking females tend to live longer than low-ranking females (Silk et al. 2010b) and also appear to experience lower mortality rates. High-ranking females may be able to minimize the threat of predation by foraging and resting in proximity to males, thereby forcing more subordinate individuals to the group's periphery, where they may be more vulnerable to attack (Ron et al. 1996). Such competitive exclusion may have contributed to low-ranking females' heightened aggression in years when the sex ratio was most skewed.

Infant mortality rates were unaffected by variation in the numbers of males and females, probably because the primary cause of infant mortality is infanticide by immigrant males. In any given year, as many as eight males may immigrate into the group. Although these males may aid in defence against predator attacks, they also represent an infanticidal threat. Whether a male is able to commit infanticide depends on whether he can attain high dominance status (Palombit et al. 2000), which seems to be unaffected by the number of males in the group.

Because female reproductive success in social mammals is determined largely by parental rather than mating effort, intrasexual competition among females has typically been assumed to occur primarily over food. Recently, however, renewed attention has been paid to the importance of mate competition among

females, with a concomitant focus on a broader definition of intrasexual selection that encompasses both competition for resources and competition for mates and social partners (Carranza 2009; Clutton-Brock 2009; Clutton-Brock & McAuliffe 2009; Huchard & Cowlishaw 2011; Rosvall 2011; Stockley & Bro-Jorgensen 2011). Such competition is predicted to be particularly intense in monogamous species and in species that exhibit high reproductive skew, where females compete for a single breeding position. The results described here indicate that intrasexual competition for social partners, mates, paternal investment, and perhaps also male protection occurs even in species where females show low skew, and that females living in groups with many other females and an imbalanced sex ratio suffer the costs of increased aggression, less stable social relationships and increased mortality.

Acknowledgments

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