Territoriality, tolerance and testosterone in wild chimpanzees

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Although testosterone (T) has well known organizational and activational effects on aggression, the relationship between the two is not always clear. The challenge hypothesis addresses this problem by proposing that T will affect aggression only in fitness-enhancing situations. One way to test the challenge hypothesis is to examine the relationship between T and different types of aggression. Chimpanzees, *Pan troglodytes*, show aggressive behaviours in several contexts and provide an opportunity for such a test. Here we show that urinary T influences a form of male chimpanzee reproductive aggression, territorial boundary patrols. In contrast, T does not affect predatory behaviour, a form of aggression that has no immediate link to male reproduction. While these results are consistent with the challenge hypothesis, our results indicate that male chimpanzees experience a significant drop in urinary T during hunts. Additional analyses reveal that males who share meat with others display this decrease. The reason for this decrement is unclear, but we hypothesize that the relative lack of aggression that results from voluntary sharing episodes and the tolerance engendered by such acts may be contributory factors.
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A central problem in the study of behavioural biology concerns the relationship between the steroid hormone testosterone (T) and aggression. While it is widely acknowledged that T plays an important role in regulating aggression in many species, studies of some taxa fail to show a connection between the two (Hirschenhauser & Oliveira 2006). The challenge hypothesis addresses these conflicting findings by proposing that T affects aggression only during periods of social instability and when individuals face challenges in fitness-enhancing contexts (Wingfield et al. 1990). Because chronically elevated T can have deleterious health consequences, its production is limited to aggression directly related to reproduction, including territorial behaviour and mate guarding. Research on several vertebrates provides support for the challenge hypothesis (Wingfield 2005), but exceptions exist, resulting in continued debate (Hirschenhauser & Oliveira 2006).

One potentially powerful way to test the challenge hypothesis is to examine the effects of T on different types of aggression. Because male chimpanzees display aggression in several contexts, they provide an opportunity to conduct such a test. Within communities, male chimpanzees behave aggressively as they compete with each other to mate with females (Bygott 1979; Muller 2002; Muller et al. 2006). Between communities, male chimpanzees are territorial. Territorial interactions occasionally escalate and result in lethal aggression (Goodall et al. 1979; Wilson et al. 2004; Mitani et al. 2010). Lethal aggression often occurs during boundary patrols, when males make deep incursions into the territories of their neighbours, in attempts to defend their community's territory and hence their access to females (Goodall et al. 1979; Williams et al. 2004). Recent research indicates that intercommunity lethal aggression can lead to chimpanzees expanding their territory at the expense of their neighbours (Mitani et al. 2010). Patrols also result in nonlethal fights, chases and vocal battles between members of different communities (Watts & Mitani 2001). Male chimpanzees also hunt vertebrate prey (Goodall 1963; Nishida et al. 1979; Boesch & Boesch 1989; Stanford et al. 1994a; Mitani & Watts 1999; Gilby et al. 2006). Here aggression takes a different form, as chimpanzee hunters interact with heterospecifics in a predatory context and compete with conspecifics for food rather than reproductive opportunities.

In keeping with the challenge hypothesis, prior research has shown that male chimpanzees display relatively high levels of T when they compete for oestrous females in their own community (Muller & Wrangham 2004; Sobolewski et al., in press). It remains unclear whether T affects males during territorial behaviour or when they hunt. The challenge hypothesis makes two straightforward predictions: T should influence territorial behaviour, but not hunting, because only the former is associated with competition for reproductive opportunities.

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In this paper we investigate the influence of T on male chimpanzee aggression in the contexts of territoriality and predation through a study of chimpanzees at Ngogo, Kibale National Park, Uganda. Chimpanzees at Ngogo live in an unusually large community, and males there frequently hunt vertebrate prey successfully and share meat with others (Mitani & Watts 1999, 2001; Watts & Mitani 2002). In addition, the Ngogo chimpanzees often engage in territorial boundary patrols (Watts & Mitani 2001; Amsler 2010; Mitani et al. 2010). The frequency with which the large number of males at Ngogo patrol their territory, hunt and share meat creates an ideal situation to test the predictions outlined above regarding the relationships between these behaviours and T.

METHODS

Study Site and Subjects

We conducted fieldwork at Ngogo, Kibale National Park, Uganda. The 30 km^2 study area lies at an altitude of about 1400 m above sea level and consists primarily of mature evergreen tropical forest. The forest is interspersed with patches of *Pennisetum purpureum* grasslands and *Phoenix reclinata* palm swamps (Struhsaker 1997). Mean annual rainfall is approximately 1400 mm and temperature fluctuates from 16.5 to 25.0 °C daily. We observed members of the Ngogo chimpanzee community. The community consisted of approximately 150 individuals at the time of study, including 27 adult males who were at least 16 years old. The Ngogo chimpanzees have been under continuous observation since 1995 (Mitani 2009). As a consequence, they are well habituated to human presence and, thus, easily followed and observed during territorial boundary patrols and hunts.

Behavioural Observations

M.E.S. conducted fieldwork over 14 months during three field seasons, May–July 2006, May–November 2007 and February–May 2008. She collected behavioural observations of adult males and recorded the size and composition of parties daily. Although chimpanzees live in fission–fusion communities whose members split apart and come together throughout the day, at Ngogo, large parties of males predictably form during periods of high food availability and around oestrous females (Mitani et al. 2002). Elevated rates of male aggression occur in large chimpanzee groups (Muller 2002), and as a result, male party size is a variable that requires examination and possible control. For purposes of this analysis, we defined large male parties as occurring on days when more than half of the adult males (= 14 males) were present during the whole or any portion of the day.

Male subjects were observed during 34 territorial boundary patrols and 36 hunts. Territorial boundary patrols are characterized by a distinctive suite of behaviours, making them readily identifiable to experienced observers (Watts & Mitani 2001; Amsler 2010; Mitani et al. 2010). During patrols, chimpanzees move en masse, typically in single file, to the boundary of their territory. Once there, they continue to travel in single file, often in complete silence. Patrollers typically scan the environment; they sniff the ground and investigate signs left behind by neighbouring chimpanzees, such as faeces, urine and discarded pieces of food. Patrollers can make deep incursions into the territories of their neighbours; aural or visual contact with neighbours occurs in about 30–40% of all patrols, with lethal aggression witnessed rarely (Mitani et al. 2010). Hunts were easily recognized as times when chimpanzees encountered and attacked vertebrate prey. Red colobus monkeys (*Procolobus* spp.) are the favoured prey of chimpanzees (Boesch & Boesch 1989; Stanford et al. 1994a; Mitani & Watts 1999; Gilby et al. 2006). Most hunts resulted in kills and the consumption of red colobus prey, as

chimpanzee hunting success at Ngogo is unusually high, averaging over 80% (Watts & Mitani 2002). At Ngogo, chimpanzees hunt opportunistically when they encounter red colobus monkeys during their normal foraging movements. Other hunts, however, occur after 'hunting patrols' (Mitani & Watts 1999). Hunting patrols are characterized by a suite of behaviours similar to those displayed by chimpanzees during territorial boundary patrols and closely resemble the behaviours described as 'searches' by chimpanzees in the Tai National Park (Boesch & Boesch 1989).

Boundary patrols and hunts occur infrequently, taking place once on average every 9 and 7 days, respectively (Watts & Mitani 2001, 2002; Amsler 2010; Mitani et al. 2010). M.E.S. therefore collected observations ad libitum. She recorded the start of each patrol and hunt, and noted individuals that participated in each. Patrols and hunts were considered to have begun when chimpanzees gathered and started to display the characteristic behaviours associated with boundary and hunting patrols described above. For hunts that occurred when chimpanzees encountered prey opportunistically, start times were recorded when chimpanzees began to climb into trees and pursue monkeys. During hunts, M.E.S. also noted the chimpanzees that made kills and the identities of individuals with whom they shared meat from kills. She recorded sharing whenever two males exchanged meat. Because meat sharing occurred rarely, priority was given to the collection of urine for hormonal analyses. It was therefore not always possible to note the precise behavioural details regarding how meat was shared. As a result, sharing was defined to occur whenever two males exchanged meat, irrespective of whether meat was actively given, passively obtained, or acquired via harassment. Although we observed sharing at all hunts, males sometimes hunted successfully and failed to share. In these cases, we could not collect urine samples from them for analysis because they typically ran away and disappeared soon after they captured prey.

Hormone Analyses

Testosterone was analysed in urine collected noninvasively from male chimpanzee subjects. All analyses were conducted by M.E.S. at the Smithsonian Conservation Biology Institute in Front Royal, Virginia, working under the supervision of J.L.B. (Kersey et al. 2010).

Urine collection

Male chimpanzee urine was typically collected from leaf litter on the ground with a pipette, or more rarely, caught in a plastic bag if chimpanzees urinated from a tree. Samples were analysed only if they were obtained from individually identified males. Samples cross-contaminated with faeces or blood were discarded. In the field, samples were placed in 5 ml tubes, which were immediately labelled with the male's name, date and time. Samples were frozen at the end of the day at 0 °C, no longer than 12 h after collection, and were subsequently shipped to the United States on ice using medically certified transport equipment from SAF-T-PAK.

We collected 1785 urine samples from 26 of the 27 adult male chimpanzees (mean ± SD = 70 ± 26 samples/male, range 30–123). We obtained 346 samples up to 4 h before and 2–4 h after the start of boundary patrols and hunts (mean ± SD samples/male: patrols: = 6.7 ± 2.4, N = 25 males; hunts: 5.8 ± 3.3, N = 26 males; see Table 1). Because of the 2–4 h time lag for hormone detection in urine (Whitten et al. 1998; Bahr et al. 2000), we considered these samples to reflect the endocrine state of males during and shortly after boundary patrols and hunts. We collected multiple samples from each male both before and after patrols and hunts (mean ± SD samples/male: before patrols: 4.2 ± 2.4, N = 25 males; after patrols: 2.8 ± 1.5, N = 25 males; before hunts: 5.1 ± 2.5, N = 26 males; after hunts: 3.8 ± 1.9, N = 24 males).

Table 1
Male chimpanzee testosterone concentrations (ng/mg of Cr)

Male	Before hunting	After hunting	No hunting	Before patrolling	After patrolling	No patrolling	Shared meat	Received meat	Unsuccessful hunt
Bt	85 (7)	47 (6)	72 (117)	77 (4)	54 (4)	71 (115)	46 (3)	51 (3)	
Bs	96 (8)	80 (6)	92 (101)	92 (5)	105 (1)	80 (100)	55 (1)	77 (1)	105 (1)
Bg	121 (7)	105 (3)	139 (95)	217 (10)	209 (3)	129 (85)	130 (2)		
Bf	89 (1)	81 (4)	93 (33)	88 (1)	223 (4)	79 (31)	47 (1)		101 (1)
Br	75 (6)	77 (4)	92 (51)	105 (1)	104 (3)	90 (50)		71 (3)	
Cr	94 (10)	58 (4)	80 (95)	88 (7)	90 (5)	78 (85)	53 (1)	50 (1)	
Dx	96 (5)	94 (3)	88 (89)	100 (3)	175 (4)	83 (84)		89 (1)	100 (1)
Di	127 (3)		128 (42)	105 (3)	98 (1)	131 (38)			
Do	86 (7)	82 (7)	88 (80)	85 (8)	77 (3)	88 (75)	72 (2)	81 (2)	79 (1)
Ga	127 (2)	82 (4)	146 (46)	141 (4)	164 (2)	144 (42)		43 (1)	
Gz	85 (4)	49 (2)	70 (38)	127 (2)	100 (1)	65 (37)	42 (1)	55 (1)	
Hr	89 (6)	82 (2)	110 (83)	94 (4)	91 (3)	111 (78)		82 (2)	
Ho	78 (6)	54 (6)	82 (45)	127 (6)	74 (2)	73 (42)	39 (3)	37 (1)	108 (1)
Lo	95 (8)	83 (5)	110 (66)	109 (4)	117 (2)	108 (64)	74 (1)	75 (3)	
Mi	139 (8)	95 (1)	127 (70)	117 (4)	116 (2)	127 (64)			
Mg	142 (8)	101 (7)	150 (89)	218 (7)	258 (4)	136 (84)	76 (4)		136 (3)
Mo	109 (7)	118 (4)	108 (87)	112 (6)	206 (2)	107 (83)	101 (2)		136 (3)
Mt	93 (6)	70 (4)	93 (95)	150 (6)	90 (5)	88 (85)		54 (1)	
Mw	92 (1)		94 (58)	100 (1)	107 (2)	93 (55)			
Or	150 (4)	111 (3)	127 (54)	195 (3)	90 (2)	125 (52)	71 (2)		93 (1)
Pk	86 (5)	50 (2)	114 (97)	156 (7)	153 (7)	106 (85)		51 (2)	
Rh	101 (3)	119 (6)	127 (52)	119 (3)	108 (5)	130 (45)		75 (1)	
Ri	110 (3)	105 (2)	139 (36)	121 (2)	206 (1)	136 (34)			99 (1)
Ro	77 (3)	77 (1)	133 (29)			105 (28)			71 (1)
Ta	158 (2)	63 (1)	129 (40)	104 (1)	102 (1)	128 (39)		63 (1)	
Wb	111 (3)	94 (3)	106 (32)	106 (4)	151 (2)	101 (28)		71 (1)	

Mean urinary T concentrations of male chimpanzees are shown. Concentrations were analysed from samples collected in different situations, with sample sizes indicated in parentheses.

Our initial analysis showed that males displayed a significant drop in T during and shortly after hunts. To explore this finding further, we examined the potential effect of meat sharing. To do so, we subdivided males that were involved in sharing episodes between those that shared with others (mean ± SD samples/male = 1.8 ± 0.8, $N = 12$ males) and those that were recipients (1.7 ± 0.9, $N = 17$ males). We collected samples from several males that failed to obtain meat after they hunted unsuccessfully, and used these to determine T concentrations of individuals that hunted but did not share (mean ± SD samples/male = 1.4 ± 0.7, $N = 10$ males).

To investigate the influence of male party size on T, we collected samples from males on days when they formed large parties. This yielded 103 samples from 25 males on 25 days (mean ± SD samples/male = 4.1 ± 1.9). We excluded samples from days that males hunted, conducted boundary patrols and followed oestrous females, as these behaviours are known or hypothesized to affect testosterone production.

Creatinine

We indexed all urine samples to their concentration of creatinine (Cr) to account for variations in water content (Taussky 1954). Creatinine is a by-product of muscle breakdown, and, under normal conditions, it is excreted at a constant rate per individual. We determined creatinine concentrations in urine (0.05 ml; diluted 1:20 in bovine serum albumin (BSA)-free phosphate buffer) using a Jaffe reaction (Taussky 1954). Samples with creatinine concentrations below 0.01 ng/ml were considered too dilute and excluded from hormone analysis; this involved less than 5% of all samples. Hormone concentration was divided by creatinine concentration and the data expressed as the concentration of T (ng) per mg of Cr.

Testosterone

We analysed urinary T using a single antibody enzyme immunoassay (EIA) provided by Coralie Munro at the University of California, Davis (Kersey et al. 2010). Microtitre plates (96 well;

Nunc-Immuno, Maxisorp) were coated with a polyclonal Tantiserum (R 156/157; 50 µl per well; diluted 1:7500 in coating buffer, 0.05 M $NaHCO_3$, pH 9.6) and allowed to set for 12–18 h at 4 °C. Unabsorbed antiserum was removed with wash solution (0.149 M NaCl, 0.5% Tween 20). Testosterone standards (50 µl, range 2.3–600 pg/well, diluted in assay buffer, 0.1 M $NaPO_4$, 0.149 M NaCl, 0.1% bovine serum albumin, pH 7.0) in triplicate and samples (50 µl) in duplicate were then added to the wells, followed immediately with testosterone-horseradish peroxidase (50 µl, 1:80 000 dilution in assay buffer). Following incubation at room temperature for 2 h, plates were washed five times before 100 µl of substrate buffer (0.4 mM 2, 2'-azino-di-(3-ethylbenzthiazoline sulfonic acid) diammonium salt, 1.6 mM H_2O_2, 0.05 M citrate, pH 4.0) was added to each well. After incubation for 30–60 min, absorbance was measured at 405 nm (540 reference filter) when the optical density in the total binding wells reached ~1.0. We maintained strict controls for individual variation, sample quality and assay variance. Intra-assay and interassay coefficients of variation (CV) for the internal controls ($N = 124$ assays) were below 10% and 15%, with 9.34% (mean binding, 23.6%) and 11.89% (mean binding, 69.5%) for the high and low samples, respectively, while the CV for the 50% binding point of the standard curve was 6.36%. Without extraction, we recovered biologically relevant T concentrations as indicated by the levels of recovery and accuracy of measurement (Kersey et al. 2010). The assay was validated for chimpanzee urine by demonstrating that serial dilutions of pooled urine samples produced displacement curves parallel to those of the T standard curve and that there was significant recovery (>90%) of exogenous T added to urine before analysis.

Statistical Analyses

We conducted a generalized linear mixed model (GLMM) analysis to examine the effects of territorial boundary patrolling and hunting on T. Testosterone concentrations were not normally distributed (Kolmogorov–Smirnov test: $Z = 5.83$, $P < 0.001$), and

we therefore used log-transformed T as the response variable in this analysis. We considered hunting status (no hunt, before hunt, after hunt) and boundary patrol status (no patrol, before patrol, after patrol) as fixed effects. Time of day was included as a covariate, as male T secretion shows a characteristic decline across the day (Muller & Wrangham 2004). Because we hypothesized that male group size might influence male T levels, we also treated group size as a covariate. We subsequently excluded male group size, however, as it had no effect on the initial model. Testosterone concentrations typically display considerable interindividual variation in vertebrates (Kempenaers et al. 2008). To control for this and the nonindependence created by using multiple samples from the same individual, we considered individual males as a random effect. We conducted a series of post hoc pairwise analyses using estimated marginal means of each subcategory of fixed effects. All statistical analyses were conducted using SPSS (version 19, SPSS Inc., Chicago, IL, U.S.A.).

Our initial model revealed that male chimpanzees experienced a significant drop in urinary T during hunts. To investigate this finding in greater detail, we conducted another GLMM analysis in which we added meat sharing as a fixed effect. Here we considered four categories: (1) individuals that shared meat with others; (2) individuals that received meat from others; (3) individuals that did not share because they hunted unsuccessfully; and (4) individuals that did not hunt.

Our research was conducted in compliance with all legal requirements of the Republic of Uganda and adhered to the ASAB/ABS guidelines for the use of animals in research. Research was approved by the University Committee on Use and Care of Animals at the University of Michigan (Research Application 9050, 27 July 2005).

RESULTS

Table 1 shows the number of samples collected from males in different contexts, as well as their mean urinary T concentrations. Results of a GLMM analysis indicated that male chimpanzee T concentrations varied across the day ($F_{1,1775} = 38.12$, $P < 0.01$), but that group size had no effect ($F_{1,1301} = 38.12$, $P < 0.78$). Territorial boundary patrol behaviour also had a significant effect on male T ($F_{2,1775} = 15.82$, $P < 0.01$; Fig. 1). A post hoc test, controlling for time of day and male identity, revealed that male chimpanzees displayed significantly higher levels of urinary T prior to conducting boundary patrols than they did on days when they did not patrol ($t_{1775} = 3.66$, $P < 0.01$; Fig. 1). Male T continued to remain high during and immediately after patrols compared to levels shown on days of no patrolling activity ($t_{1775} = 4.39$, $P < 0.01$; Fig. 1). Elevated T during boundary patrols could not be attributed to males forming large parties on these days because male group size did not influence T (see above).

In the initial model, hunting also had a significant effect on male chimpanzee T concentrations, but in the opposite direction as that during boundary patrols ($F_{2,1775} = 4.15$, $P < 0.02$). A post hoc test revealed that males failed to show an anticipatory response to hunting, as samples collected before they hunted did not differ from those obtained on days when they did not hunt ($t_{1775} = 0.39$, $P > 0.72$). In contrast, males displayed a pronounced decrease in their urinary T concentrations during hunts ($t_{1775} = 2.83$, $P < 0.01$).

The finding that male T dropped during hunts was unexpected. An additional GLMM analysis suggested that meat sharing had a significant effect on male T levels ($F_{3,1775} = 6.94$, $P < 0.001$; Fig. 2). Interestingly, when meat sharing and hunting were considered together in the same model, the effect of hunting per se disappeared ($F_{2,1775} = 0.14$, $P > 0.87$). Instead, meat sharing alone predicted T levels ($F_{3,1775} = 6.94$, $P < 0.001$). Post hoc analyses indicated that both sharing and receiving meat influenced male T concentrations. Males that hunted successfully and shared meat with others
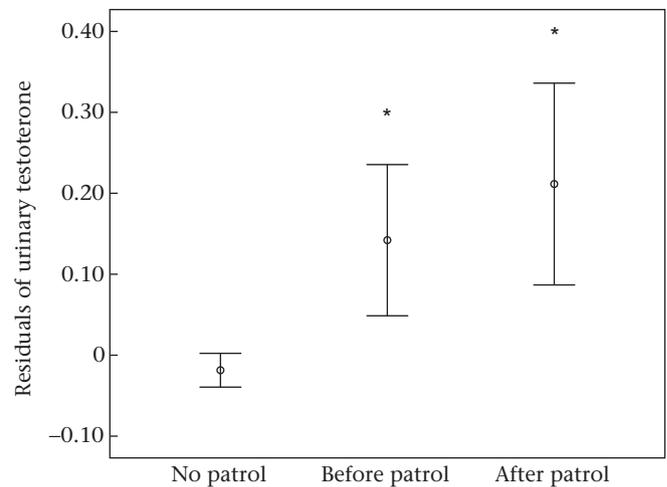

Figure 1. Effect of territorial boundary patrols on urinary testosterone concentrations in male chimpanzees. The Y axis represents the residuals of log-transformed testosterone concentrations obtained from an LMM including time of day as a covariate and male identity as a random factor. Shown are the means (±SE) of individual male means for each patrol subcategory: No patrols: $N = 26$ males; Before patrols: $N = 25$ males; After patrols: $N = 25$ males. For comparisons between males before and after patrols versus no patrolling: *$P < 0.01$.

displayed significantly lower T concentrations than males that did not hunt ($t_{1775} = 2.80$, $P < 0.01$; Fig. 2). Similar decrements were shown by males that received meat from others ($t_{1775} = 2.33$, $P < 0.02$; Fig. 2). The patterns displayed by males that were involved in sharing episodes differed considerably from those of males that hunted unsuccessfully and did not obtain meat. Testosterone levels of males that failed to acquire meat did not differ from their levels on days when they did not hunt ($t_{1775} = 1.76$, $P > 0.08$; Fig. 2).

DISCUSSION

The preceding results provide novel tests of and support for the challenge hypothesis in chimpanzees. While T is linked to territorial aggression in male chimpanzees, it does not appear to be
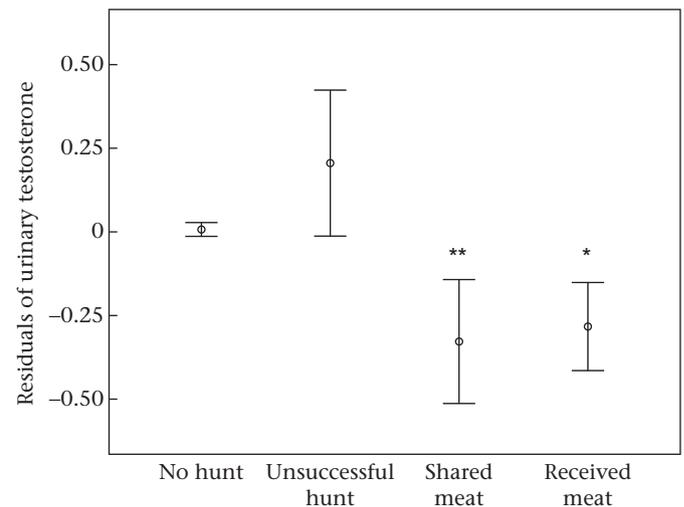

Figure 2. Effect of meat sharing on urinary testosterone concentrations in male chimpanzees. The Y axis represents the residuals of log-transformed testosterone concentrations obtained from an LMM including time of day as a covariate and male identity as a random factor. Shown are the means (±SE) of individual male means in four sharing categories: No hunt and no sharing: $N = 26$ males; Unsuccessful hunt and no sharing: $N = 10$ males; Shared meat: $N = 12$ males; Received meat: $N = 17$ males. For comparisons between males that shared and received meat versus no hunting and no sharing: *$P < 0.02$; **$P < 0.01$.

associated with their aggression in the context of predation. Territorial boundary patrols are conspicuous aspects of male chimpanzee behaviour and have significant reproductive consequences (reviewed in: Muller & Mitani 2005; Mitani 2009). Recently we have shown that male chimpanzees use an extreme form of territorial behaviour, lethal aggression committed largely during boundary patrols, to expand their territory at the expense of neighbours (Mitani et al. 2010). By acquiring new territory, males are able to enhance the feeding success of others in their community, and as a consequence, increase female reproduction (Williams et al. 2004). Because of these important fitness consequences, the challenge hypothesis predicts that T will be associated with male chimpanzee territorial behaviour. Our findings, however, indicate that T increases before as well as during these events. This raises two important questions regarding chimpanzee physiology and behaviour. First, does the increase in the production of T act in a similar way to the anticipatory T response observed in captive male chimpanzees prior to competitive events (Wobber et al. 2010)? Second, how do male chimpanzees know or anticipate that a patrol is imminent? Are there overt behavioural cues associated with elevated T levels that might provide an observer information about an impending patrol? Additional study will be required to answer these questions.

While territorial aggression affects chimpanzee reproduction, the reproductive consequences of hunting are less clear. Controversy exists over whether male chimpanzees hunt to obtain meat that they use to swap for matings with females (Stanford et al. 1994b; Mitani & Watts 2001; Gomes & Boesch 2009; Gilby et al. 2010). Doing so would implicate predatory aggression as a part of an evolved male chimpanzee reproductive strategy. Our results, however, do not support this hypothesis, as they indicate that male urinary T is low while chimpanzees hunt. This finding mirrors a study of human hunters where hunting success did not correlate with male serum T concentrations (Worthman & Konner 1987).

The pronounced decrease in urinary T in male chimpanzee hunters was unanticipated. One possible explanation is that success at hunts accounted for this drop, but we were unable to test this hypothesis directly. As noted above (see Methods), some males captured prey and failed to share, but it was impossible to obtain samples from them because they fled. Despite our inability to test of this hypothesis formally, it is unlikely that successful hunting alone can account for the decrease in T in sharers because males still displayed low levels when they shared but did not make kills themselves.

Two additional factors related to differences in patterns of sharing may explain the relatively low T concentrations exhibited by males at hunts. Some sharing represents a form of tolerated theft (Blurton-Jones 1984), as individuals are forced to relinquish meat to others that harass them (Gilby 2006). In these cases, decreases of T in sharers might reflect social failure or loss of dominance. Decrements of T in beggars are more difficult to explain, but one possibility is that persistent beggars might display a transient decline in T as they subjugate themselves in front of others.

Voluntary sharing provides another potential explanation for the relatively low T concentrations exhibited by males at hunts. Meat is sometimes shared actively between individuals, without resistance by sharers or aggression by recipients (Nishida et al. 1992; Mitani & Watts 2001). There can also be a remarkable respect for ownership, whereby carcass holders maintain possession in the absence of harassment by others (de Waal 2009). At Ngogo, there is a considerable amount of voluntary sharing between maternal half-siblings (Langergraber et al. 2007) and between unrelated individuals that use meat to develop and maintain social bonds with each other (Mitani & Watts 2001). Moreover, sharing is reciprocated at the group level, and males

exchange meat for coalitionary support (Mitani & Watts 2001). These observations of how meat is shared, who shares, and why sharing occurs indicate that hunting may constitute a form of tolerance and affiliation between males instead of a form of aggression and reproductive competition. In these situations, T might be down-regulated in the same way that it is in vertebrate males when they care for and affiliate with their young, another key prediction of the challenge hypothesis (Wingfield et al. 1990).

Because of our inability to record the precise circumstances under which food was shared between givers and receivers, we currently lack the necessary behavioural data to test these two alternative explanations. Obtaining such observations and analysing the effects of harassment and voluntary sharing on T remain important tasks for future research. These data will contribute to our understanding of the mechanisms underlying and evolution of chimpanzee behaviour, and promise to help clarify the precise role that T plays in animal social interactions (Eisenegger et al. 2011).

Acknowledgments

References

Amsler, S. J. 2010. Energetic costs of territorial boundary patrols by wild chimpanzees. *American Journal of Primatology*, **72**, 93–103.

Bahr, N. I., Palme, R., Mohle, U., Hodges, J. K. & Heistermann, M. 2000. Comparative aspects of the metabolism and excretion of cortisol in three individual nonhuman primates. *General and Comparative Endocrinology*, **117**, 427–438.

Blurton-Jones, N. 1984. A selfish origin for human food sharing: tolerated theft. *Ethology and Sociobiology*, **1**, 1–3.

Boesch, C. & Boesch, H. 1989. Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology*, **78**, 547–573.

Bygott, D. 1979. Agonistic behavior, dominance, and social structure in wild chimpanzees of the Gombe National Park. In: *The Great Apes* (Ed. by D. Hamburg & E. McCown), pp. 405–427. Menlo Park: Benjamin–Cummings.

Eisenegger, C., Haushofer, J. & Fehr, E. 2011. The role of testosterone in social interaction. *Trends in Cognitive Science*, **15**, 263–271.

Gilby, I. C. 2006. Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Animal Behaviour*, **71**, 953–963.

Gilby, I. C., Eberly, L. E., Pintea, L. & Pusey, A. E. 2006. Ecological and social influences on the hunting behaviour of wild chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour*, **72**, 169–180.

Gilby, I. C., Emery Thompson, M. E., Ruane, J. D. & Wrangham, R. W. 2010. No evidence of short-term exchange of meat for sex among chimpanzees. *Journal of Human Evolution*, **59**, 44–53.

Gomes, C. M. & Boesch, C. 2009. Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS One*, **4**, e5116.

Goodall, J. 1963. Feeding behavior of wild chimpanzees: a preliminary report. *Symposium of the Zoological Society of London*, **10**, 39–48.

Goodall, J., Bandora, A., Bergmann, E., Busse, C., Matama, H., Mpongo, E., Pierce, A. & Riss, D. 1979. Intercommunity interactions in the chimpanzee population of the Gombe National Park. In: *The Great Apes* (Ed. by D. Hamburg & E. McCown), pp. 13–54. Menlo Park: Benjamin/Cummings.

Hirschenhauser, K. & Oliveira, R. F. 2006. Social modulation of androgens in male vertebrates: meta-analyses of the challenge hypothesis. *Animal Behaviour*, **71**, 265–277.

Kempenaers, B., Peters, A. & Foerster, K. 2008. Sources of individual variation in plasma testosterone levels. *Philosophical Transactions of the Royal Society B*, **363**, 1711–1723.

Kersey, D. C., Wildt, D. E., Brown, J. L., Huang, Y., Snyder, R. J. & Monfort, S. L. 2010. Parallel and seasonal changes in gonadal and adrenal hormones in male giant pandas (*Ailuropoda melanoleuca*). *Journal of Mammology*, **91**, 1496–1507.

Langergraber, K. E., Mitani, J. C. & Vigilant, L. 2007. The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Sciences, U.S.A.*, **104**, 7786–7790.

Mitani, J. C. 2009. Cooperation and competition in chimpanzees: current understanding and future challenges. *Evolutionary Anthropology*, **18**, 215–227.

Mitani, J. C. & Watts, D. P. 1999. Demographic influences on the hunting behavior of chimpanzees. *American Journal of Physical Anthropology*, **109**, 439–454.

Mitani, J. C. & Watts, D. P. 2001. Why do chimpanzees hunt and share meat? *Animal Behaviour*, **61**, 915–924.

Mitani, J. C., Watts, D. P. & Lwanga, J. 2002. Ecological and social correlates of chimpanzee party size and composition. In: *Behavioural Diversity in Chimpanzees and Bonobos* (Ed. by C. Boesch, G. Hohmann & L. Marchant), pp. 102–111. Cambridge: Cambridge University Press.

Mitani, J. C., Watts, D. P. & Amsler, S. J. 2010. Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology*, **20**, 507–508.

Muller, M. N. 2002. Agonistic relations among Kanyawara chimpanzees. In: *Behavioural Diversity in Chimpanzees and Bonobos* (Ed. by C. Boesch, G. Hohmann & L. Marchant), pp. 112–124. Cambridge: Cambridge University Press.

Muller, M. N., Emery Thompson, M. E. & Wrangham, R. W. 2006. Male chimpanzees prefer mating with old females. *Current Biology*, **16**, 2234–2238.

Muller, M. N. & Mitani, J. C. 2005. Conflict and cooperation in wild chimpanzees. *Advances in the Study of Behavior*, **35**, 275–331.

Muller, M. N. & Wrangham, R. W. 2004. Dominance, aggression and testosterone in wild chimpanzees: a test of the 'challenge hypothesis'. *Animal Behaviour*, **67**, 113–123.

Nishida, T., Uehara, S. & Nyundo, R. 1979. Predatory behavior among wild chimpanzees of the Mahale Mountains. *Primates*, **20**, 1–20.

Nishida, T., Hasegawa, T., Hayaki, H., Takahata, Y. & Uehara, S. 1992. Meat-sharing as a coalition strategy by an alpha male chimpanzee. In: *Topics in Primatology. Vol. 1: Human Origins* (Ed. by T. Nishida, W. McGrew, P. Marler, M. Pickford & F. deWaal), pp. 159–174. Tokyo: Tokyo University Press.

Sobolewski, M.E., Brown, J. L. & Mitani, J. C. In press. Female parity, male aggression, and the challenge hypothesis in wild chimpanzees. *Primates*.

Stanford, C. B., Wallis, J., Matama, H. & Goodall, J. 1994a. Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park, 1982–1991. *American Journal of Physical Anthropology*, **94**, 213–228.

Stanford, C. B., Wallis, J., Mpongo, E. & Goodall, J. 1994b. Hunting decisions in wild chimpanzees. *Behaviour*, **131**, 1–18.

Struhsaker, T. T. 1997. *Ecology of an African Rainforest*. Gainesville: University Press of Florida.

Taussky, H. H. 1954. A microcolorimetric determination of creatine in urine by the Jaffe reaction. *Journal of Biological Chemistry*, **208**, 853–861.

de Waal, F. B. M. 2009. *The Age of Empathy: Nature's Lessons for a Kinder Society*. New York: Three Rivers Press.

Watts, D. P. & Mitani, J. C. 2001. Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, **138**, 299–327.

Watts, D. P. & Mitani, J. C. 2002. Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, **23**, 1–28.

Williams, J. M., Oehlert, G. W., Carlis, J. V. & Pusey, A. E. 2004. Why do male chimpanzees defend a group range? *Animal Behaviour*, **68**, 523–532.

Wilson, M. L., Wallauer, W. R. & Pusey, A. E. 2004. New cases of intergroup violence among chimpanzees in Gombe National Park, Tanzania. *International Journal of Primatology*, **25**, 523–549.

Wingfield, J. C. 2005. A continuing saga: the role of testosterone in aggression. *Hormones and Behavior*, **48**, 253–255.

Wingfield, J. C., Hegner, R. E., Dufty, A. M. & Ball, G. F. 1990. The challenge hypothesis: theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist*, **136**, 829–846.

Whitten, P. L., Brockman, D. K. & Stavisky, R. C. 1998. Recent advances in noninvasive techniques to monitor hormone–behavior interactions, techniques to monitor hormone–behavior interactions. *Yearbook of Physical Anthropology*, **41**, 1–23.

Wobber, V., Hare, B., Maboto, J., Lipson, S., Wrangham, R. & Ellison, P. T. 2010. Differential changes in steroid hormones before competition in bonobos and chimpanzees. *Proceedings of the National Academy of Sciences, U.S.A.*, **107**, 12457–12462.

Worthman, C. M. & Konner, M. J. 1987. Testosterone levels change with subsistence hunting effort in Kung San men. *Psychoneuroendocrinology*, **12**, 449–458.