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 consortship 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.

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 Sluijter, 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

show greater inter-individual variation in testosterone levels. More specifically, we expected more pronounced effects of age and rank on testosterone levels in adult male chacma baboons. We also expected to find a relationship between consortships and testosterone levels in both species, but predicted this would be less pronounced in Guinea baboons as the relatively permanent association between males and females seems to be rarely challenged and thus mate-guarding is less intense. Generally, we expected to find a relationship between testosterone and agonistic interactions only during periods when males are competing over high rank or access to females; in Guinea baboons, however, previous observation suggested that such periods may not occur.

Due to the importance of dominance ranks and aggression for reproductive success in chacma baboons we expected that rank, rank changes and aggression would exert a stronger effect on male GC levels compared to Guinea baboons. More specifically, we expected to replicate the finding that dominant male chacma baboons have higher GC levels during rank instability as their reproductive success is highly dependent on high rank position (Bergman et al., 2005; Cheney et al., 2015). In male Guinea baboons, we expected no or only a weak effect of rank position on GC levels, as ranks were assumed to be of less importance to reproductive success. As for testosterone, we expected to find a stronger relationship between consortships and GC levels in chacma baboons.

Methods

Study sites and populations

Behavioral and hormonal data were collected from wild chacma baboons in the Moremi Game Reserve, Botswana, and wild Guinea baboons in the Niokolo Koba National Park in Senegal. Data collection in Botswana took place between March and September 2011. The observed group ('C-Troop') had been under continuous observation between 1978 and 2007 (see Cheney and Seyfarth (2007)). Despite the end of continuous observations in 2007, the group was still well habituated in January 2011. At that time, the group was composed of 10 adult males, 25 adult females and their immature offspring (Table 2). At the end of April, however, the group fissioned into two smaller groups, the 'Airstrip subgroup' (ASG) and the 'Hamerkop subgroup' (HSG). Five of the adult males and 13 of the adult females went into the ASG; two of these females disappeared during the remaining study period. The other five adult males went into the HSG with 12 females, and were immediately joined by a new male who took over the alpha position. One of the HSG males disappeared at the end of June and another male was found dead at the end of August 2011. After the fission, both subgroups stayed within the same territory and regularly encountered each other. The frequency and quality of these encounters are briefly described in the supplementary material (SM, Group Encounters).

The 11 adult male chacma baboons included in data collection were put into three broad age categories, estimated by tooth wear and other morphological characteristics (see Method S1, SM). Three adult males were categorized as 'young', five as 'middle-aged', and three as 'old'.

Data collection in Senegal took place between February and July 2012 at Simenti (described in Patzelt et al. (2011)). As outlined above, Guinea baboons live in a multi-level society in which several 'parties' form 'gangs'. While males of different gangs rarely interact with each other, males within the same gang have regular interactions even if they belong to different parties (Patzelt et al., 2014). It therefore seems that Guinea baboon gangs are the social units most comparable to chacma baboon groups (see also Maciej et al. (2012)). We therefore compared male behavior between chacma baboon groups and Guinea baboon gangs.

We collected data on two different gangs (Table 2). The 'Mare-gang' was composed of three different parties and we collected data on two of these, the 'OSM-party' (4 males and 9–10 females) and the 'SNE-party' (4 males and 5–6 females). The third party associated with the Mare-gang, the 'AND-party', was a bachelor group of two young adult males and 3–4 subadult males. We also collected data on one party of the 'Simenti-gang', the 'JKY-party'. This party represented the larger of two parties constituting this gang. Males of the 'MST-party', the second party of this gang, could not be included in data collection. The 14 males included in the Guinea baboon data set consisted of four young, seven middle-aged, and three old individuals. The number of females associated with a male was determined ad libitum by observations on spatial proximity, copulations and other interactions.

Behavioral data collection

U.K. conducted focal observation on males of both species to make data as comparable as possible. Observations always took place between 6 am and 1 pm and were balanced over different times of the day for each individual. Focal subjects were chosen randomly whenever possible. Focal observations included observations of 20 and 30 min, respectively, depending on the availability of males (i.e. longer observations in small groups after the fission in chacma baboons, and when Guinea baboon parties were separated).

During focal observation, U.K. recorded all agonistic behaviors (i.e. fights, chases, charges, threats and submissive behaviors; for definitions see Table S1, SM). He also noted all approaches and leaves within 1 m and 10 cm (i.e. 'body-contact') of the focal individual to compare supplants and general patterns of interactions among males. When individuals were only briefly in close proximity (i.e. for less than 5 s) we labeled such interactions as either a supplant (when A approached B and B left); an 'in&out' (when A approached and immediately left B, or A and B approached each other and both left), or a 'bump-in' (when A approached B and both left in different directions). During all these interactions we noted whether individuals exchanged 'greetings' (including all non-agonistic and non-affiliative physical contact; for a definition see Table S1, SM), as these have been associated with the non-agonistic negotiation of dominance relationship (e.g. Colmenares, 1991) and the formation of bonds (Whitham and Maestripieri, 2003). During group movements we only recorded such interactions when proximity was clearly directed, meaning that one individual headed

Table 2
Study groups, compositions, and periods of observation.

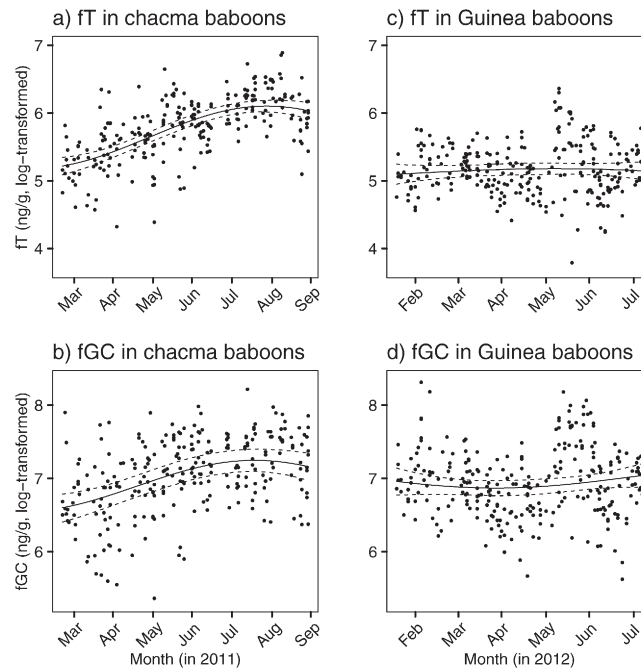| Species	Group/gang	Party	Period of data collection	Number of males/focal males	Number of females	Number of cycling females	Focal hours
Chacma baboons							260h
	C–Troop	(Before fission)	03.–04.2011	10/10	25	6–9	
	ASG	(After fission)	05.–09.2011	5/5	11–13	2–5	
	HSG		05.–09.2011	4–6/4–6	12	3–5	
Guinea baboons							231h
	Mare–gang			10/8	15	3–5	
		OSM	02.–07.2012	4/4	9–10		
		SNE	02.–07.2012	4/4	5–6		
		AND	–	2/0	0		
	Simenti–gang			11/6	17	4-6	
		JKY	03.–07.2012	7/6	10–11		
		MST	–	4/0	6–7		

Fig. 1. Temporal variation in hormone metabolite values. Plots show values for a) fT and b) fGC in male chacma baboons, and c) fT and d) fGC in male Guinea baboons. The solid line depicts the predicted values for metabolites from models with trigonometric functions (see Model 1.1–Model 1.4, SM). Dashed lines indicate 2.5% and 97.5% confidence intervals of the models.

directly towards another; mere proximity while the group was traveling was not included.

When one individual approached another and both stayed in close proximity for longer than five seconds, this could potentially result in three different behaviors related to spatial tolerance or affiliation: '1 m proximity' (feeding, resting or standing within 1 m), 'contact sitting' (resting, feeding, or standing within body-contact), or grooming. For all these behaviors we determined durations using recorded start and end times.

In addition to recordings during focal observations, we noted all agonistic interactions ad libitum to improve the assessment of dominance relationships. Further, we recorded whether fights resulted in injuries since we were interested in the intensity of fights. As fights are rarely observed, however, we also recorded each time a male had a fresh wound which could potentially have resulted from a fight, including slashes, cuts, or punctures of the skin.

To assess the effect of mating activity on hormone values, we recorded consortships ad libitum. A male was considered as consorting when 1) a female showed visible signs of swelling of the perineal skin and 2) the male followed and regularly mated with that female (Bergman et al., 2005; Cheney et al., 2015). Consorting male chacma baboons typically threaten other males approaching that female (Cheney et al., 2015). Consortships seem to be less pronounced in Guinea baboons (personal observation, U.K.), but males nevertheless follow females more closely when they have full swellings than during other times (Goffe and Fischer, in revision). Due to a 24–48 h delay of hormone excretion in feces (Heistermann et al., 2006; Möhle et al., 2002), all hormone samples collected one or two days after a male has been observed to consort were classified as 'in consort' (as in Cheney et al. (2015)).

Hormone data

For the non-invasive assessment of hormone levels, we regularly collected fecal samples from all focal individuals. Only samples uncontaminated with urine were collected immediately after defecation and only samples collected between 6.30 am and 1 pm were included to avoid diurnal effects on hormone levels (Hodges and Heistermann, 2011). For chacma baboons, we collected 251 samples in total, ranging

between 13 and 27 per individual (mean ± sd = 22.82 ± 4.87) and for Guinea baboons 268 samples, ranging between 10 and 27 per individual (mean ± sd = 19.14 ± 6.74). Average levels of hormone metabolites for all males under different conditions are shown in Table S4 (SM; see below for further details).

Hormone metabolites were extracted from fecal samples directly in the field according to Shutt et al. (2012) and as described in Method S2 (SM). The extracts were stored in a gas-refrigerator until transport to the German Primate Center (DPZ) for analysis. The maximum storage duration of extracts in the refrigerator was less than six months, which has been shown not to affect testosterone or glucocorticoid metabolite levels (Kalbitzer and Heistermann, 2013). Once samples arrived in the DPZ they were immediately put into a freezer at −20 °C and assayed within five months thereafter.

Fecal extracts were assayed for immunoreactive testosterone (fT) and 11ß-hydroxyetiocholanolone (fGC), a major cortisol metabolite in the feces of primates, by using validated enzyme immunoassays (see Method S3, SM). For hormone measurements in samples collected from chacma baboons, inter-assay coefficients of variation (CVs) for the fT assay were 11.4% and 15.7% for high and low value quality controls, respectively, while for fGC-assays CV values were 7.7% and 16.5%. For samples collected from Guinea baboons, CVs for fT were 11.2% and 14.0%, and for fGC 4.4% and 8.4%.

Data analysis

We used individual number of agonistic interactions (i.e. how often each focal male was involved in agonistic interactions with other individuals) to compare aggressiveness between both species. As male–male competition is usually more intense when many males have to compete over few females (e.g. Kvarnemo and Ahnesjo, 1996), we categorized females as lactating, pregnant, or cycling, and controlled differences in male–male agonism for the ratio between number of adult males and cycling females ($M:F_{cycling}$). There was always at least one cycling female in each group/gang (see Table 2). To determine whether chacma baboon males are generally more aggressive we also analyzed male–female aggression in both species.

In order to analyze dominance relationships, we included all direct-ed dominance interactions in which the dominant and subordinate individual could be assigned (i.e. chases, charges, supplants, and submissive behaviors). We also included agonistic behaviors that occurred in two directions within one bout; for example if a chase turned in direction, we included both chases.

For chacma baboons, we analyzed dominance relationships in the C-troop before the group split. We excluded the first week of focal data collection because a young male took over the alpha position one week after the start of observations, and we therefore had very little data from the time before this event occurred. After the group fission (7 weeks later), we analyzed data on both new groups separately until the end of the study period. To assess the effect of rank changes in the upper rank position (i.e. unstable periods; Beehner et al., 2006; Bergman et al., 2005) on behavior and hormones, we labeled the two weeks following such changes as unstable. This included two periods: the first two weeks analyzed for the C-troop, and after the fission of the C-troop the first two weeks for both smaller groups (ASG and HSG).

In Guinea baboons, we analyzed dominance relationships for all of the five following constellations: First, we assessed dominance relation-ships for the two observed parties of the Mare-gang (OSM- and SNE-parties) separately. We then combined data from the two parties and included interactions with other males of this gang that were not part of focal observations (the two males of the AND-party). For the Simenti-gang, we assessed relationships within the JKY-party (including the young non-focal male) and then included data on inter-actions with males of the other party (the MST-party) which belonged to this gang but which was not included in focal observations. We did not observe changes in the upper rank positions and could therefore not detect any unstable period.

Statistics

We compared rates of interactions between species using general-ized linear mixed model (GLMMs) calculated in R 3.1.2 (R Core Team, 2014; for details see Method S5, SM). The different behaviors were in-cluded as response variables (as counts), species as test variable, M:F$_{cycling}$ as control variable (only for male–male agonistic interac-tions), focal individual as random effect, and log-transformed focal durations as offset (for details see Models 2.1, 2.2, 3.1, and 3.2, SM). For most behaviors we used models with a Poisson error structure, but for behaviors that did never occur more than once during a focal we used a binomial error structure.

We used two-sided, exact Wilcoxon–Mann–Whitney-tests (function 'wilcox.test') to compare within each species whether interac-tions occurred more often with or without greeting. We used the same test to compare time engaged in behaviors indicating spatial tolerance and affiliation between species.

To compare dominance relationships we used the directional consis-tency index (DCI). This index is robust against variation in sample size and the number of unknown dyads, and therefore represents the most appropriate parameter to compare dominance relationships among groups (Koenig and Borries, 2006). The DCI was calculated in MatMan 1.1 (Noldus, Wageningen, Netherlands; first described in de Vries et al., 1993). The same program was used to calculate ranks (I&SI meth-od) and the Landau's linearity index h' (corrected for unknown relation-ships). Similar to the steepness of hierarchies (de Vries et al., 2006), h' is strongly affected by sample size and number of unknown dyads (Klass and Cords, 2011; Koenig and Borries, 2006), which makes group or species comparisons meaningless. Nevertheless, we used the linearity test using the h' index to assess whether calculated ranks could be used in further analyses.

To test whether adult males of one of the species varied generally more strongly in hormone levels, we calculated average monthly fT and fGC levels for each male. Using these values, we calculated CVs (CV[%] = 100*sd/mean) for each month and then compared average CVs between species using the Wilcoxon–Mann–Whitney test.

To test relations between hormone levels and behavior, age, rank, and rank stability we used linear mixed models (LMMs, see Method S5, SM) with fT and fGC as response variables, respective predictor var-iables, and focal individual as a random effect (for further details see Models 5.1, 5.2, 6.1, 6.2, SM). To meet the assumption of normal distribution we log-transformed fT and fGC values. We furthermore z-transformed all included covariates. We scaled ranks from 0 to 1 with 0 for the lowest ranking individual and 1 for the highest-ranking individual in order to make rank positions comparable among groups. To test the effect of agonism on fGC levels, we calculated the rate of agonistic interactions and, alternatively, the rate of received agonistic behaviors (i.e. 'agonism received') per hour during the two weeks before sample collection and included these as predictor variables. To test whether agonism was related to fT levels, we calculated the rate of agonism given (i.e. fights, chases, charges, threats, and supplants) during the two weeks corresponding to sample collection. We did not include submissive behaviors in the calculation of agonism given and received, as it does not reflect the tendency of an individual to show, or the frequency of an individual to receive, agonistic behaviors.

We were mainly interested in inter-individual variation in metabo-lite values (e.g. due to differences in age) rather than temporal variation affecting the entire group. Nevertheless, fT and fGC often show seasonal variation, which can have methodological or biological causes. Method-ological effects can occur due to seasonally varying availability of differ-ent food items, as diet can change the way hormones are metabolized (Goymann, 2012). Biological effects can occur for various reasons. For example, testosterone levels can be affected by temperature (e.g. Gesquiere et al., 2011b), and GC levels can be affected by daylight hours (Weingrill et al., 2004) or rainfall patterns (e.g. Gesquiere et al., 2011b), as these factors affect the availability of food and water re-sources and activity budgets.

A visual inspection of hormone data from chacma baboons indicated considerable variation over the course of the study with gradually in-creasing fT (Fig. 1a) and fGC (Fig. 1b) levels until peak values in August 2011 followed by a decline. Variation in temperature, rainfall, and the seasonal flooding of the delta strongly affect habitat characteristics of the study population (Cheney and Seyfarth, 2007), but our study was not designed to investigate endocrine correlates of this ecological varia-tion. Nevertheless, we needed to take this pattern into account in order to investigate relationships between steroid levels and variables of in-terest (e.g. age, rank, and consortships), which should be relatively in-dependent of seasonal variation in ecology. As there was no clear distinction between different seasons we could not consider season as a factor variable with discrete levels. Instead, we modeled the (gradual) seasonal variation by the inclusion of a trigonometric term (sine and co-sine of the day in radian). This term was highly significant for both fT ($X_2^2 = 134.04$, P < 0.001) and fGC levels ($X_2^2 = 53.72$ P < 0.001; see also Figs. 1a and 2b and Models 1.1 and 1.2, SM). Furthermore, models predicted peak levels for both hormone metabolites within the same 14 days, indicating the same factor underlying the variation in both me-tabolites. We therefore included these terms as control variables in all models for chacma baboons. Hormone samples from Guinea baboons were all collected during the dry season and the data showed no season-al variation (Fig. 1c and d). Models with the same trigonometric terms were also not better than models without (fT: $X_2^2 = 0.82$, P = 0.664; fGC: $X_2^2 = 2.96$, P = 0.228; see Models 1.3 and 1.4, SM).

Results

Agonistic interactions among males

Male chacma baboons were involved in agonistic interactions with other males at higher rates than male Guinea baboons (Table 3; for de-tails see Model 2.1, SM). The majority of agonistic interactions consisted

of supplants, which also occurred at a higher rate in male chacma baboons. Additionally, male chacma baboons showed a higher rate of submissive behaviors than male Guinea baboons. Other, less frequent, agonistic behaviors (chases, charges, and threats) were also more frequent in male chacma baboons. The low number of these behaviors, especially among Guinea baboons, prevented us from including $M:F_{cycling}$ into the models (models became unstable, thus model results were highly dependent on the inclusion of specific individuals).

Fights among males were extremely rare: we recorded only two fights in chacma baboons during all focal observations and six additional fights ad libitum. Four of these fights included bite attacks, but we could only observe injuries after one of these fights; one participant had a deep cut in the leg and the other one was bleeding at the neck and the shoulder. Additionally, we observed 17 injuries in which we did not observe the wounding event, including 11 injuries to the face, four to the shoulder, one to the buttocks, and one to the flank of a male. In Guinea baboons, we observed nine fights ad libitum, but none of these fights included a bite-attack or an injury. Furthermore, we never recorded injuries on our focal males during the entire study period.

Agonistic interactions between males and females

Male chacma baboons were also involved in agonistic interactions with females at higher rates than were male Guinea baboons (Table 3; for details see Model 2.2, SM). More specifically, we detected significant differences between species in supplants and threats (rates in chacma baboons were higher in both cases). During focal observation we recorded three fights of male chacma baboons with females, and two fights of male Guinea baboons with females.

During male–female interactions in chacma baboons males were always dominant over females with the exception of 6.25% of supplants, in which a male left after the approach of a female. In Guinea baboons, males were supplanted in 15.09% of all male–female supplants. Furthermore, in 12.50% of chases, the male was chased by the female, and in 16.65% of threats, the male was threatened by a female. In contrast, female chacma baboons were never observed to chase or threaten males.

Interactions within close proximity and greeting rates

Male Guinea baboon had more interactions in close proximity than male chacma baboons (Table 4; for details see Model 3.1, SM). As mentioned above, supplants were more common in chacma than in Guinea baboon males (Table 3), but Guinea baboon males were more often involved in bump-ins and in&outs (Table 4). Interactions in male chacma baboons were more likely to occur without greetings (Wilcoxon–Mann–Whitney tests: P < 0.001; see Table S2, SM), while interactions

of male Guinea baboons typically included greetings (P = 0.001). This generalization held for supplants (chacma baboons: more supplants without than with greeting, P < 0.001; no difference in Guinea baboons), bump-ins (no difference in chacma baboons; Guinea baboons: more bump-ins with greetings than without, P = 0.001) and in&outs (chacma baboons: more in&out without than with greeting, P < 0.001; Guinea baboons: more in&outs with than without greeting, P < 0.001).

With respect to male–female interactions, there were the same differences in the rate of supplants (more in chacma baboons, Table 3) and bump-ins (more in Guinea baboons; Table 4). The pattern for the involvement of greetings in male–female interactions was similar to male–male interactions in chacma baboons (1 m-interactions, supplants, and in&outs more often without than with greeting, all P < 0.001; see Table S2, SM). In Guinea baboons, the majority of male–female supplants occurred without a greeting (P = 0.016, see Table S2, SM), while male–female bump-ins occurred slightly more often with than without greeting (P = 0.002).

Spatial tolerance and affiliation

There were obvious differences between males in the time spent in behaviors related to spatial tolerance and affiliation (Fig. 2). Male Guinea baboons regularly spent time resting, feeding or standing with at least one male within 1 m, while such behavior was extremely rare in chacma baboons (Fig. 2a). Contact-sitting occurred occasionally among male Guinea baboons but was never recorded for male chacma baboons (Fig. 2b). Male–male grooming followed a similar pattern (Fig. 2c). In Guinea baboons, 9.96% of all grooming interactions during focal observations were with another male. In contrast, male chacma baboons were never observed in a grooming interaction. For male–female behavior, the direction of species differences was similar for 1 m-proximity (Fig. 2a) and contact-sitting (Fig. 2b; see Table S3, SM). Only in the context of male–female grooming did we not detect a difference between species (Fig. 2c).

Dominance relationships

As agonistic interactions were much more frequent in chacma baboons, the number of interactions available to calculate characteristics of dominance relationships differed between species (Table 5). The DCI in chacma baboons was similar among groups, and was always higher than in Guinea baboons. In Guinea baboons, the DCI was similar for most gangs and parties, and only the males of the OSM-party showed a lower consistency in dominance relationships.

In chacma baboons, the linearity of dominance hierarchies (h') within groups varied with a lower linearity before than after the fission, but both the C-troop and the HSG showed significantly linear hierarchies (P < 0.05; we could not test the linearity of the hierarchy for the ASG
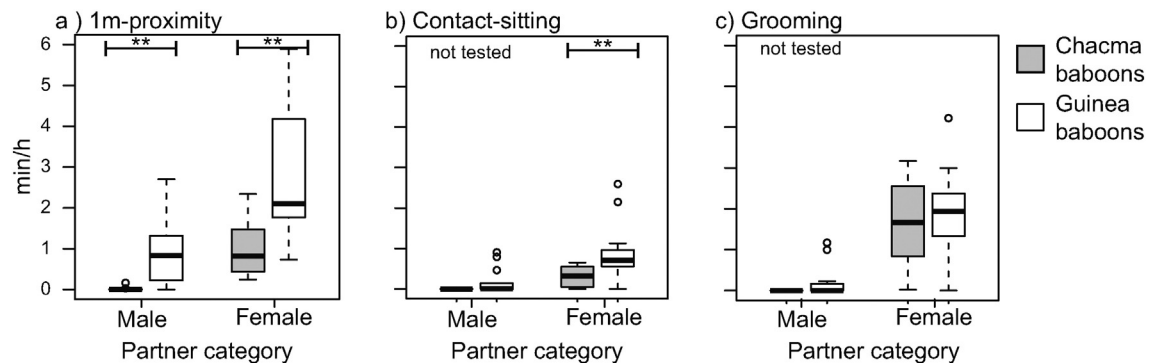

Fig. 2. Relative time males spent in a) 1 m-proximity, b) contact sitting and c) grooming with male and female partners. Durations are shown in minutes per hour of focal observation. Stars indicate significant differences (Wilcoxon–Mann–Whitney tests) with **P < 0.01. See Table S3, SM for details. We did not test differences between species for male–male contact-sitting or grooming because this never occurred in chacma baboons and thus represents a qualitative rather than quantitative difference.

Table 3
Differences in number of agonistic interactions between chacma and Guinea baboons. Stars indicate significant differences (GLMMs) with *P < 0.05, **P < 0.01, and ***P < 0.001. For detailed results see Model 2.1, SM. [1]The total number of agonistic interactions is lower than the sum of specific behaviors as several behaviors occurring in the same bout (e.g. threats and supplants) were counted separately for the number of specific behaviors but summarized as one agonistic interaction (i.e. one bout; for details see Methods). [2]M:F$_{cycling}$ could not be included as control-variable as there were too few interactions.

		Chacma baboons		Guinea baboons		
		Total	Mean ± sd/male	Total	Mean ± sd/male	More in chacma baboons?
Focal hours		261 h	23.70 ± 5.13 h	231 h	16.52 ± 4.14 h	
Male–male agonism	Agonistic interactions	268[1]	1.04 ± 0.26/h	65[1]	0.28 ± 0.29/h	***
	Supplants	157	0.62 ± 0.18/h	52	0.23 ± 0.27/h	***
	Submissive	93	0.35 ± 0.17/h	6	0.02 ± 0.04/h	***
	Threats	26	0.10 ± 0.12/h	3	0.01 ± 0.02/h	**[2]
	Chases	21	0.08 ± 0.05/h	8	0.03 ± 0.06/h	*[2]
	Charges	8	0.03 ± 0.03/h	1	0.00 ± 0.01/h	*[2]
Male–female agonism	Agonistic interactions	186[1]	0.71 ± 0.28/h	96[1]	0.41 ± 0.27/h	**
	Supplants	112	0.44 ± 0.18/h	53	0.23 ± 0.16/h	**
	Submissive	28	0.11 ± 0.05/h	23	0.09 ± 0.10/h	No effect
	Threats	27	0.09 ± 0.10/h	6	0.03 ± 0.05/h	*
	Chases	24	0.08 ± 0.07/h	17	0.08 ± 0.07/h	No effect
	Charges	10	0.03 ± 0.04/h	5	0.02 ± 0.04/h	No effect

as only five males were in the group). During the fission, there was no indication that relative dominance rank influenced which new group a male joined. Males ranked 1, 3, 5, 7, and 8 joined the ASG, and males ranked 2, 4, 6, 9, and 10 joined the HSG. Following changes in the upper rank positions (i.e. unstable periods) we did not observe an increase in rates of agonistic interactions ($X_1^2 = 1.09$, P = 0.58; model was controlled for effects of rank and M:F$_{cycling}$ on agonism; see Model 4, SM).

In Guinea baboons, linearity of hierarchies varied widely between gangs and parties. None of the Guinea baboon hierarchies including at least six males (Mare-gang, Simenti-gang, Jky-party) had a significantly linear hierarchy even though there was a trend for linearity in the JKY-party. Accordingly, we could assess rank positions for male chacma but not for male Guinea baboons.

Variation in testosterone levels (fT) among adult males

Inter-individual variation in fT levels as assessed by monthly CVs was relatively similar in both species (chacma baboons: CV ± sd = 17.42 ± 5.86%, Guinea baboons: 22.07 ± 3.78%; CV ± sd of log-tranformed fT-levels: 3.12 ± 1.02% and 4.16 ± 0.86% respectively). Comparisons of CVs using both non-transformed and log-transformed fT-levels did not indicate a significant difference between species (Wilcoxon–Mann–Whitney test: W = 10 P = 0.138 and W = 9 and P = 0.101 respectively).

The full model in chacma baboons testing the relation between fT and rank, rank stability, agonism given, the interaction between agonism given and rank stability, and age was not significantly better than the null model ($X_7^2 = 11.56$, P = 0.116; Model 5.1, SM). Initially, we also planned to include future rank positions into the model (e.g. Beehner et al., 2006), but during our study no resident male chacma baboon challenged a higher-ranking male.

The analysis of the model stability (see Method S5, SM) indicated that the model was relatively unstable with regard to rank due to one very influential subject, an old male at the bottom of the hierarchy with relatively high fT values. By excluding this individual from the dataset, the full model became significantly better than the null-model ($X_7^2 = 17.34$, P = 0.015). The interaction between agonism given and rank stability was not significant ($X_1^2 = 0.33$, P = 0.566) and was thus removed from the model in order to establish P-values for the main effects (Table 6). Using the reduced dataset, high-ranking males showed higher fT levels than lower ranking males, and males also showed elevated fT levels during consortships. There was no significant relation between fT levels and rate of agonism given, stable/unstable periods or age.

As previously described, male rank predicts access to receptive females in chacma baboons. We could not establish linear hierarchies in male Guinea baboons, but males are permanently associated with specific females. Therefore, we included the number of females instead of rank into the model testing predictors for fT levels in Guinea baboons (Model 5.2, SM). However, the model including the number of females, agonism given, and age as predictor variables was not better than the null model ($X_5^2 = 2.55$, P = 0.769).

Variation in glucocorticoid levels (fGC) among adult males

Inter-individual variation in fGC levels as assessed by monthly CVs was relatively similar in both species (chacma baboons: CV ± sd = 30.07 ± 6.59%, Guinea baboons: 27.76 ± 6.48%; CV ± sd of log-tranformed fGC-levels: 4.46 ± 1.32% and 3.99 ± 0.88% respectively). For both non-transformed and log-transformed fGC-levels we did not detect a significant difference in CVs between species (Wilcoxon–Mann–Whitney test: W = 24, P = 0.731 and W = 25, P = 0.628 respectively).

Table 4
Variation in 1 m-interactions between chacma and Guinea baboons. '↑Chacma' indicates more interactions in chacma baboons and '↑Guinea' indicates more interactions in Guinea baboons. Stars indicate significant differences (GLMMs) with *P < 0.05, **P < 0.01, ***P < 0.001, and [T]P < 0.1. For details see Model 3.1, SM.

		Chacma baboons		Guinea baboons		Species differences
	Duration	Total	Mean ± sd/male	Total	Mean ± sd/male	
		261 h	23.70 ± 5.13 h	231 h	16.52 ± 4.14 h	
Male–male 1 m-IAs	Total	280	1.09 ± 0.24	352	1.62 ± 0.88	↑Guinea *
	Supplants	157	0.62 ± 0.18	52	0.23 ± 0.27	↑Chacma ***
	Bump-ins	7	0.03 ± 0.04	56	0.28 ± 0.26	↑Guinea ***
	In&outs	116	0.44 ± 0.17	244	1.11 ± 0.43	↑Guinea ***
Male–female 1 m-IAs	Total	411	1.57 ± 0.48	287	1.22 ± 0.54	↑Chacma [T]
	Supplants	112	0.44 ± 0.18	53	0.23 ± 0.16	↑Chacma **
	Bump-ins	20	0.08 ± 0.05	40	0.18 ± 0.12	↑Guinea **
	In&outs	279	1.06 ± 0.42	194	0.81 ± 0.37	No effect

Table 5

Characteristics of dominance relationships. Linearity h' = Landau's linearity index h' of hierarchies; DCI = directional consistency index (see Methods for details). Significant results are highlighted. [1]The number of males in the gangs is higher than the sum of males in the shown parties as we only calculated values for parties included in the focal observations.

	Chacma baboons			Guinea baboons				
	Before fission	After fission		Mare-Gang			Simenti-Gang	
	C-Troop	ASG	HSG	Gang[1]	OSM	SNE	Gang[1]	JKY
Males in group	10	5	6	10	4	4	11	7
Focal males	10	5	6	8	4	4	6	6
Interactions included	94	167	150	50	9	30	39	30
Focal hours included	41 h	107 h	105 h	159 h	80 h	79 h	72 h	72 h
Consistency (DCI)	0.85	0.87	0.95	0.76	0.56	0.73	0.74	0.73
Linearity h'	0.62	1.00	1.00	0.33	0.20	1.00	0.39	0.71
Significance of linearity (P)	**0.021**	NA	**0.023**	0.360	NA	NA	0.223	0.072

For chacma baboons, we included rank, rank stability, the interaction between rank and rank stability, rate of agonistic interactions, consort status, and the interaction between consort status and rank stability as predictor variables (Model 6.1, SM). The full model was significantly better than the null model ($X_6^2 = 25.98$, P < 0.001). Neither interaction was significant (rank*rank stability: $X_1^2 = 0.03$, P = 0.868; consort*rank stability: $X_1^2 = 2.47$, P = 0.112) and interactions were therefore removed to establish the P-values for the main effects (Table 7). High-ranking males showed higher fGC levels than lower ranking males and males showed higher fGC levels during consortships than during other periods. Furthermore, fGC levels were higher during unstable periods, but this result has to be considered with care given the terms included into the model to account for seasonal variation in hormone levels. The rate of agonistic interactions was not related to fGC levels and we obtained very similar results when we replaced agonistic interactions by agonism received as predictor variable (Model 6.1, SM). Excluding the same low-ranking male with high fT levels as done for the fT model did not change the results for fGC patterns (the P-value for the effect of rank on fGC decreased from <0.05 to P < 0.01 but all other significance levels remained the same; see Model 6.1, SM).

In Guinea baboons, we included the number of females of a male, consort status, and the rate of agonistic interactions as predictor variables (Model 6.2, SM). Full-null comparisons revealed that these variables did not affect fGC levels in Guinea baboons ($X_3^2 = 5.26$, P = 0.154), and we obtained similar results when we replaced agonistic interaction by agonism received (Model 6.2, SM).

Table 6

Results of reduced LMM with fT levels of male chacma baboons as response variable. The non-significant interaction between agonism given and rank and one influential subject were removed from the model. fT values were log-transformed, rank was scaled from 0 to 1, and rank and rate of agonism given were z-transformed. Mean ± sd before z-transformations: Rank = 0.557 ± 0.32, Agonism given = 0.419 ± 0.72. N = 10 males. Significant results are highlighted. For details, see Model 5.1, SM.

Effect	Estimate	SE	X_1^2	P
(Intercept)	5.503	0.074	NA	NA
Agonism given	−0.015	0.026	0.32	0.570
Stability (unstable)	0.108	0.072	2.21	0.137
Rank (scaled)	0.091	0.033	7.14	**0.008**
Consort	0.196	0.078	5.70	**0.017**
Age (middle-aged)	0.044	0.072	1.69	0.430
Age (old)	0.091	0.072		
Sine (day) (in null model)	−0.329	0.039	60.85	<0.001
Cosine (day) (in null model)	−0.434	0.071	34.42	<0.001

Table 7

Results of reduced LMM with fGC levels of male chacma baboons as response variable. Non-significant interactions of rank*stability and consort*stability were excluded. fGC values were log-transformed, rank was scaled from 0 to 1, and rank and rate of agonistic interactions were z-transformed. Mean ± sd before z-transformations: Rank = 0.495 ± 0.35, agonistic interactions = 1.039 ± 1.14. N = 11 males. For details see Model 6.1, SM.

Effect	Estimate	SE	X_1^2	P
(Intercept)	6.710	0.079	NA	NA
Rank (scaled)	0.132	0.052	4.93	**0.026**
Consort	0.348	0.107	7.01	**0.008**
Stability (unstable)	0.276	0.078	10.79	**0.001**
Agonistic interactions	−0.042	0.026	2.47	0.116
Sine (day) (in null model)	−0.232	0.043	25.83	0.000
Cosine (day) (in null model)	−0.486	0.078	35.91	0.000

Discussion

Our comparison of behavioral and endocrine profiles between male chacma and Guinea baboons suggests that these closely related species differ fundamentally in their intensity of male contest competition, and these differences have consequences for endocrine profiles. Male chacma baboons showed higher levels of aggression than male Guinea baboons. In contrast, Guinea baboons were more affiliative to each other and showed pronounced spatial tolerance. Despite some individual variation, our results suggest that rank and consortship status were related to fT levels in chacma but not in Guinea baboons. In both species, rates of agonistic interactions were not significantly correlated with fT and fGC levels, but in chacma baboon higher-ranking males and those involved in consortships showed elevated fGC levels. Because we applied the same sampling protocols for both species, we can rule out methodological issues as a cause of these species (or population) differences.

Adult male chacma baboons were generally more aggressive than male Guinea baboons, in terms of both the frequency and the intensity of aggressive interactions. This observation was not the result of general differences in interaction rates, as male Guinea baboons interacted more often with each other. Furthermore, differences in aggression were more pronounced for male–male than for male–female behavior, suggesting that selection pressures in baboons acted more strongly on male–male aggression than male aggression per se.

In contrast to chacma baboons, we were not able to detect linear hierarchies, and therefore clear rank relationships, in Guinea baboons. Furthermore, male chacma baboons formed more consistent dominance relationships, indicating more intense contest competition in this species (Koenig et al., 2013). A decrease in male contest competition has been associated with lower potential to monopolize receptive females (e.g. van Hooff and van Schaik, 1994), which is mainly determined by the spatio-temporal distribution of the latter (Altmann, 1990; Emlen and Oring, 1977). This hypothesis, however, cannot explain the observed variation between chacma and Guinea baboons. Females in all species of this genus, including female chacma (Cheney and Seyfarth, 2007) and Guinea baboons (personal observation) show only a low degree of estrous synchrony. Furthermore, differences in rates of male–male agonism were not explained by different ratios between males and cycling females. Notably, this ratio was higher in Guinea than in chacma baboons, which should have resulted in more intense competition among male Guinea baboons (Kvarnemo and Ahnesjo, 1996). In combination with reports that chacma baboons show stronger sexual size dimorphism and canine size than Guinea (and all other) baboons (Patzelt, 2013; Plavcan and Ruff, 2008; Thorén et al., 2006), our results suggest that variation in competition represents true differences between species (or at least between populations), rather than plastic responses to environmental variation. Future comparative studies will be necessary to determine whether other baboon species show intermediate levels of male aggressiveness as predicted by data on morphological differences and reproductive strategies.

In contrast to previous studies (Beehner et al., 2009), we did not detect a relationship between fT levels and age in either species. Because we included very young and old adult males in our study, narrow age ranges are unlikely to explain this pattern. Perhaps, variation in fT levels among adult male baboons is generally low, and therefore hard to detect, which is supported by relatively low CVs (~20%) calculated for both species. Although Beehner et al. (2009) reported that fT levels of adult male chacma baboons decreased with age, some of the very old males (~18–20 years) exhibit similar levels as prime-aged males (~8–10 years; see Beehner et al. (2006)). A potential explanation for the low variation is that all adult male baboons keep a relatively high testosterone 'breeding baseline' (Wingfield et al., 1990) after reaching maturity, which is linked to non-seasonal mating patterns and occasional mating opportunities for subordinate males in chacma (Bulger, 1993) and most other baboon species (e.g. yellow baboons: Alberts et al., 2003, olive baboons: Packer, 1979).

These factors might also explain why fT levels showed an inconsistent relationship with rank and consort activity in male chacma baboons, and why we did not find a relationship between fT levels and consort activity or number of females in Guinea baboons. In species where alpha males almost entirely monopolize reproduction and show exaggerated secondary sexual characteristics, such individuals also show considerably elevated testosterone levels (e.g. in white-faced capuchin monkeys, *Cebus capucinus*, Jack et al., 2014). In contrast, in most species of baboons, there is no consistent relation between dominance rank and testosterone levels. High-ranking olive baboon males only exhibit elevated testosterone levels during unstable periods (Sapolsky, 1993). Similarly, although high-ranking yellow baboon males have higher testosterone levels than low-ranking males, alpha males do not have higher levels than beta males (Gesquiere et al., 2011a). Finally, elevated testosterone levels in male chacma baboons seem to be important in the preparation for mating activity and competition over high rank in the future but not strongly correlated with current mating activity or rank position (Beehner et al., 2006; Bergman et al., 2006). Thus, subordinate male baboons (which are also often older males) or males without much mating activity may also maintain a high testosterone breeding baseline, as illustrated by the low-ranking male chacma baboon in our dataset. In Guinea baboons, fT levels were not related to number of females associated with a male, suggesting that in this species, too, males with few (or any) females may keep a high testosterone breeding baseline to be prepared for potential mating opportunities.

As a consequence of the importance of rank for reproductive success in chacma baboons, we expected that rank would have a stronger effect on fGC levels than in Guinea baboons. We were not able to test this hypothesis, as we could not determine rank in Guinea baboons. In chacma baboons, high-ranking males showed higher fGC levels than low-ranking males. This has been previously observed only during unstable periods (Bergman et al., 2005; Cheney et al., 2015), but the group fission and the frequent group-encounters might have created a similar stressful situation for high-ranking males in our study. Generally, high-ranking chacma baboon males seem to have higher or similar fGC levels compared to low-ranking males, and therefore high ranks seem to impose more energetic stress in this species.

As predicted, we observed differences in the energetic stress related to consortships. fGC levels were elevated in consorting male chacma but not consorting male Guinea baboons, probably reflecting differences in the stress and costs of mate-guarding (cf. Girard-Buttoz et al. (2014)). During consortships, male chacma baboons must constantly prevent other males from approaching and mating with the female they are guarding, and consequently have more aggressive interactions than when not in consort (Bergman et al., 2005). Male Guinea baboons, in contrast, are associated with females for several months or even years at a time (Goffe and Fischer, in revision) and – comparable to the 'respect of possession' shown by hamadryas baboons (Kummer et al., 1974) – other males might not challenge this association during that

time, resulting in less intense mate-guarding. Additionally, mate-guarding has been suggested to impose fewer energetic costs in species with male bonds, and less intense contest competition (e.g. discussed for Assamese Macaques, *M. assamensis*, Schülke et al., 2014). This might also be true for Guinea baboons, though comparable studies on costs of mating-effort and mate-guarding are necessary to test this hypothesis.

Despite the high costs of aggressive competition in chacma baboons, including elevated fGC levels in high-ranking and in consorting males, and regularly observed injuries, contest competition seems to represent the most adaptive way for a male chacma baboon to maximize his reproductive success. By contrast, in Guinea baboons the ability to form social bonds may be more important than aggressive competition with other males. Furthermore, subtle interactions and honest signals may regulate the access to females in this species (see Jolly (2007) for a discussion of this topic). For example, most interactions within 1 m among male Guinea baboons included greetings, and these have been suggested to represent a non-agonistic behavior to negotiate dominance relationships (e.g. Colmenares, 1991).

With regard to ultimate causes, the behavior of contemporary male chacma baboons has been interpreted as adapted to their historical ecology, which only allowed for small groups (Henzi and Barrett, 2003, 2005). According to this hypothesis, one or few males monopolized most of the mating in these groups, resulting in high paternity certainty, high risk of infanticide, and associated counter-strategies. The large size of groups of yellow and olive baboons was hypothesized to result in less potential for a single male to monopolize females, which favored the evolution of male–male coalitions. These coalitions, however, appear to be mainly formed opportunistically rather than constituting long-term bonds (Noe and Sluijter, 1995), and behaviors typically associated with the occurrence of male bonds are extremely rare. For example, in yellow baboons from Amboseli, Kenya (which represents a population with some anubis admixture; Tung et al., 2008), only 0.2% of all grooming interactions involving at least one adult male occurred with another male (S.C. Alberts, personal communication; compared to 9.96% in Guinea baboons). The absence of male coalitions in chacma baboons was therefore interpreted as a phylogenetic constraint (Henzi and Barrett, 2003). However, the mechanisms preventing contemporary male chacma baboons from forming coalitions, even in groups as large as our study group, are unknown.

According to Jolly (2007, 2009) the distinct social behavior of male Guinea and hamadryas baboons is closely linked to a shift in dispersal patterns in baboons. As previously mentioned, dispersal in Guinea (Kopp et al., 2015) and hamadryas baboons (Städele et al., 2015) is female-biased and thus males are more philopatric than females. Jolly suggested that this dispersal pattern evolved at the 'frontier' during the rapid range expansion of the genus into baboon free territory (Jolly, 2009; see also Patzelt et al. (2014)) and that this change represented the main driver for the evolution of relaxed dominance relationships and social bonds among male Guinea and hamadryas baboons. The evolution of non-agonistic mechanisms to negotiate dominance relationships (see Jolly (2007) and above) could have further attenuated frequency and intensity of overt aggressive interactions.

Our results support the view that different social systems create differential selection pressures for male aggression, reflected by differential hormone profiles. When aggressive contest competition represents the almost exclusive male reproductive strategy, males have to bear the physiological costs to achieve and maintain high ranks and defend receptive females, while in male-bonded societies with a lower reproductive skew and long-term male–female associations, the physiological costs but also the possible gains associated with aggressive competition may be less palpable. Future studies need to assess long-term male reproductive success in Guinea baboons, to contribute to a better understanding of the diversity of male reproductive strategies in different social systems.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.yhbeh.2015.08.013.

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