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Social correlates of fecal testosterone in male ursine colobus monkeys (*Colobus vellerosus*): The effect of male reproductive competition in aseasonal breeders

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ABSTRACT

Male testosterone (T) levels are thought to be linked with the mating system, degree of parental care, and male–male aggression in reproductive contexts (The 'challenge hypothesis'; Wingfield et al., 1990). In many species though, T increases associated with mating behavior cannot be separated from those associated with male–male aggression. We tested the challenge hypothesis on aseasonally breeding ursine colobus (*Colobus vellerosus*), where male–male competition is intense outside of mating contexts. Fecal samples ($N = 109$) were collected from >27 subadult and adult males in seven groups during 13-months of research in Ghana in 2004–2005. Fecal T (fT) levels were determined by enzyme immunosorbant assays. Behavioral data was collected using focal-animal and *ad libitum* sampling. The number of receptive females in each group did not positively correlate with male fT. There was a trend for adult males to have higher fT than subadult males; however there was no effect of rank on fT. The level of male–male aggression experienced was positively correlated with fT and individual males showed higher mean fT during 'challenge' than during 'non-challenge' periods. The number of male incursions experienced positively correlated with fT whereas the number of between-group encounters did not. Males attempt to gain reproductive opportunities during incursions, thus these results support the 'challenge hypothesis' in *C. vellerosus*. Outside of mating contexts, higher male fT levels are associated with increased aggression. Male parental investment in the form of infant defense was associated with increased fT, rather than the decline expected from other forms of paternal care.

Introduction

For vertebrates, the anabolic steroid testosterone (T), is associated with reproductive functions (Balthazart, 1983; Griffin, 1996), the formation of male secondary sexual characteristics (Wickings and Dixson, 1992; Dixson, 1998), muscle mass gain (Kemnitz et al., 1988; Welle et al., 1992; Bardin, 1996), and the maintenance of musculoskeletal performance (Bribiescas, 2001). In primates, there is a link between high T levels and risk taking and initiative behaviors (Donovan, 1985; Archer, 1991; Booth et al., 2006), but T's effect on behavior is dependent on previous experiences and the social context (Sapolsky, 1993). Thus, T does not cause aggressive or 'status-maintaining' behaviors but increases the likelihood that they will be expressed (Booth et al., 2006) and appears most important in direct competition between males when some change in status may occur (Mazur, 1985; Mazur and Booth, 1998; McCaul et al., 1992).

These conditions suggest that male T levels and social rank should be positively correlated, which has been found for several species of primates (e.g. Rhesus macaques, *Macaca mulatta*, Bercovitch, 1983; lesser mouse lemurs, *Microcebus murinus*, Perret, 1992; mountain gorillas, *Gorilla beringei beringei*, Robbins and Czekala, 1997; Verreaux's sifakas, *Propithecus verreauxi*, Brockman et al., 2001; mandrills, *Mandrillus sphinx*, Setchell and Dixson, 2001; chimpanzees, *Pan troglodytes schweinfurthii*, Muller and Wrangham, 2004; bonobos, *Pan paniscus*, Marshall and Hohmann, 2005). However, a higher number of studies failed to show such a correlation (e.g. Rhesus macaques, *Macaca mulatta*, Gordon et al., 1976; vervet monkeys, *Chlorocebus aethiops sabaeus*, Steklis et al., 1985; stump-tailed macaques, *M. arctoides*, Nieuwenhuijsen et al., 1987; muriquis, *Brachyteles arachnoides*, Strier et al., 1999; red colobus, *Piliocolobus tephrosceles*, Firos, 2000; Japanese macaques, *M. fuscata*, Barrett et al., 2002; tufted capuchins, *Cebus apella nigritus*, Lynch et al., 2002; redfronted lemurs, *Eulemur fulvus rufus*, Ostner et al., 2002; bonobos, *Pan paniscus*, Sannen et al., 2004). Beyond variation in methodology and social systems that may explain some of the differences, it appears that maintaining high T is costly in terms of immunosuppression (Grossman, 1985; Grossman et al., 1991) and increased time and energy expenditure, which is detrimental to survivability (Marler and Moore, 1988; Muehlenbein and Bribiescas, 2005; Hau, 2007). Thus, rank differences in T levels for some species may only be apparent when there is instability in the hierarchy (Sapolsky, 1993) or when males are contesting for a limiting resource, such as estrus females (e.g. Japanese macaques, *M. fuscata*, Muroyama et al., 2007).

The 'challenge hypothesis' was developed from research on birds and states that T levels in adult males are closely linked with the

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mating system, degree of parental care, and male–male aggression in reproductive contexts (Wingfield et al., 1990). It predicts that, in the absence of mating behavior, males should maintain only the low baseline T level (Level A) required for the feedback regulation of GnRH and gonadotrophin release. For seasonally breeding species, environmental cues such as increased day length should lead to an androgen response in males sufficient for spermatogenesis and the expression of reproductive behaviors (Level B). Increases in T beyond Level B to Level C should be seen facultatively when males compete in reproductive contexts or during interactions with receptive females (Goymann et al., 2007). High levels of T (at Level C) seem to interfere with parental behavior, so the challenge hypothesis predicts a decrease in T levels when males are required to show a high degree of parental care. When no male parental care is required, males should maintain a high level of T throughout the breeding season (Level B-C), while if only some male parental care is needed a compromise between these two androgen patterns should be seen (Wingfield et al., 1990; Goymann et al., 2007).

The challenge hypothesis has been supported in many bird species (Wingfield et al., 2000) but for most nonavian vertebrates the results have been equivocal (Hirschenhauser and Oliveira, 2006). Several recent primate studies have found that the hypothesis generally appears valid for this group of animals (ring-tailed lemurs, *Lemur catta*, Cavigelli and Pereira, 2000; Gould and Ziegler, 2007; tufted capuchins, *Cebus apella nigitus*, Lynch et al., 2002; redfronted lemurs, *Eulemur fulvus rufus*, Ostner et al., 2002; chimpanzees, *Pan troglodytes schweinfurthii*, Muller and Wrangham, 2004; moustached tamarins, *Saguinus mystax*, Huck et al., 2005; bonobos, *P. pansicus*, Marshall and Hohmann, 2005; golden lion tamarins, *Leontopithecus rosalia*, Bales et al., 2006; chacma baboons, *Papio hamadryas ursinus*, Beehner et al., 2006; mantled howlers, *Alouatta palliata*, Cristóbal-Azkarate et al., 2006). However, for many of these studies it has been difficult to examine increases in T due to male aggression without the confounding increases that are caused by courtship and mating behaviors, an association often due to seasonal breeding (e.g. Cavigelli and Pereira, 2000; Lynch et al., 2002; Ostner et al., 2002; Gould and Ziegler, 2007).

Ursine black-and-white colobus monkeys (*Colobus vellerosus*) provide the opportunity to examine the correlation between social factors and T excretion under conditions where male–male aggression and mating behavior often occur separately. We therefore tested the challenge hypothesis on this species at the Boabeng–Fiema Monkey Sanctuary in Ghana to determine the social situations associated with increased T levels for males. Variation in male T levels has never been investigated in a black-and-white colobus species and has rarely been studied in colobines (but see: Firos, 2000; Wich et al., 2003; Gao et al., 2003; Ren et al., 2003). *Colobus vellerosus* shows aseasonal mating behavior but male competition for group membership and high dominance rank (both of which increase mating possibilities in the future) is intense. Interactions with extra-group males (during between-group encounters and male incursions) may threaten resident male(s)' reproductive investment in their group because extra-group copulations, attacks on immatures, and take-over attempts may occur (Sicotte and MacIntosh, 2004; Teichroeb et al., 2005; JAT, unpubl.data). Indeed, the immigration of new males often leads to takeovers and infanticide (Saj and Sicotte, 2005; Sicotte et al., 2007; Teichroeb and Sicotte, 2008). High-ranking males tend to monopolize receptive females in multi-male groups through mate-guarding (males stay in close proximity to receptive females and prevent lower-ranking males from mating with them), thus dominance relationships between males appear to mediate access to fertile females in this species (JAT, unpubl. data). A similar effect of dominance is reported in many primate species (reviewed in: Smuts, 1987) and may skew paternity in favor of dominant males (reviewed in: Campbell, 2007). We therefore looked at fecal T (fT) levels for individual males in relation to the number of receptive females in the group, age, rank, the number of between-group encounters and male incursions, and the overall level of male–male aggression experienced to test the challenge hypothesis. We predicted that fT would be higher in adult males compared to subadults and that males would show an increase in fT when their aggression rates were high (during times of 'challenge') and when encounter rates with extra-group males were frequent. In the absence of challenges, we did not expect that dominant males would maintain higher fT than subordinates.

Methods

Study site and subjects

Research on ursine colobus monkeys (*C. vellerosus*) has been conducted at the Boabeng–Fiema Monkey Sanctuary (BFMS), central Ghana (7° 43′N and 1° 42′W) under the direction of PS since 2000. This is a dry semi-deciduous forest fragment, 191.6 ha in size, located 350 m above sea level in the Nkoranza district of the Brong–Ahafo Region. The vegetation is a mosaic of primary forest, regenerating farmland (secondary forest), and woodland (Fargey, 1991; Saj et al., 2005). Annually, there are two rainy seasons and two dry seasons. Rainfall was monitored daily during this study in a rain gauge located <1 km from the study groups' home-ranges. The annual rainfall at BFMS during this time (July 2004–June 2005) was 1329 ml (monthly range: 0.4 to 227.6 ml). Nineteen bisexual groups of *C. vellerosus* reside at the site with a growing population of Campbell's mona monkeys (*Cercopithecus campbelli lowei*) (Kankam, unpub. data). Group sizes vary considerably (range: 9–38, mean: 15.0, $N=15$; Wong and Sicotte, 2006) and group composition is multi-male and uni-male, with the presence of all-male bands (Teichroeb et al., 2003; Saj and Sicotte, 2005). *Colobus vellerosus* at BFMS is mainly folivorous, with leaves representing 79–89% of the diet.

Behavioral observations and sample collection

Behavioral observations and fecal sample collection were done on four groups of *C. vellerosus* (WW, DA, B2 and RT) and an all-male band (AMB) during 13-months (July–November 2004, January–August 2005). Additional fecal samples were also taken from the single adult male of two additional groups (OD and SP), although no behavioral data was collected on them. The size and composition of the groups and the number of hours of data collection are provided in Table 1. All males except those in the AMB were individually recognized by features of the face and tail. Two-hundred and eleven full-day follows were conducted for the four study groups and the AMB. The four focal groups were followed for two, two-day periods per month from dawn to dusk (6:00 am to 6:00 pm) by JAT with the help of a research assistant. Behavioral observations were recorded during 10-min focal samples that were alternated among adult and subadult individuals. *Ad libitum* datum collection was employed to record aggressive events and copulations that occurred outside of focal-samples (Altmann, 1974).

Male age was sometimes known from previous contact with that individual but in most cases, it was estimated from the size of the individual relative to individuals of known age. Subadult males were either smaller or the same size as adult females and ranged in age from approximately 3–6 years old. Males were defined as adult when they had achieved full body size (i.e. were larger than adult females) and regularly participated in loud call bouts with the other adult males (at ≥7 years of age). Male dominance relationships were determined from the direction of aggressive displacements and submissive avoids and pant-grunts during focal samples and contact hours. Dominance relationships within each group were linear and males could be assigned a number ranking. The intensity of male–male aggressive events was taken from both focal-animal and *ad libitum* data and was categorized daily for each male in three levels: 0 = no aggression observed; 1 = low-intensity aggression: threats (aggressive stiff-legs and jump displays (Oates, 1977)) were given or received by the focal-male; and 2 = high-intensity aggression: chases or contact aggression was observed between the focal-male and other males.

Between group encounters and male incursions occurred whenever individuals from two groups came within 50 m of one another (Oates, 1977). They differed in that

Table 1
Study group composition, contact and focal hours

Name	Group size	Adults		Subadults		Juveniles/ infants	Contact hours[a]	Focal hours
		M	F	M	F			
RT	13	1	5	1	1	5	567.5	106.5
B2	13–17	1–3	4	2–4	0–1	4–5	574.5	102
DA	21–31	3–8	9–10	3–5	1–3	4–5	574	99.8
WW	28–33	6–10	10–11	2–6	2–3	2–5	690	125
AMB	4–10	0–3	0–1	4	0–2	0	101	1
OD	18	1	8	0	4	5	20	0
SP	7	1	4	0	0	2	20	0
Totals							2547	434.3

[a] Including JAT and research assistants.