ORIGINAL ARTICLE

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Testosterone predicts future dominance rank and mating activity among male chacma baboons

Abstract Despite the many benefits that testosterone has on male reproduction, sustaining high levels of testosterone for long periods can be costly. The challenge hypothesis predicts that males will show temporarily sustained elevations of testosterone at critical periods, counterbalanced by decreased levels during noncritical periods. We investigated male testosterone measures extracted from fecal samples in a group of chacma baboons (*Papio hamadryas ursinus*) living in the Okavango Delta, Botswana. Because rank serves as a proxy for competition for mates, we examined how male testosterone was related to dominance rank, age, aggression, and mating activity. Males showed an elevation in testosterone at maturity; young adult males had the highest testosterone levels followed by a steady decline with age. Among dispersing males, testosterone was temporarily elevated in the month following dispersal. After controlling for age, testosterone and rank were unrelated, but testosterone and changes in rank were positively correlated, such that males rising in rank had higher testosterone than males falling in rank. Thus, for males in this group, testosterone was predictive of a male's rank trajectory, or future rank. Similarly, male testosterone levels predicted future, rather than current, mating activity.

Finally, male testosterone and aggression rates were unrelated during stable periods in the dominance hierarchy but positively related during unstable periods when high ranks were being contested. In general, our results support the challenge hypothesis with males exhibiting elevated testosterone in association with the acquisition of high rank (ensuring access to mates), rather than with mating itself.

Keywords Testosterone · Aggression · Dominance rank · Baboon · Challenge hypothesis

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Introduction

The importance of testosterone in regulating many aspects of male reproductive physiology is widely documented. Testosterone is associated with physiological changes that accompany male sexual maturation, including the development of reproductive anatomy, the production of sperm, and the onset of secondary sexual characteristics (Wickings and Dixson 1992; Woodley 1994; Hews and Moore 1995; Soliman et al. 1995; Terasawa and Fernandez 2001). Testosterone secretion is also correlated with many behavioral traits that relate to competition for mates, such as reproductive motivation, territoriality, mate guarding, heightened aggression, and display behaviors (Hart 1974; Wingfield et al. 1990; Wickings and Dixson 1992; Dixson 1998).

Despite the clear benefits of testosterone for male reproductive function, increasing evidence suggests that sustaining high titers of testosterone for extended periods is costly (Wingfield et al. 1997, 1999). For example, testosterone increases an organism's overall energetic costs (primarily via the anabolism of expensive muscle tissue; Bardin 1996; Bhasin et al. 1996; Bribiescas 1996) while increasing the risk of injury that accompanies elevated levels of aggression (Marler and Moore 1988; Marler et al. 1995; Wikelski et al. 1999). Consistently high testosterone levels can also result in reduced immune function (Grossman 1985; Grossman et al. 1991; Folstad and Karter 1992; Olsen and Kovacs 1996; Klein 2000; Tanriverdi et al. 2003). The

cost–benefit trade-off for testosterone may be responsible for the highly variable testosterone profiles that many males exhibit throughout their lives, with temporarily sustained elevations of testosterone occurring at critical periods (Wingfield et al. 1990) counterbalanced by decreased levels of testosterone during less critical periods (Ketterson and Nolan 1992). The "challenge hypothesis," originally proposed for seasonally breeding birds, posits that male testosterone rises slightly from baseline levels at the onset of the breeding season to facilitate basic reproductive behavior. As competition for mates intensifies, testosterone levels reach a physiological maximum to promote responses to aggressive challenges (Wingfield et al. 1990). By regulating testosterone secretion according to anticipated need, organisms can maintain a balance between the costs and benefits of elevated testosterone levels.

Seasonally breeding species offer fairly widespread support for the challenge hypothesis (but see Creel et al. 1993; Strier et al. 1999). Male competitive behavior during the breeding season has been linked to elevated testosterone concentrations across a wide variety of taxa, including birds (Wingfield et al. 1999; Smith et al. 2005), reptiles (Klukowski and Nelson 1998), and mammals (Higely et al. 1996; Mehlman et al. 1997; Brockman et al. 1998; Cavigelli and Pereira 2000; Ostner et al. 2002; Buck and Barnes 2003). The duration and quality of male–male competitive interactions vary widely across species, but generally, they are characterized by social instability, the establishment of a breeding territory, or confrontations with a conspecific male.

Nonseasonally breeding species also provide some support for the challenge hypothesis (but see Klinkova et al. 2004). In these taxa, the relationship between testosterone and aggression appears to be mediated primarily by the instability in male dominance ranks rather than a seasonal onset of mate competition. For males living in multimale and multifemale groups, a dominance hierarchy often regulates access to mates. In such groups, males invest considerable effort in competing for and maintaining high rank, and males of high rank usually achieve the highest mating success (Bulger 1993; see review in Ellis 1995; Owens and Owens 1996; Alberts et al. 2003; Takahashi 2004). Several studies of nonseasonally breeding primates have shown that competition to achieve high rank is associated with elevated testosterone among competing males (e.g., Marshall and Hohmann 2005). In unstable and newly formed social groups, male testosterone increases as rates of aggression increase (Bernstein et al. 1979; Sapolsky 1982, 1993; Alberts et al. 1992). In contrast, there is no clear relationship between testosterone and rates of aggression in well-established groups with stable male dominance hierarchies (e.g., Sapolsky 1982, 1993; Steklis et al. 1985; Nieuwenhuijsen et al. 1987). Among wild chimpanzees, Muller and Wrangham (2004) found that high-ranking males generally had both higher levels of aggression and higher levels of testosterone than low-ranking males. Due to the stability of the hierarchy throughout their study, the authors conclude that testosterone is correlated with male rank regardless of rank stability

among chimpanzees. Furthermore, they (and others) suggest that the relationship between testosterone and rank depends on the relationship between rank and aggression (Whitten 2000; Muller and Wrangham 2004).

Although changes in testosterone are thought to promote aggression rather than to facilitate sexual behavior (e.g., Higely et al. 1996), there is some evidence that testosterone may also rise in response to real or perceived mating opportunities. First, several studies link elevations in testosterone to courtship and mating behaviors but not to male–male aggression (Lynch et al. 2002; Wiley and Goldizen 2003). Second, experimental evidence from a variety of mammalian taxa indicates that visual or olfactory exposure to sexually receptive females can cause testosterone levels to rise (Purvis and Haynes 1974; Macrides et al. 1975; Harding and Feder 1976; Bernstein et al. 1977; Eberhardt et al. 1980; Ruiz de Elvira et al. 1982). Additionally, studies on human males demonstrate that sexual activity itself can result in elevated testosterone concentrations (Dabbs and Mohammed 1992). These studies highlight the importance of distinguishing between causal sources of elevated testosterone in males, particularly if the same males have high rank, show high rates of aggressive behavior, and have priority of access to fertile females.

In this study, we investigated male testosterone profiles in relation to dominance rank, aggression, and consort status in a group of chacma baboons (*Papio hamadryas ursinus*) living in the Okavango Delta, Botswana. We also assessed the relationship between male testosterone measures and two life history variables: age and dispersal. Our predictions (below) are based on three characteristics of the chacma social system. First, among chacma males, competition for high rank serves as a proxy for competition for mates. The highest-ranking (alpha) male generally monopolizes mating access to any female with a sexual swelling, particularly during maximum tumescence or the periovulatory period. If more than one female is maximally swollen at a time, then the second highest-ranking male can monopolize a female, and so on, until all swollen females are accounted for (Bulger 1993). As such, the male dominance hierarchy acts as a queue for mating opportunities (see also Alberts et al. 2003), and agonistic encounters over specific females are relatively infrequent. In a recent study on the same population, (Bergman et al.in press) found that consorting males did not show significantly higher rates of aggression, but rather went out of their way to avoid other males (see also Smuts 1985). In contrast, males did exhibit elevated rates of aggression when ranks were being contested (Bergman et al. in press).

Second, chacma baboons are nonseasonal breeders, and opportunities for mating occur throughout the year (although there is a birth peak from July to October; Cheney et al. 2004). With one exception (September), all months of the current study period had one or more adult females exhibiting maximally tumescent sexual swellings at least 30% of the time. Furthermore, there is little seasonality to hormone secretion among males in this group. Bergman et al. (in press) demonstrated that mean monthly gluco-

corticoids for males were unrelated to rainfall. Similarly, mean monthly testosterone for males was also unrelated to cumulative monthly rainfall (Cheney and Seyfarth, unpublished data). Due to the unique ecology of the Okavango Delta, the annual flood generally arrives shortly after the rainy season ends, ensuring a constant source of water throughout the year.

Third, because dominance relationships among males are influenced primarily by age, size, and fighting ability (Hamilton and Bulger 1990; Bulger 1993; Kitchen et al. 2003), changes in the male hierarchy are common. Upon reaching maturity (8–10 years), males generally disperse to a neighboring group where they compete to attain high dominance rank. Some males, however, remain in their natal groups for their entire lives (Hamilton and Bulger 1990; Kitchen et al. 2003) and occasionally achieve the alpha position. Typically, a male is only able to maintain alpha status for a short period of time (~6 months) before he is usurped by another male (Palombit et al. 2000; Kitchen et al. 2003). Moreover, a "lag time" of 1–2 months between acquiring high rank and achieving high mating success has previously been observed in this population of baboons (Bulger 1993). Consequently, even high-ranking males have only a short, transient window of opportunity for mating success.

Therefore, following the logic of the challenge hypothesis, we expected that chacma male testosterone levels would be more closely associated with acquiring access to mates than with mating per se. In other words, we predicted that high-ranking males would have higher testosterone levels than low-ranking males; moreover, males in the process of acquiring high rank (securing greater access to mates) should have the highest testosterone. Because aggression is frequently associated with acquiring high rank, we also expected that male testosterone measures would be correlated with aggression rates during periods of social instability. Finally, based on the short reproductive tenure for males, we also expected that testosterone levels would rise with age among subadults, as these males typically disperse and begin competing for high rank, but fall with age among older adults.

Methods

Study site and population

Subjects for this research were members of a group of wild chacma baboons located in the Moremi Game Reserve in the Okavango Delta of Botswana. This study group has been observed regularly since 1978 (e.g., Bulger and Hamilton 1987) and almost daily since 1992 (Cheney et al. 2004). We know all the ages and matrilineal relationships for natal individuals, as well as the origins and destinations of immigrant males. During the course of this study, the group contained 82–91 individuals, including 9–10 adult males (>8.5 years of age), 29–31 adult females (>6 years of age), and their immature offspring. A total of 13 adult males were observed in this study. Two of these males

(hereafter "roaming" males) entered and left the group at least twice, and thus, behavioral and demographic data for these two males were limited. Roaming males were only included in the analysis of testosterone measures and male migration.

Behavioral observations

Behavioral observations were conducted on adult males from January 2002 to February 2003. All behavioral data were collected using focal animal sampling (10-min samples) and ad libitum observations (Altmann 1974). Males were sampled at the same rate for a total of 1,201 focal animal samples or 23.3 h of observation for each male present for the entire study. We used behavioral data to calculate rates of aggression for individual males. In addition to overt fighting, aggressive interactions were scored each time a male supplanted, threatened, chased, or exhibited submissive behavior toward another male. Threats included quick head movements, eyelid flashes, lunges, ground slaps, and threat–grunt vocalizations. Submissive behavior included crouching, fear grimacing, and retreating. Contact aggression comprised 9.4% of all male–male aggressive behavior.

We recorded a consortship each time a male was observed mate-guarding a sexually swollen female. Because fecal steroids in baboons reflect cumulative hormone secretion over the previous 12–48 h with peak excretion occurring at 26 h (Wasser et al. 1994), we designated each fecal sample as a "consort" or "nonconsort" sample depending on whether the male was observed in consort for any period of time during the 48 h prior to the collection of the sample. Consortships in the Okavango population typically last for several days, making it unlikely that we missed a short consortship. If the male was not observed on either of the 2 days preceding fecal sample collection, that sample was not included in the consort analysis (*N*=136) resulting in a sample size of 324 fecal samples.

We used ad libitum observations (in addition to focal animal sampling) to record approach–retreat interactions between males; these data were used to calculate the male dominance hierarchy (see below).

Age determination

The exact birth dates of three natal males were known (Table 1). Immigrant males were assigned approximate ages on the basis of tooth wear and color (for details, see Kitchen et al. 2003) and length of residence in the group. If an immigrant male arrived with white, intact canines, we designated him as "young" and assigned him an age of 111 months, based on the mean age of dispersal for 20 natal males in this population. For most age analyses, we split males into eight age categories (20 months each) from 80 months (the earliest age at which males rise above one or more adult males in the dominance hierarchy) to 220

Table 1 Ages and tenure of adult males and number of fecal samples collected

ID	Age (months)	Age category	Dispersal status[a]	Date of birth	Date of immigration	Tenure	N fecal samples
NK	86	Young	Natal	Nov 94	–	Oct 02–End[b]	19
BG	108	Young	Immigrant	–	Apr 02	Apr 02–End	42
GM	108	Young	Immigrant/emigrant	–	Apr 02	Apr 02–Jun 02	11
MG	113	Young	Natal	Aug 92	–	Entire study	50
BJ	134	Young	Resident	–	Feb 00	Entire study	56
PO	141	Young	Natal	Apr 90	–	Entire study	55
TH	152	Old	Resident	–	Aug 98	Entire study	53
RY	157	Old	Resident	–	Mar 98	Entire study	53
AP	182	Old	Resident	–	Feb 96	Entire study	56
AU	191	Old	Resident	–	May 95	Entire study[c]	46
WA	228	Old	Resident	–	May 92	Start–Mar 02	8
FG	–	Old	Roaming	–	–	Start–Sep 02	26
SO	–	Old	Roaming	–	–	May 02–Jul 02, Sep 02	7

[a]Dispersal status refers to events that occurred during the study period. "Immigrant" and "emigrant" refer to males who entered or left the group during the study period, whereas "resident" refers to nonnatal males who entered the group prior to July 2001
[b]The "start" of the study was July 2001; the "end" was March 2003
[c]AU was an old male that was occasionally absent from the group

months (the estimated age of the oldest male). For our analysis of age and dispersal, we divided males (at the median age) into "young" and "old."

Dominance rank

Rank relationships were scored daily using approach–retreat interactions. Ranks were linear, and changes were abrupt and salient. Therefore, if we observed a change in the dominance hierarchy, we recalculated the hierarchy on that day. We controlled for variation in group size by expressing each male's rank as the proportion of adult males that he outranked ("relative" rank). Rank changes were calculated by subtracting each male's rank at the beginning of the study (or when he entered the group) from each male's rank at the end of the study (or when he left the group). Males entering the group were assigned an initial rank at the bottom of the hierarchy. If a male both gained and lost the same number of rank positions, his rank change across the study was zero.

For some analyses, we divided the study into four categories based on changes at the top of the male hierarchy. These four periods are described in detail elsewhere (Bergman et al. in press). Briefly, they consisted of the following: (1) *stable periods*, when there were no changes in the top two ranks of the male hierarchy (two periods of 74 and 45 days each); (2) *natal male rise periods*, when a natal male reached the second-ranking position (two periods of 73 and 52 days each); (3) *resident male takeover periods*, when a male who had been resident in the group for at least 3 months attained the highest-ranking position (three periods of 29, 31, and 16 days each); and (4) an *immigrant male takeover period*, when a recent immigrant attained the highest-ranking position (one period of 29 days). In another analysis, we compared male aggression rates during periods of stability (*stable periods* only) to periods of instability (the other three periods combined).

Our definition of stability differs from that of Sapolsky (1983), who used "instability" to refer to ambiguity in dominance relationships. There was never a case where rank ambiguity existed in the study population; rather, all rank changes were conspicuous, abrupt, and permanent. Therefore, we primarily define "instability" as approximately 1-month periods following changes in the first two rank positions.

Hormone collection and preservation

We collected 460 fecal samples from 13 males over a 14-month period (Table 1). Fecal samples were collected from each male approximately once per week using a targeted collection schedule. For most weeks, we were able to obtain a fecal sample from each male before any male was sampled twice. Because males were in the group for different lengths of time, the total number of samples from each male varied. For males that remained in the group throughout the study (N=6), this variation was minimal (range, 50–56 samples/male). For males that arrived and/or disappeared during the study (N=7), the number of samples varied in proportion to their residency in the group (range, 7–46 samples/male). In all cases, fecal sampling was evenly distributed across males for any given period of time.

We extracted hormones from feces in the field using methods described by Beehner and Whitten (2004). All samples were collected in the morning, placed in a methanol/acetone solution, homogenized, filtered, and loaded onto a reverse-phase C18 cartridge (Sep-Pak Plus, Waters Associates, Milford, MA). Following solid-phase extraction, all samples were immediately frozen (−10°C) until transported to Emory University for analysis. There, steroids were eluted from cartridges with methanol and subsequently frozen (−80°C) until the time of radioimmunoassay (RIA). Immediately prior to RIA, aliquots of samples were evaporated under nitrogen and reconstituted

at a fivefold dilution in working buffer (phosphosaline gelatin). All samples were assayed for testosterone using a testosterone RIA kit (Equate RIA ^{125}I Testosterone Kit) previously validated for use in baboons (Beehner and Whitten 2004). Interassay coefficients of variation were $9.43\pm0.94\%$ (high control, $N=36$) and $14.31\pm0.11\%$ (low control, $N=36$). The intra-assay coefficient of variation was $2.90\pm0.78\%$ (fecal extract pool, $N=6$). All samples were run in duplicate, and values are expressed as ng/g dry feces.

Data analysis

Because we found significant testosterone variation among individual males (ANOVA: $F_{12,447}=4.74$, $p<0.001$), for most hormone analyses, we calculated a mean testosterone value per male for each month of the study. This allowed us to make comparisons between male testosterone measures and other individual characteristics that changed from month to month, such as age and dominance rank. Our sample size for most analyses was 121 male months with a few exceptions. First, because no consortships were observed during 1 month (September), we did not include testosterone data from this month in our analyses of consort activity ($N=113$ male months). Second, for baseline testosterone measures (determined only from nonconsort samples), there were several months for which males did not have nonconsort samples available ($N=88$ male months). Third, we calculated each male's mean testosterone level over the entire study period in relation to overall rank and change in rank ($N=11$ males), and for our analysis of dispersal, we added hormone means from the two roaming males ($N=13$ males). Lastly, for our analysis of stable vs unstable periods, we calculated one testosterone mean per male per period ($N=39$ male means, 9 males with a hormone mean for each of four periods and 1 male with a hormone mean for three periods before disappearing; 1 male was excluded because we had hormone samples from the unstable period only).

Because the raw hormone measures were not normally distributed, we log-transformed all values. Following this transformation, hormone values approached an approximately normal distribution (Kolmogorov–Smirnov test, $p=0.61$). Like hormone means, mean male dominance ranks were also calculated separately for each month. We tested for differences across independent groups using ANOVA. Where results were significant, we used a post-hoc Tukey's test to determine which groups were significantly different. Because we had no a priori assumption about the causal relationship between testosterone measures and our other variables, we use correlation statistics rather than linear regression for all bivariate analyses. For all of our analyses that did not include behavioral variables, we used Pearson's product-moment correlations. To correct for multiple testing, we used Qvalue (version 1.0; Storey 2002), which controls the proportion of true null hypotheses that are rejected. Qvalue is a more equitable compromise between type I and type II errors than is a Bonferroni correction, particularly when statistical power

is low (Storey and Tibshirani 2001; Nakagawa 2004). For all analyses that involved aggression rates, which are not normally distributed, we used a Spearman's rank-order correlation. We used a Wilcoxon signed ranks test to compare males' testosterone levels in consorting and nonconsorting periods. All statistical analyses (except corrections for multiple testing) were carried out using the SPSS statistics package (SPSS 11.0), and all tests were two-tailed.

Results

Age

In a monthly analysis, testosterone measures varied considerably across the eight age categories (ANOVA: $F_{7,113}=4.65$, $p<0.001$), rising sharply to peak at 100–120 months followed by a steady drop throughout the remainder of a male's life (Fig. 1). Males aged between 100 and 120 months had significantly higher testosterone levels than all categories from 160 to 220 months ($p<0.02$), but the differences between males aged 100–120 months and all other age groups were not significant (80–100, 120–140, and 220–240 months, $p>0.250$).

Dominance rank

We found a significant correlation between male rank and testosterone measures in a monthly analysis ($r=0.34$, $p<0.001$, $N=121$) and across the entire study period ($r=0.61$, $p=0.047$, $N=11$), such that high-ranking males had higher testosterone levels than low-ranking males. The relationship between *changes* in male rank and testosterone
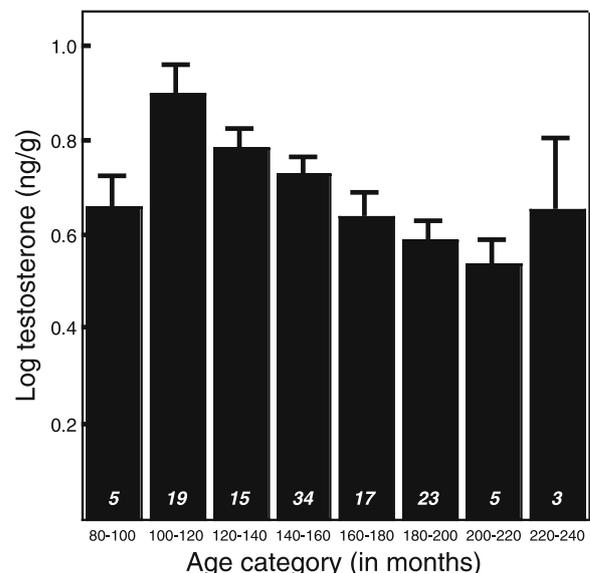
Fig. 1 Mean log testosterone (±SEM) for adult males in each age category. Age categories are divided into 20-month periods. *Numbers inside the bars* represent sample sizes (i.e., number of male monthly means)
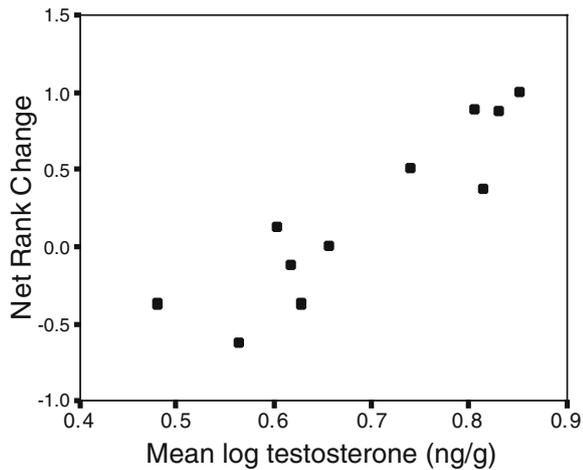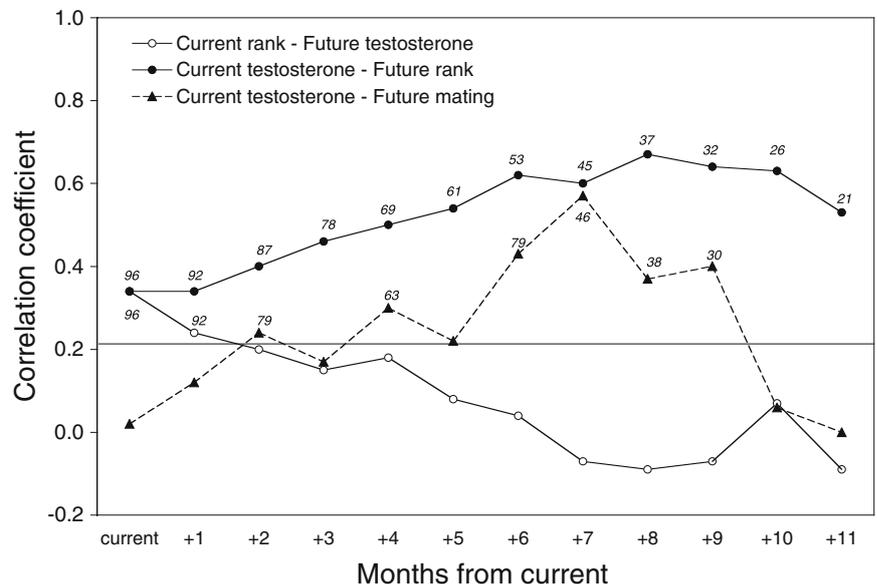
Fig. 2 Scatterplot of the relationship between each male's mean log testosterone level (ng/g) and net rank change for the study period (see text for calculation of net rank change)

and one subsequent month but not for future months (Fig. 3).

Rank and age

Males in different age categories had significantly different dominance ranks (ANOVA: $F_{7,113}=29.7$, $p<0.001$), with most of the high-ranking males in the 100- to 120-month age category (Fig. 4). When we evaluated male age and dominance rank for the entire study period, younger males had significantly higher ranks across the entire study period ($r=-0.77$, $p<0.01$, $N=11$). Age was also significantly correlated with rank change ($r=-0.66$, $p=0.03$, $N=11$), with young males ascending the hierarchy and older males descending. After controlling for age, the association between dominance rank and testosterone disappeared (partial correlation: $r=0.19$, $p=0.60$, $N=11$), but the significant correlation between testosterone and rank change remained (partial correlation: $r=0.84$, $p<0.01$, $N=11$). Thus, while age accounted for much of the variation between testosterone and rank, it did not sufficiently explain the relationship between testosterone and changes in rank.

Dispersal

Overall, mean testosterone measures of males who dispersed during the study were significantly higher than those of nondispersing males (ANOVA: $F_{1,11}=7.02$, $p=0.02$). Two types of males dispersed during the study period: (1) young males that recently emigrated from their natal group, and (2) older roaming males that entered and left the group at least twice. Among old males, dispersing males had higher testosterone levels than nondispersing males (ANOVA: $F_{1,5}=12.18$, $p=0.02$), but this was not the case among young males (ANOVA: $F_{1,4}=0.97$, $p=0.38$).

measures across the study period was even more pronounced ($r=0.91$, $p<0.001$, $N=11$; Fig. 2); males who ascended the hierarchy had significantly higher testosterone levels than males who descended. Two immigrant males that arrived in the group and immediately achieved high rank might represent two high-leverage points; these males had two of the greatest rank changes in the group and also had very high testosterone measures. However, removing these two males from the analysis did not change the significance of the result ($r=0.87$, $p<0.01$, $N=9$).

Following post-hoc corrections for multiple testing using Qvalue (see "Methods"), each male's testosterone mean for any given month was significantly correlated with his dominance rank for that month and all future months up to 11 months (see Fig. 3 for correlation coefficients, significance, and sample sizes). In contrast, a male's dominance rank for any given month was only significantly correlated with his testosterone mean for the current month

Fig. 3 Correlation coefficients between males' current dominance rank and future testosterone concentrations (*open circles*), current testosterone concentrations and future dominance rank (*closed circles*), and current testosterone concentrations and future mating activity (*closed triangles*) for current and subsequent months up to 11 months. Samples sizes (in *italics above each significant point*) necessarily decrease with each subsequent month. All points above the *horizontal line* are significant correlations at $p<0.05$ (after post-hoc correction for multiple testing using Qvalue, see text for details)

Although the small sample size (N=6) gave us little statistical power to detect a difference in young males, the effect of migration in old males (N=7), a similar sample size, was large enough to detect a difference. All dispersing males (young and old) had higher testosterone concentrations in the month immediately following dispersal when compared to other months (ANOVA: $F_{1,45}$=4.06, p=0.05).

Consortships

Overall, testosterone was significantly higher in hormone samples from consorting males than those from nonconsorting males (ANOVA: $F_{1,322}$=4.50, p=0.04). In a paired comparison between consort and nonconsort testosterone measures for each male, we found that 8 of 11 males had higher testosterone levels during consort, but this difference was not significant (Wilcoxon signed ranks test, Z= −1.78, p=0.08). A post-hoc power analysis (statistical power=43.7%) indicates that we did not have sufficient power to detect a difference of the magnitude observed (23.8%). Thus, while males had higher testosterone during consortships, this relationship warrants further investigation with more individual males. When we compared each male's monthly "baseline" testosterone (nonconsort testosterone) to his monthly consort activity (percentage of all consort days attributed to that male), baseline testosterone measures were unrelated to consort activity (r=0.02, p=0.88, N=88). Because testosterone levels were higher in high-ranking males (results above) and because high-ranking males formed consortships at a higher rate than low-ranking males (r=0.45, p<0.001, N=113), we explored this relationship further. Following corrections for multiple testing using Qvalue (see "Methods"), each male's current (nonconsort) testosterone measures were able to predict his
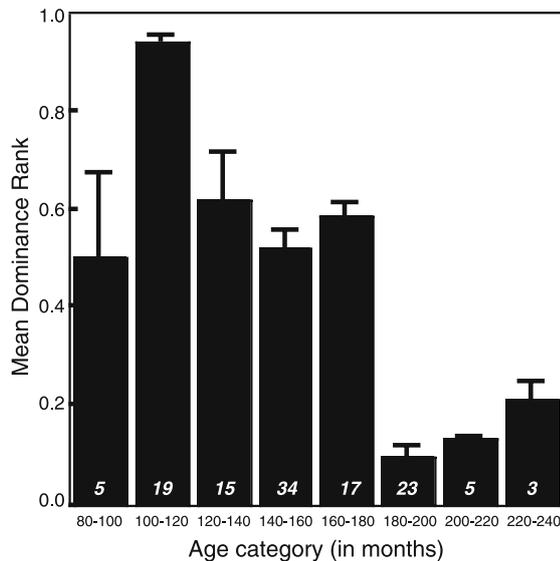

Fig. 4 Mean dominance rank (±SEM) for adult males in each age category. *Numbers inside the bars* represent sample sizes (i.e., number of male monthly means). Dominance ranks are expressed as relative ranks; 1.0 is the highest-ranking male and 0.0 is the lowest
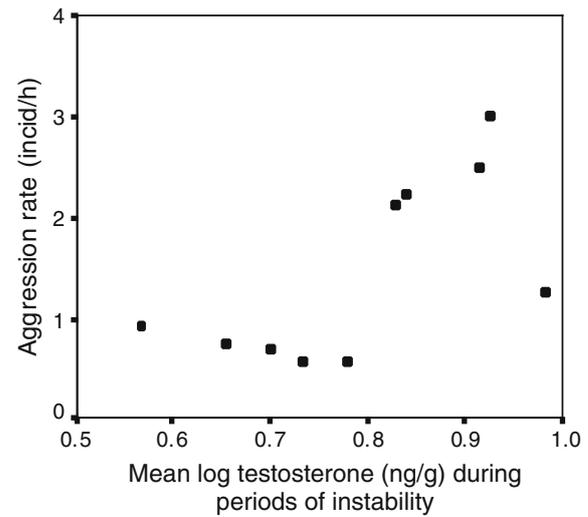

Fig. 5 Scatterplot of the relationship between each male's mean log testosterone (ng/g) and mean dominance rank during periods of rank instability

consort activity 2 months later, and during subsequent months up to 9 months (see Fig. 3 for correlation coefficients, significance, and sample sizes), months 3 and 5 were not significant (0.05<p<0.10).

Behavior

We found no significant differences in testosterone levels across stability periods (ANOVA: $F_{3,35}$=1.64, p=0.20). During stable periods, there was no relationship between each male's testosterone level and his aggression rate (Spearman's rank-order correlation: r_s=0.35, p=0.32, N=10). However, during periods of rank instability, there was a significant correlation between the two, such that males with higher testosterone also had higher rates of aggression (r_s=0.65, p=0.04, N=10; Fig. 5).

Discussion

Testosterone variation was strongly tied to life history in this group of chacma baboons. Testosterone levels were highest in young adult males (100–120 months), the age period when males typically leave their natal troop, achieve high rank, and sometimes commit infanticide (Bulger and Hamilton 1988; Hamilton and Bulger 1990; Palombit et al. 2000). However, testosterone was not associated directly with dispersal in young males since all young males had equally high testosterone measures regardless of whether or not they dispersed from their natal group during the study. In contrast, higher testosterone was associated with dispersal among older "roaming" males. All dispersing males (young and old) exhibited elevated testosterone concentrations during the month immediately following dispersal. Therefore, although dispersal was associated with a temporary surge in testosterone for all males, the role that testosterone plays in natal male dispersal remains

unclear. Other vertebrate studies have found a positive relationship between testosterone and dispersal status, with immigrants exhibiting higher testosterone titers than natal animals (Reyer et al. 1986; Alberts et al. 1992; Woodroffe et al. 1995; Holekamp and Smale 1998). In one study on voles, testosterone implants stimulated dispersal in females (Taitt and Krebs 1982), supporting the hypothesis that testosterone activates dispersal behavior for some species (Phoenix et al. 1959). Other studies on spotted hyenas and Belding's ground squirrels, however, did not find evidence that testosterone activates dispersal behavior (Holekamp et al. 1984; Holekamp and Smale 1998; Nunes et al. 1999). As we accumulate data on additional dispersal events, we hope to explore possible causal connections between male testosterone and natal dispersal in this population.

Testosterone measures were strongly associated with dominance rank and, more importantly, with changes in rank. The relationship between testosterone and rank appeared to be primarily age-dependent, with younger males exhibiting both higher rank and higher testosterone. The relationship between testosterone and rank changes, however, remained significant after controlling for age. Thus, males of similar ages may have very different testosterone profiles depending on whether they are ascending or descending the dominance hierarchy. A similar relationship between testosterone measures and changes in rank has also been reported in captive male talapoin monkeys (Eberhardt et al. 1980). It has become increasingly apparent that dominance rank is not an individual trait, but rather a dynamic interaction of behaviors and events (Sapolsky 1993). Consequently, in systems where the dominance hierarchy is dynamic, an individual's rank trajectory may be more informative (both physiologically and behaviorally) than any single rank position.

Monthly male testosterone means predicted future dominance positions; high testosterone levels predicted higher dominance ranks, and low testosterone levels predicted lower dominance ranks. In contrast, the reverse relationship, that dominance rank predicted future testosterone levels, was not supported by our data. This suggests that testosterone, or more likely the change in aggressive behavior and motivation that is associated with testosterone, exerts a strong influence on future rank. Many studies on primates, including humans, have demonstrated corresponding changes in testosterone concentrations after winning or losing a dominance interaction (Bernstein et al. 1974; McCaul et al. 1992; Mazur and Booth 1998). The possibility that elevated testosterone may contribute to achieving high rank, particularly in a species where rank is a major determinant of mating success, suggests that males who are able to maintain high titers of testosterone may achieve higher reproductive success as a result.

Male testosterone was directly associated with dominance rank changes, and the acquisition of high rank increased the potential for consort activity. Although we found no relationship between current testosterone and consort activity, there was a significant relationship between current testosterone and future consort activity after at least a 2-month delay. These results suggest that the high testosterone levels shown by consorting males probably resulted both from temporary testosterone elevations resulting from consortship and from the indirect relationship between baseline testosterone and mating, as mediated through rank. Testosterone elevations associated with mating activity have been reported in several species, including humans (Dabbs and Mohammed 1992; Lynch et al. 2002; Wiley and Goldizen 2003), suggesting that slight elevations in male testosterone levels during mating may serve to facilitate basic reproductive function. More importantly, however, males with higher baseline testosterone measures consorted with females at slightly higher rates in the short term and at significantly higher rates in the long term. As such, a male's testosterone level predicted his future rank trajectory, which, in turn, predicted his future mating. This observation is consistent with the hypothesis that elevations in testosterone concentrations are more closely related to mate acquisition (via rank acquisition) than to mating activity itself (Wingfield et al. 1990).

Male testosterone was related to aggression, but only during periods of rank instability when rank positions were being contested. In other words, aggression temporally associated with rank changes was more closely linked to testosterone measures than aggression in other contexts. In a previous study on this group, we demonstrated that rates of male–male aggression were higher during periods of rank instability (Bergman et al. in press). Studies across a wide variety of vertebrate taxa have shown that testosterone is closely associated with aggression rates, but only during critical periods such as territory acquisition (reviewed in Wingfield and Farner 1993) or the formation of a new dominance hierarchy (Bernstein et al. 1979; Sapolsky 1982, 1993). Furthermore, the relation between testosterone and aggression during periods of instability coincides with experimental evidence from this same group, suggesting that males with high testosterone levels perceive themselves to be in competition with other high testosterone males (Bergman et al. 2005). In playback experiments that simulated the approach of one male using recorded grunts, Bergman et al. found that a male subject was most likely to move away from a simulated approach (1) when the male was adjacently ranked to him and (2) when both he and the approaching male had high testosterone levels. Responses were therefore strongest in pairs of males that were most likely to be competing for each other's rank.

In this population, males that have achieved alpha status typically retain this rank for about 6 months before being usurped by a rival (Palombit et al. 2000; Kitchen et al. 2003, unpublished data). Having fallen in rank, former alpha males often switch reproductive strategies from "mating" to "parenting." Rather than (or in addition to) competing for access to estrous females, former alpha males typically form nonsexual "friendships" with lactating females. These friendships appear to be a sexually selected strategy for protecting offspring against infanticidal attacks (Hamilton 1984; Palombit et al. 1997, 2000). The high rate of infanticide in this population and the potential for paternal care suggest that males must mediate the trade-off between investment in mating (maintaining

high rank) and investment in current offspring (protecting offspring from infanticidal males). Once a male has fathered several offspring, the marginal benefit of maintaining high testosterone may be reduced, suggesting a benefit to switching to a low testosterone, parenting role. Significant decreases in testosterone have been documented in many species where males switch from mating to parenting (e.g., Ketterson and Nolan 1992), and the rapid fall in testosterone after 120 months of age in chacma males is consistent with this trade-off. The role of male testosterone in mating vs parenting strategies deserves to be evaluated further in baboons, particularly in populations with varying degrees of reproductive skew and paternal care.

The data presented here provide additional support for the challenge hypothesis as it applies to nonseasonally breeding, multimale species; mainly, those elevations in testosterone were associated with (1) rising in rank, (2) increased aggression during periods of social instability, and (3) future mating success. In two recent studies on wild chimpanzees (Muehlenbein et al. 2004; Muller and Wrangham 2004), male testosterone was positively related to dominance rank even during extended periods of social stability. Both sets of authors explain the testosterone–rank relationship in the context of the fission–fusion sociality of chimpanzees that makes male competition and mating opportunities unpredictable throughout the year. In the present study, the male hierarchy experienced some degree of social instability for the majority of the study (9 of 14 months; Bergman et al. in press). Thus, male social instability may be more common than stability for this group of chacma baboons. As such, even though testosterone and aggression were only correlated during periods of social instability, male chacma baboons may maintain rank-appropriate titers of testosterone throughout the year in anticipation of frequent challenges from other males. Consequently, male chacma baboons may be similar to wild chimpanzees because males must be physiologically ready to defend their rank at all times.

The testosterone profiles manifested by males in this study differed in several interesting ways from their glucocorticoid profiles. Unlike testosterone levels, glucocorticoid levels did not differ among individuals and did not vary systematically with age or rank (Bergman et al. in press). Glucocorticoids did, however, differ significantly across periods depending on the stability of the male dominance hierarchy. Furthermore, glucocorticoids were significantly elevated following immigration and during consortships. This suggests that glucocorticoid levels were largely influenced by events, with temporary elevations occurring during and after certain stressful events. In contrast, testosterone varied across individuals, age, rank, and rank trajectory, but did not fluctuate significantly in association with events. Thus, while glucocorticoids appear useful for monitoring the impact of specific events, testosterone may be more usefully considered as an individual attribute (albeit an unstable one). Thus, for multimale groups, measuring testosterone for males may represent a way to measure determinants of behaviors that influence reproductive fitness.

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