



Social behavior and patterns of testosterone and glucocorticoid levels differ between male chacma and Guinea baboons



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ABSTRACT

In multi-male, multi-female groups of mammals, males usually compete aggressively over access to females. However, species vary in the intensity of male contest competition, which has been linked to differences in testosterone and glucocorticoid profiles. Chacma (*Papio ursinus*) and Guinea (*P. papio*) baboons constitute an intriguing model to examine variation in male competition and male endocrine correlates, because of the differences in their social systems. Chacma baboons live in stable female-bonded groups with linear male dominance hierarchies and a high male mating skew, whereas Guinea baboons live in male-bonded, multi-level societies. We recorded male behavior and assayed testosterone (fT) and glucocorticoid metabolite (fGC) levels from fecal samples in one population of each species. Male chacma baboons were more frequently involved in agonistic interactions, and dominance relationships were more consistent than in Guinea baboons, where we could not detect linear hierarchies. Notably, male chacma baboons were also more aggressive towards females, indicating an overall higher aggressiveness in this species. In contrast, male Guinea baboons showed higher levels of affiliative interactions and spatial tolerance. High-ranking and consorting male chacma baboons showed elevated fGC levels and also tended to show elevated fT levels, but there was no effect of consorting in Guinea baboons. Agonism was not related to hormone levels in either species. Thus, predictors of fT and fGC levels in Guinea baboons seem to differ from chacma baboons. Our results support the view that different social systems create differential selection pressures for male aggression, reflected by different hormone profiles.

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Introduction

In most mammalian species, male reproductive success is determined primarily by mating rather than parental effort (Trivers, 1972) and males in multi-male, multi-female groups commonly compete intensely with other group members over access to females (i.e. contest competition). This intense competition strongly shapes male behavior, life-history traits, and associated endocrine profiles. The establishment of dominance hierarchies can be considered as an adaptation to regulate access to females without frequent, and potentially costly, conflicts. Positions in such hierarchies are often based on differences in competitive abilities (reviewed in Zinner and Wheeler (2012)), and dominant males usually have priority of access to receptive females (Altmann, 1962). This generally results in a reproductive skew among males of different ranks (reviews: Alberts, 2012; Ellis, 1995). To circumvent dyadic contest competition for high

rank, males sometimes employ alternative tactics, most importantly through coalitionary behavior (Alberts, 2012; e.g. in bottlenose dolphins, *Tursiops* sp., Connor et al., 1992; feral horses, *Equus caballus*, Feh, 1999; yellow baboons, *Papio cynocephalus*: Alberts et al., 2003).

The intensity of male contest competition is related to the length of time that a male breeds during his life (Lukas and Clutton-Brock, 2014), potentially because only prime-aged males can successfully defend mating opportunities against other males in species with intense dyadic contest competition. The resulting interspecific differences in male reproductive trajectories are reflected in long-term patterns of the androgen testosterone, which affects traits related to competition (e.g. stimulation of muscle tissue growth: Kemnitz et al., 1988) and mating (e.g. promotion of spermatogenesis: McLachlan et al., 1996). In long-lived mammals, testosterone levels increase until males become sexually mature, remain relatively high during breeding years, and decline once males cease breeding (shown e.g. in Papionini: Beehner et al., 2009; feral Soay sheep, a form of the domestic sheep *Ovis aries*: Preston et al., 2012). Furthermore, the ‘challenge hypothesis’ – originally postulated for birds (Wingfield et al., 1990) – predicts that elevation of testosterone

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enhances aggression in the context of reproductive competition (Muller and Wrangham, 2004). In accordance with this idea, males may show elevated testosterone levels during the mating season (e.g. feral horses, Khalil et al., 1998, long-tailed macaques, *Macaca fascicularis*: Girard-Buttoz et al., 2015), in the presence of receptive females (e.g. in chimpanzees, *Pan troglodytes*: Muller and Wrangham, 2004), during mate-guarding periods (e.g. *M. fascicularis*: Girard-Buttoz et al., 2015) or during competition for high rank (e.g. in bighorn sheep, *Ovis canadensis*: Pelletier et al., 2003). Indeed, in some species, an association between individual testosterone levels and aggressiveness has been observed during such periods (bighorn sheep: Pelletier et al., 2003; chacma baboons: Beehner et al., 2006).

The type and intensity of competition is also reflected in patterns of glucocorticoid (GC) levels (Abbott et al., 2003; Goymann and Wingfield, 2004). Glucocorticoids are responsible for the mobilization of energy reserves and suppression of non-essential metabolic processes (reviewed in Sapolsky et al. (2000)). As a result, high GC levels can be adaptive in response to acute stressors, but detrimental when sustained over long times (e.g. Sapolsky, 2005). With regard to dominance relationships, relative GC levels of dominant animals depend on how ranks are acquired and maintained, while in subordinate animals levels depend on the degree of threat they suffer from dominants, the ability to avoid these threats or to gain social support, and the availability of resources or mating partners (Abbott et al., 2003; Goymann and Wingfield, 2004). In addition to a relation with dominance position, males' GC levels often increase during high mating activity, most likely as a result of the energetic stress of mating and mate guarding (e.g. Bercovitch and Ziegler, 2002; Cheney et al., 2015; Girard-Buttoz et al., 2014; Higham et al., 2013). Accordingly, GC and testosterone levels are sometimes observed to increase synchronously in males during intense mating activity (Bercovitch and Ziegler, 2002).

Baboons (*Papio* spp.) are well-suited to an investigation of the causal and proximate factors underlying differences in male–male competition, including the endocrine correlates of these differences, because they vary in terms of their social organization and males show a great diversity of behavioral adaptations when competing with other males (Henzi and Barrett, 2003; Jolly, 2007). There are presently six recognized baboon morphotypes, which diverged only about 2 million years ago (Zinner et al., 2013). According to the phylogenetic species concept, these have been identified as species, although considerable interbreeding and hybridization have been reported (e.g. Tung et al., 2008).

Chacma (*P. ursinus*), yellow (*P. cynocephalus*), and olive baboons (*P. anubis*) form stable female-bonded multi-male, multi-female groups. Males usually emigrate into neighboring groups where they aggressively compete for high ranks (e.g. Drews, 1996; Kitchen et al., 2003, 2005; MacCormick et al., 2012). In all three species males form linear hierarchies and rank positions largely predict which males form sexual 'consortships' during females' receptive periods (Alberts et al., 2003, 2006; Bulger, 1993; Packer, 1979). Coalitions among male chacma baboons are virtually absent (Bulger, 1993; Henzi and Barrett, 2003), while opportunistic coalitions among male yellow and olive baboons are relatively common (e.g. Smuts, 1985; Bercovitch, 1988; Noe and Sluiter, 1995). As a consequence, mating skew, and possibly intensity of dyadic contest competition, seem to be most pronounced in chacma baboons (Alberts et al., 2003; Beehner et al., 2009; Packer, 1979).

Hamadryas baboons (*P. hamadryas*), in contrast, live in multi-level societies (Abegglen, 1984; Kummer, 1968; Schreier and Swedell, 2009) with female-biased dispersal (Städele et al., 2015). Within this society, one-male units (OMUs) form the smallest entity, and 'leader' males almost entirely monopolize reproduction within their OMUs (Swedell et al., 2014).

Guinea baboons also live in multi-level societies, where several males and females form 'parties', which aggregate into 'gangs' (Patzelt et al., 2014). Dispersal patterns seem to be female-biased (Kopp et al., 2015). Males are spatially tolerant, sometimes groom each other, and often form coalitions (Galat-Luong et al., 2006; Patzelt et al., 2014;

Sharman, 1981), indicating the existence of male bonds in this species. The degree of mating skew is probably lower than in other species as most of the adult males, even non-prime aged males, are closely associated with a variable number of females (Boese, 1973; Patzelt et al., 2014; Goffe and Fischer, in revision).

Because male chacma and male Guinea baboons have evolved clearly different reproductive strategies, the aim of this study was to compare behavioral and endocrine profiles between males of these two species to better understand causes and consequences of variation in male–male competition. Previous studies of male chacma baboons have indicated that testosterone levels increase before individuals reach their maximum dominance position and decline afterwards (Beehner et al., 2006, 2009). Furthermore, high testosterone levels are correlated with high aggression rates during periods in which upper rank positions are contested (i.e. 'unstable' periods; Beehner et al., 2006), and they are predictive of rises in dominance rank (Beehner et al., 2006; Bergman et al., 2006). During unstable periods, dominant males show higher GC levels than subordinate males, while during stable periods dominant males tend to have similar or lower levels (Bergman et al., 2005; Cheney et al., 2015). This probably reflects the stress (social and/or metabolic) of defending a high rank against frequent challenges during unstable periods (Cheney et al., 2015). Furthermore, involvement in consortships increases male GC levels (Bergman et al., 2005), and this effect is most pronounced during unstable periods (Cheney et al., 2015). Comparable data on testosterone and GC levels for Guinea baboons are missing. Although much information has already been collected for chacma baboons, we nevertheless undertook a comparative study of both species to ensure that methodological differences could be ruled out as a source of variation between species.

As an expected consequence of differences in reproductive strategies, we predicted that male chacma baboons would show higher levels of aggression and more consistent (i.e. unidirectional) dominance relationships, indicating a higher degree of contest competition (Koenig et al., 2013). For Guinea baboons, we predicted that behaviors associated with the occurrence of male bonds [male–male affiliation and high spatial tolerance (van Hooff and van Schaik, 1994)] would occur more often (for all prediction see Table 1). Given the assumption that reproductive success is monopolized by a few males in chacma but not in Guinea baboons, we predicted that adult male chacma baboons would

Table 1
Predictions.

Prediction	Confirmed?	Fig./Table
Male–male behavior		
More frequent and intense agonistic interactions in chacma baboons	Yes	Table 3
More consistent dominance relationships in chacma baboons	Yes	Table 5
More affiliation and higher spatial tolerance in Guinea baboons	Yes	Fig. 2
Testosterone		
More variation in chacma baboons	No	Text
Stronger age and rank effects in chacma baboons	Potential rank effect in chacma baboons. No ranks in Guinea baboons.	Table 6, text
Stronger relation with consortships in chacma baboons	Potential effect in chacma baboons but not in Guinea baboons.	Table 6, text
Relation to agonism during periods of aggressive competition	No	Text
Glucocorticoids		
More variation in chacma baboons	No	Text
Stronger effect of rank in chacma baboons, especially during rank instability	Related to rank in chacma baboons. No ranks in Guinea baboons and not related to number of females.	Table 7, text
Stronger effect of agonistic interactions in chacma baboons	No effect found in either species	Table 7, text
Stronger effect of consortships in chacma baboons	Yes	Table 7, text

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