



Context dependence of female reproductive competition in wild chacma baboons

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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.

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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'

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reproductive states, which are characterized by different needs and limiting resources (Gowaty, 2004; Huchard & Cowlshaw, 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 & Cowlshaw, 2011). Thus, reproductive synchrony between females is likely to intensify female reproductive competition, for instance in species with a short breeding season (e.g. Bebié & McElligott, 2006; Bro-Jørgensen, 2002; Bro-Jørgensen, 2007), 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 et al., 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 & Cowlshaw, 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 & Cowlshaw, 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 & Cowlshaw, 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; Wheeler, Scarry, & Koenig, 2013; van Schaik, 1989), 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; Cowlshaw, 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, Cowlshaw, & Huchard, 2016), which are typically associated with high infanticide risk (Lukas & Huchard, 2014; Palombit, 1999; Zippel 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

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