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# Dominance, aggression and testosterone in wild chimpanzees: a test of the 'challenge hypothesis'

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The 'challenge hypothesis' posits that variation in male testosterone levels is more closely associated with aggression in reproductive contexts than it is with changes in reproductive physiology. Numerous bird studies support this idea, but few tests have been conducted with primates. We conducted behavioural observations and noninvasive hormone sampling of 11 male chimpanzees, *Pan troglodytes schweinfurthii*, in the Kanyawara study site, Kibale National Park, to test predictions of the challenge hypothesis. Results indicated that adult male chimpanzees showed significant testosterone increases during periods when parous females showed maximally tumescent sexual swellings. These periods were also marked by increased rates of male aggression. Male testosterone levels did not increase in the presence of maximally tumescent nulliparous females. Such females are less attractive to males: they are not mate-guarded, nor do rates of male aggression increase when they are swelling. Male chimpanzees copulate with parous and nulliparous females at similar rates, however, suggesting that testosterone increases in the presence of cycling parous females are associated with aggression rather than sexual behaviour. High-ranking chimpanzees were more aggressive than low-ranking males and produced higher levels of urinary testosterone. Thus, the predictions of the challenge hypothesis were generally upheld. This suggests that the hypothesis may have wider applicability among primates, including humans.



The steroid hormone testosterone influences multiple aspects of male reproductive physiology, from the development of the reproductive anatomy, to the maintenance of both reproductive function and motivation (Dixson 1998). It has also classically been linked with aggressive behaviour, and a large body of research, mostly on birds, suggests that variation in circulating testosterone levels during the breeding season is more closely associated with male aggression in reproductive contexts than with changes in reproductive physiology (Wingfield et al. 1990). Formally known as 'the challenge hypothesis', this idea has had notable success in explaining both inter- and intraspecific patterns of testosterone production across more than 60 species (Wingfield et al. 2000).

Specifically, in seasonally breeding birds, testosterone levels rise modestly with the onset of the mating season to support basic reproductive functions, such as spermatogenesis and courtship behaviour. During periods of heightened male aggression, testosterone levels increase further to a maximum physiological level. This additional testosterone appears to facilitate agonistic responses to threats from conspecifics, particularly during territory formation and mate guarding. When males need to provide care to offspring, testosterone levels decrease. Experimental manipulations of male birds have shown that high levels of testosterone suppress paternal behaviour in favour of aggression (Hegner & Wingfield 1987).

Across species, basal levels of breeding-season testosterone are predictably associated with mating system. Monogamous birds maintain high testosterone levels during territory formation and breeding, decrease testosterone production while providing paternal care, and react strongly to challenges from conspecifics with increased testosterone production. Polygynous birds, on the other hand, engage in less paternal care and show high levels of testosterone throughout the breeding season. They generally do not show a heightened endocrine response to challenges, because their testosterone levels are already close to the physiological maximum. Elegant field experiments have shown that testosterone implants can induce polygyny in normally monogamous species (Wingfield 1984; De Ridder et al. 2000).

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Few tests of the challenge hypothesis have been performed on mammals, despite a substantial body of data on endocrine function in wild populations, particularly social carnivores (e.g. meerkats, *Suricata suricata*: Moss et al. 2001; spotted hyaenas, *Crocuta crocuta*: Holekamp & Smale 1998; African wild dogs, *Lycaon pictus*: Creel et al. 1997). One exception is a study of dwarf mongooses, *Helogale parvula*, in which the predictions of the hypothesis were not upheld (Creel et al. 1993).

Among primates, explicit tests of the challenge hypothesis are also rare, but several lines of evidence suggest that it may apply (Whitten 2000; Muller & Wrangham 2001). For example, in seasonally breeding primates, significant increases in circulating testosterone are regularly observed during the breeding season (Dixson 1998). Studies in semiwild settings have found that such increases frequently correlate with male–male aggression (e.g. Cavigelli & Pereira 2000, ringtailed lemur, *Lemur catta*). The strongest demonstration comes from Higley et al. (1996), who found that variations in breeding-season concentration of cerebrospinal fluid free testosterone were positively correlated with individual rates of aggression in male rhesus monkeys, *Macaca mulatta* (Mehlman et al. 1997).

Male rhesus monkeys compete aggressively over mating opportunities. Male muriquis, *Brachyteles arachnoides*, in contrast, do not (Strier 1992). As expected by the challenge hypothesis, faecal testosterone levels in male rhesus rise during the breeding season, but no such rise occurs in male muriquis (Strier et al. 1999). This suggests that acute changes in testosterone have more to do with facilitating aggression in reproductive contexts than with sexual behaviour, even in species like muriqui that show intense sperm competition (Strier et al. 1999).

In this paper we test the challenge hypothesis in wild chimpanzees, *Pan troglodytes schweinfurthii*. Chimpanzee males show high rates of intrasexual aggression and do not provide direct paternal care. Thus, under the standard formulation of the challenge hypothesis, they would be expected to maintain high levels of testosterone during the breeding season and show little response to challenges from other males. Unlike most birds, however, chimpanzees are not seasonal breeders. Rather, mating periods are distributed unpredictably throughout the year, with the availability of conceptible females showing enormous inter- and intra-annual variability (Goodall 1986). Accordingly, we modify the predictions of the challenge hypothesis to take account of this nonseasonal breeding system (Muller & Wrangham 2001).

Among chimpanzees, mating is generally restricted to females with maximally tumescent sexual swellings, which last 10–14 days (Goodall 1986). Males typically show little overt competition for nulliparous females or parous females in the early part of the midfollicular phase (Wrangham 2002). However, towards the end of the follicular phase, when ovulation occurs, aggressive competition over parous females is intense (Watts 1998; Wrangham 2002). During this periovulatory period, high-ranking males are often able to maintain exclusive or near-exclusive access to females (Muller & Wrangham 2001). Preliminary genetic data from two sites indicate that this is a successful reproductive strategy, as high-ranking males, and particularly alphas, appear to systematically father more offspring than lower-ranked males (Constable et al. 2001; Vigilant et al. 2001).

Accordingly, the challenge hypothesis suggests three predictions. First, males should show increased testosterone production during the periovulatory periods of parous females.

Second, these oestrous-period rises in testosterone should be associated specifically with aggression rather than simply with copulation. We test this hypothesis by comparing males mating parous versus nulliparous females, because among chimpanzees, parous females tend to induce more male aggression than nulliparous females do (Wrangham 2002). Specifically, mean copulation rates for parous and nulliparous females do not differ in our study population. However, mating males show more possessive behaviour to parous than to nulliparous females (Wrangham 2002). Parous females should therefore induce a greater rise in male testosterone than nulliparous females.

Third, testosterone levels should be correlated with dominance rank. In olive baboons, *Papio anubis*, the relationship between testosterone and dominance rank depends on the stability of the dominance hierarchy: higher-ranked males are more aggressive only when the hierarchy is unstable (Sapolsky 1993). Only during these unstable periods do they show higher levels of circulating testosterone than low-ranking males. In chimpanzees, by contrast, higher-ranking males are more aggressive at all times (Muller 2002). Hence, high-ranking males are expected to maintain generally higher levels of circulating testosterone than low-ranking males.

## METHODS

### Study Site and Population

M.N.M. observed chimpanzees from November 1997 through December 1998 at the Kanyawara study site in Kibale National Park, Uganda (0°34′N and 30°21′E). The data presented here are from 1998 only (see Table 1 for observation hours). The Kanyawara chimpanzees occupy a territory of at least 15 km$^2$ that incorporates areas of primary forest, logged forest, grassland, swamp, exotic softwood plantation and agriculture (Chapman & Wrangham 1993). Struhsaker (1997) provides a detailed description of the site.

The Kanyawara community were first studied systematically by Isabirye-Basuta (1989) in the early 1980s. They have been studied continuously since September 1987, when R.W.W. established the Kibale Chimpanzee Project. During this study, all of the males and most of the females were well habituated to human observers, and could be observed at close range without disturbance. They have never been provisioned.

At the beginning of this study, the Kanyawara community consisted of 50 chimpanzees, including 11 adult males, 15 parous females, one subadult male, two nulliparous females, eight juveniles and 13 infants. Males were considered to have reached adulthood after successfully

**Table 1.** Individual rates of male aggression in reproductive (R) and nonreproductive (NR) contexts (i.e. in parties with and without maximally swollen parous females, respectively)

| | Observation hours | | Charging displays/h | | Chases and attacks/h | |
|---|---|---|---|---|---|---|
| Male | R | NR | R | NR | R | NR |
| MS | 50 | 114.7 | 0.720 | 0.759 | 0.340 | 0.113 |
| AJ | 44.7 | 105.3 | 0.179 | 0.190 | 0.358 | 0.095 |
| TU | 44.7 | 64.7 | 0.224 | 0.294 | 0.201 | 0.108 |
| BB | 25.3 | 81.3 | 0.118 | 0.148 | 0.158 | 0.049 |
| LB | 42.7 | 110.7 | 0.539 | 0.208 | 0.141 | 0.054 |
| ST | 46.7 | 90 | 0.086 | 0.044 | 0.021 | 0.000 |
| SY | 27.3 | 71.3 | 0.183 | 0.028 | 0.110 | 0.014 |
| YB | 20 | 119.8 | 0.250 | 0.159 | 0.050 | 0.017 |
| LK | 35.3 | 97.3 | 0.028 | 0.082 | 0.142 | 0.144 |
| $\bar{X} \pm$ SE | $37.4 \pm 3.6$ | $95 \pm 6.5$ | $0.259 \pm 0.075$ | $0.212 \pm 0.074$ | $0.169 \pm 0.039$ | $0.066 \pm 0.017$ |

Includes data from nine adult males for whom at least 20 observation hours were available in each condition. Parties containing fewer than two adult males were excluded. Parous females represented were AL, EK and GO.

dominating all females in the community (e.g. Goodall 1986). Male ages are estimates from observations by Isabirye-Basuta in the early 1980s, and R.W.W. from the late 1980s to present. Young chimpanzees (15–20 years) show a suite of morphological characteristics that include thick glossy black hair, unbroken teeth and light facial creasing. Older chimpanzees (>35 years) display thinning brown or grey hair with less sheen, worn or broken teeth and saggy, wrinkled faces. Older individuals also move more slowly and deliberately. Because observations at Kibale have continued since 1983, the males in this study have been seen in a variety of conditions, allowing for reliable age estimates.

## Behavioural Observations

With the help of long-term field assistants, chimpanzees were followed, whenever possible, from the time that they woke in the morning until the time that they constructed their night nests. All-male and bisexual parties were followed preferentially to facilitate data collection on male aggression.

We used 40-min group focal follows to generate rates of aggression for individual chimpanzees. Such all-occurrence sampling (Altmann 1974) was possible because the boisterous nature of chimpanzee agonism renders it highly conspicuous to observers. If a party could not be observed for the full 40 min, then the focal follow was abandoned. If a party fissioned during the focal period, then only data from individuals who were observed for the full 40 min were used in rate calculations. In practice such fissioning was rare, occurring in fewer than 8% of the 40-min follows. M.N.M. collected all data taken during January–November. Four field assistants from the Kibale Chimpanzee Project collected most of the observations in December; these account for less than 4% of the total.

Party composition was recorded every 10 min during focal follows. We used a simple three-point scale to record the degree of tumescence of the sexual swelling for each adult female in a party (e.g. Wallis 1992): (1) No swelling: females with sexual skins that were completely flat. (2) Partial swelling: females with sexual skins that were partly inflated, but wrinkled and droopy. (3) Maximally tumescent: females with sexual skins that were fully expanded (i.e. tense and shiny with no drooping).

Behavioural categories followed those of Bygott (1979) and Goodall (1986); these are summarized in Nishida et al. (1999). Charging displays involved exaggerated locomotion, piloerection and branch shaking. Chases were recorded when an individual pursued a fleeing conspecific, who was generally screaming. All incidents of contact aggression were recorded as attacks. These included hits, kicks, or slaps delivered in passing, as well as extended episodes of pounding, dragging and biting. In behavioural analyses, charging displays are considered low-level aggression, while chases and attacks are classified together as high-level aggression.

Ad libitum observations of aggression and submission were also recorded by M.N.M. and field assistants. These were pooled with focal aggression data to rank the adult males in a linear dominance hierarchy. Ad libitum data were used only to assign male dominance ranks; they were not included in estimates of individual aggression rates.

## Dominance Ratings

Male dominance ratings were based on the distribution of pant-grunt vocalizations (e.g. Goodall 1986). Pant-grunt orientation is highly directional and reliably correlates with multiple measures of dominance (Bygott 1974; Hayaki et al. 1989; Boesch & Boesch-Achermann 2000). The observed distribution of pant-grunts (Table 2) was insufficient to distinguish male rank beyond the basic categories of alpha, high, middle and low (e.g. Bygott 1974; Watts 1998). These designations are referred to as dominance levels.

To enhance resolution of male dominance relationships, we applied the Batchelder et al. (1992; Jameson et al. 1999) model to data on decided agonistic bouts. This model takes into account the number of opponents that an individual has successfully defeated, and the relative success of those opponents in their own agonistic encounters. Its designations are referred to as dominance ranks.

**Table 2.** Dominance relationships among adult males at Kanyawara

| | MS | AJ | BB | TU | LB | SL | BF | ST | YB | SY | LK |
|---|---|---|---|---|---|---|---|---|---|---|---|
| MS | — | 0/1 | | 0/1 | | | | | | | |
| AJ | 6/5 | — | | | | | | | | | |
| BB | 4/3 | 0/2 | — | | | | | | | | |
| TU | 4/2 | 0/1 | 0/1 | — | | | | | | | |
| LB | 13/11 | 1/4 | 1/2 | 2/1 | — | 0/1 | | | | | |
| SL | 12/3 | 0/0 | 0/0 | 1/2 | 0/2 | — | | | | | |
| BF | 1/2 | 0/1 | 0/0 | 0/0 | 0/0 | 0/3 | — | | | | |
| ST | 1/3 | 0/4 | 1/4 | 0/2 | 0/2 | 0/0 | 0/0 | — | | | |
| YB | 0/1 | 4/1 | 0/1 | 0/4 | 0/2 | 0/0 | 0/1 | 1/0 | — | | |
| SY | 7/4 | 4/6 | 1/2 | 1/1 | 2/2 | 1/2 | 0/1 | 0/0 | 2/0 | — | |
| LK | 9/4 | 2/3 | 1/2 | 2/0 | 1/2 | 1/1 | 0/0 | 1/3 | 2/0 | 0/1 | — |

Entries are the number of times that the row male pant-grunted to/lost a dyadic agonistic bout with the column male. Data are from focal follows and ad libitum observations in 1998.

## Comparing Mating and Nonmating Periods

Individual rates of aggression during both mating and nonmating periods were calculated by dividing the number of agonistic acts committed by each adult male by his total observation hours. Only males for whom at least 20 observation hours were available in each period were considered (9/11). Observations from parties containing fewer than two adult males were excluded from rate calculations.

Parous females were considered separately from nulliparous females because previous research indicated that they are not as attractive to males (reviewed in Wrangham 2002). Males at Kanyawara do not mate-guard nulliparous females, nor do they show increased aggression during the periovulatory period of such females. We observed two nulliparous females (NL and NE) and three parous females (AL, EK and GO) cycling at Kanyawara in 1998. Cycles from all five were included in this study.

One parous female, AL, was followed continuously through 14 days of maximal tumescence (25 September–8 October 1998). Thus, it was possible for observers to clearly discern her periovulatory period (here defined as the last 5 days of maximal swelling). We examined this one cycle in detail to ascertain whether the frequency of aggression increased during the periovulatory period compared to previous days of maximal tumescence. Mean daily rates of party aggression were calculated by summing the number of aggressive acts observed during a day's 40-min focals, and dividing by the number of focals performed.

## Urine Collection and Preservation

We regularly collected first-morning urine samples from chimpanzees, who predictably urinate upon waking. When a chimpanzee urinated from a tree, we trapped urine in a disposable plastic bag attached to a 2-m pole. Urine samples were also collected opportunistically throughout the day. Whenever possible, we captured samples on plastic; if a bag could not be placed in time, then urine was pipetted from leaves in the ground layer of vegetation. After collection, we recorded the identity of the chimpanzee, the date and the time of urination.

Within 1–24 h of collection (mean: 6.5 h), urine samples were processed and stored in a propane-powered freezer that consistently maintained a temperature between −18 and −23 °C. Frozen samples were transported on ice and dry ice to the Reproductive Ecology Laboratory at Harvard University, where M.N.M. performed all hormone analyses.

The risk of sample cross-contamination was mitigated by collecting urine from vegetation only when it was clear that multiple individuals had not urinated in the same area. This situation was easy to avoid with first-morning samples, because chimpanzees nest alone, and build fresh nests in new locations nightly. When collecting samples during the day, caution had to be exercised, particularly when several individuals were feeding in the same tree.

Care was taken to avoid collecting urine contaminated with faeces. However, upon close inspection in the field laboratory, small amounts of faecal matter were visible in some samples. Heavily contaminated samples were discarded. When trivial amounts of faecal material were present, this was noted and the offending particles were removed from the sample before freezing.

Because some urine samples passed through leaves in the canopy before they reached the ground, and others were collected from the ground layer of vegetation, it was theoretically possible that contaminants from leaf surfaces could affect the results of the hormone assays. In July 1997, M.N.M. performed two tests at Kanyawara to address this issue.

First, we collected branches from 22 of the tree species most frequently used by chimpanzees. Human volunteers were asked to make clean collections of urine. These were separated into an untreated control and an experimental sample, which was poured over specified branches. After 5–10 min, urine was collected from the leaves with a disposable pipette, following the procedures used for chimpanzee urine collection. The samples were frozen and returned to the Reproductive Ecology Laboratory, where they were assayed for testosterone and creatinine, following the procedures detailed below. Paired comparisons of testosterone and creatinine measurements from the control and experimental samples revealed no significant differences. Testosterone measurements between the two sets of samples were highly correlated ($r^2 = 0.97$,

$P<0.0001$); the same was true for creatinine ($r^2 = 0.93$, $P<0.0001$).

In a second test, 19 branches were collected from 18 of the most common species in the ground layer of vegetation. Approximately 250 ml of water was poured over each branch to simulate urination. Within 5–10 min, water was collected from the leaves, following the procedures used for chimpanzee urine collection. The samples were frozen and returned to the Reproductive Ecology Laboratory, where they were assayed for testosterone and creatinine. In all 19 samples, testosterone levels were indistinguishable from zero, and creatinine was undetectable.

### Hormone Analysis

Steroid levels were quantified by radioimmunoassay according to published protocols (Ellison 1988; Lipson & Ellison 1989) adapted for use with primate urine. Because most testosterone appears in the urine as the metabolite testosterone glucuronide, samples were deconjugated before they were assayed. This was accomplished by hydrolysis; 100 μl of urine was combined in a test-tube with 20 μl of the enzyme β-glucuronidase-arylsulfatase (Boehringer Mannheim, La Jolla, California, U.S.A.) and 300 μl of pH 5 buffer (Fisher Scientific, Pittsburg, Pennsylvania, U.S.A.) and incubated overnight in a 37 °C water bath.

The testosterone assay is based on a four-position tritium competitor (Amersham-Searle, Arlington Heights, Illinois, U.S.A.) and an antiserum raised against testosterone-11-BSA provided by Gordon Niswender of Colorado State University (No. 250). This antiserum has reported cross-reactivities of 46% with DHT and 17% with androstenedione and dihydroepiandrosterone. Hydrolysed urine samples were extracted twice in diethyl ether prior to assay, with recoveries individually monitored by the addition of trace amounts of tritiated testosterone (T). Recoveries averaged 90.3% (coefficient of variation, CV = 8.9%). Separation of bound and free steroid after 24 h of incubation at 4 °C was accomplished by adsorption of free steroid to dextran-coated charcoal. Bound competitor was measured in a RackBeta liquid scintillation counter (LKB/Wallac, Turku, Finland).

For a small number of samples ($N = 22$), recoveries were less than 50%. These samples were hydrolysed and extracted a second time, but recoveries remained low. Visual inspection revealed nothing aberrant about these samples, which highlights the importance of monitoring individual recoveries. These samples were excluded from all analyses.

Quality control was maintained by monitoring values of urine pools at three different levels. Assay sensitivity, the least amount distinguishable from 0 with 95% confidence, averaged 11 000 pmol/litre. Intra-assay variability (CV) at the 50% binding point of the standard curve was 6.6%. Interassay variability averaged 6.6, 6.2, and 6.4% for high, medium and low pools ($N = 17$). Linearity of response was verified by assaying serial dilutions of testosterone standard (predicted versus observed values: $r^2 = 1$, $P<0.0001$) and chimpanzee urine (predicted versus observed values: $r^2 = 0.99$, $P<0.0001$).

To correct for variation in urine concentration, steroid levels were indexed to creatinine (Erb 1970; Cook & Beastall 1987). Creatinine is produced when creatine phosphate, a high-energy compound in skeletal muscle, is nonenzymatically dephosphorylated. This is assumed to occur at a relatively constant rate. Creatinine levels were quantified colourimetrically using the Jaffee reaction (Taussky 1954). Samples with creatinine measurements below 0.05 mg/ml ($N = 6$; all from different males) were excluded from all analyses.

Testosterone production in male hominoids shows a clear diurnal pattern (see below) with the highest levels in the early morning, followed by a steady decline throughout the day. We controlled for this effect by analysing morning samples (those collected before 1000 hours) separately from afternoon samples (those collected after 1000 hours).

In order to compare individual testosterone values between different periods, we calculated mean daily values for each male for the period in question. To control for the diurnal effect described above, we used only morning samples to calculate daily values. When multiple morning samples were collected from an individual on a single day, the average of these was taken as the daily value.

### Statistical Procedures

Comparisons between independent groups were made with the Fligner–Policello rank-based test (Fligner & Policello 1981). This nonparametric test is equivalent to the Mann–Whitney test, but it eliminates the assumption of equal variances that can result in poor power and wide confidence intervals (Wilcox 1997).

Paired comparisons were made with the Agresti–Pendergrast rank-based procedure (Agresti & Pendergrast 1986). This nonparametric test is similar to the standard Wilcoxon matched-pairs signed-ranks test, but it appears to have better power properties over a wide range of situations, particularly when sampling from heavy-tailed distributions (Kepner & Robinson 1988; Wilcox 1997).

Unless noted, all correlations presented in this study use Pearson's product-moment correlation coefficient ($r$). Regression lines were fitted with the standard least squares method. Statistical tests are two tailed. Where rank statistics are used, figures report means and standard errors.

## RESULTS

### Temporal Variation in Testosterone Excretion

Consistent with results from studies of gorillas, *Gorilla gorilla* (Czekala et al. 1994) and humans (Van Cauter 1990), mean morning testosterone values for male chimpanzees were significantly higher than afternoon testosterone values (Agresti–Pendergrast procedure: $F = 10.76$, $N = 11$, $P<0.01$). Furthermore, means of mean male testosterone levels calculated across 14 1-h intervals (0500–1800 hours) showed a strong, statistically significant decline through the day ($r^2 = 0.83$, $F = 60.31$, $N = 14$, $P<0.0001$).

The possibility that male age and urinary testosterone excretion were independent could not be rejected; this was true for both morning (Kendall's partial correlation: $\tau = 0.073$, $N = 11$, NS) and afternoon ($\tau = -0.18$, $N = 11$, NS) samples. Male dominance rank and age were also independent ($\tau = -0.07$, $N = 11$, NS).

## Aggression and Mating Competition

Male chimpanzees became more aggressive during periods when parous females were sexually receptive (Fig. 1). Males increased their display rate, on average, by 24% in parties containing maximally tumescent parous females ($0.26 \pm 0.08$ displays/observation hour), compared with their display rate in parties without such females ($0.21 \pm 0.07$ displays/observation hour; Agresti–Pendergrast procedure: $F = 2.69$, $N = 9$, $P = 0.14$). The effect on high-level aggression was more pronounced. Males engaged in chases and attacks almost 2.5 times more frequently when in parties containing maximally tumescent parous females ($0.17 \pm 0.04$ incidents/h) than when in parties without such females ($0.07 \pm 0.02$ incidents/h; Agresti–Pendergrast procedure: $F = 22.23$, $N = 9$, $P = 0.002$). Individual rates of aggression are summarized in Table 1.

The rise in rates of high-level aggression during mating competition resulted in a significant increase in the overall intensity of aggression. In parties containing maximally tumescent parous females, $46 \pm 9\%$ of male agonism took the form of chases and attacks. In other parties only $29 \pm 6\%$ of male agonism took this form (Agresti–Pendergrast procedure: $F = 6.3$, $N = 9$, $P = 0.036$).

Detailed observations of a single cycle from the parous female AL support the prediction that male aggression increases in the late follicular phase. During the first 9 days of maximal swelling, low-level aggression was observed, on average, $0.63 \pm 0.22$ times/h; in the final 5 days this figure increased to $1.25 \pm 0.44$ times/h. This difference was not significant (Fligner–Policello procedure: $Z_{fp} = -1.079$, $N_1 = 7$, $N_2 = 5$, $P = 0.28$). High-level aggression, on the other hand, increased significantly in the periovulatory period. Chases and attacks were observed, on average, $0.67 \pm 0.24$ times/h during the 9 days of maximal swelling; in the final 5 days this figure rose to $2.0 \pm 0.42$ times/h (Fligner–Policello procedure: $Z_{fp} = -4.8$, $N_1 = 7$, $N_2 = 5$, $P < 0.0001$).

## Testosterone and Mating Competition

Males showed significant increases in urinary testosterone excretion during periods of reproductive competition (Fig. 2). Mean male testosterone levels were almost 40% higher in parties containing maximally tumescent parous females ($784 \pm 76$ pmol/mg creatinine) than in parties without such females ($570 \pm 50$ pmol/mg creatinine) (Agresti–Pendergrast procedure: $F = 8.34$, $N = 11$, $P = 0.016$).

Detailed analysis of samples collected during and immediately following a single cycle from one parous female (AL) was consistent with this pattern (Fig. 3). In the 14-day period when AL was maximally tumescent, mean morning testosterone levels for eight adult males averaged $885 \pm 79$ pmol/mg creatinine. In the 14-day period following AL's detumescence, testosterone levels in the same males averaged $597 \pm 81$ pmol/mg creatinine (Agresti–Pendergrast procedure: $F = 8.6$, $N = 8$, $P = 0.022$).

Male testosterone levels did not appear to increase in the presence of maximally tumescent nulliparous females (Fig. 2). Samples were available from eight of the 11 adult males on days when nulliparous females were present. In parties containing such females, urinary testosterone levels for eight males averaged 537 pmol/mg creatinine. In parties containing no maximally tumescent females, mean morning testosterone levels for the same males appeared to be slightly higher, at 652 pmol/mg creatinine. This difference was not statistically significant (Agresti–Pendergrast procedure: $F = 4.01$, $N = 8$, NS).

## Dominance, Aggression and Testosterone

Only 89 pant-grunts were observed among the 11 adult males (Table 2). Fifty-seven of these (64%) were directed towards the alpha male, MS. Thus, it was impossible to determine precise dominance relationships from this signal alone. Males could be assigned to dominance levels, however. No reversals were recorded in any of the pant-grunt interactions.

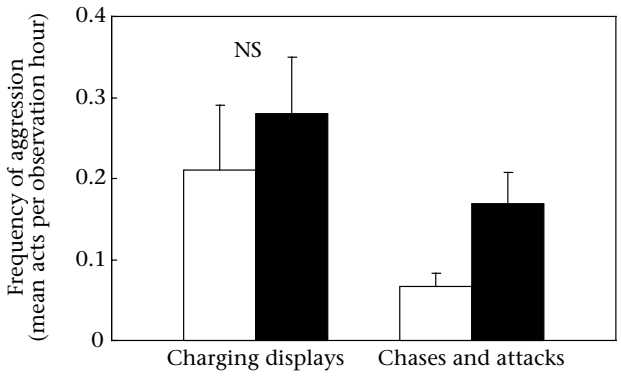


**Figure 1.** Rates of male aggression in parties with (■) and without (□) maximally tumescent parous females.

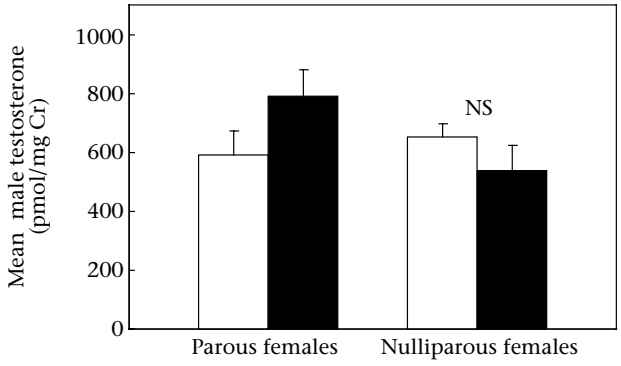


**Figure 2.** Male testosterone in mating (■) and nonmating (□) contexts.

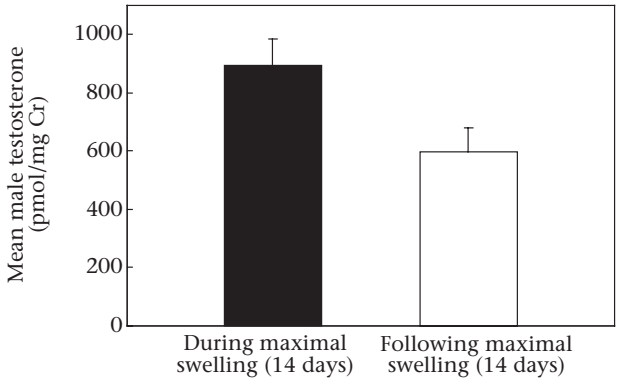


**Figure 3.** Male testosterone during and immediately following one mother's (AL's) maximal swelling.

We recorded 107 decided agonistic encounters between male dyads (Table 2). These data were used to generate a probabilistic dominance rank for each male. Males received scaled values between −1 and 1, with 1 representing high rank (Table 3). The distance between the scaled values indicates a difference in the magnitude of dominance. Only three of these encounters represented dominance reversals.

High-ranking males were generally more aggressive than low-ranking males (Fig. 4). Across the adult males, dominance rank and frequency of low-level aggression (charging displays) were positively and significantly correlated ($r_9 = 0.75$, $P = 0.008$). The same was true for dominance rank and the frequency of high-level aggression (chases and attacks) ($r_9 = 0.71$, $P = 0.014$). These relationships were consistent during both mating and nonmating periods.

The alpha male, MS, showed markedly high rates of aggression. His frequency of display was 4.5 times the male average, and more than twice that of the next highest male. His rate of high-level aggression was twice the male average.

Across the adult males, mean morning testosterone levels did not correlate significantly with either dominance level ($r_9 = 0.28$, $P = 0.41$) or dominance rank ($r_9 = 0.20$, $P = 0.56$). However, morning testosterone levels in the alpha male were consistently higher than those of lower-ranked individuals. Pairwise comparisons using all morning samples collected from 11 adult males revealed significant differences between the alpha and all males save the beta (AJ) and one other male (ST) (Table 4).

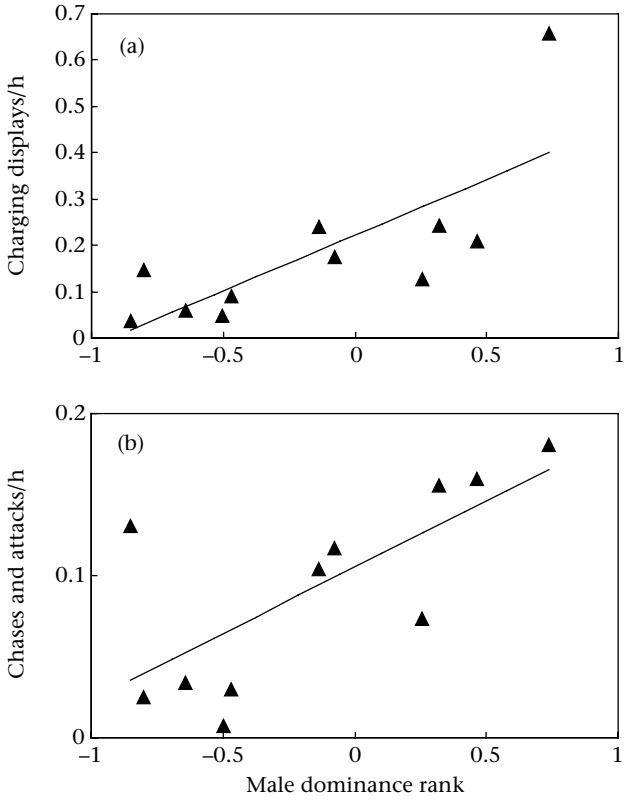


**Figure 4.** Male dominance rank and the frequency of (a) low and (b) high levels of aggression.

For afternoon samples, mean male testosterone levels were positively and significantly correlated with both dominance level ($r_9 = 0.62$, $P = 0.04$) and dominance rank ($r_9 = 0.62$, $P = 0.04$; Fig. 5). As in the morning, the alpha male had higher mean urinary testosterone levels than lower-ranked males. However, limited afternoon samples precluded pairwise comparisons between males.

**Table 3.** Mean morning and afternoon testosterone values (pmol/mg Cr) for 11 adult males

| | | Dominance | | Morning | | Afternoon | |
|---|---|---|---|---|---|---|---|
| Male | Age | Rank | Level | Mean T | *N* | Mean T | *N* |
| MS | 23 | 0.739 | Alpha | 900 | 33(34) | 552 | 15(16) |
| AJ | 24 | 0.465 | High | 751 | 30(32) | 466 | 8(9) |
| TU | 38 | 0.320 | High | 463 | 20(20) | 421 | 5(5) |
| BB | 32 | 0.258 | High | 378 | 12(12) | 479 | 6(6) |
| SL | 27 | −0.078 | Medium | 406 | 7(7) | 411 | 4(5) |
| LB | 30 | −0.138 | Medium | 568 | 36(49) | 314 | 25(31) |
| BF | 32 | −0.467 | Medium | 594 | 13(14) | 451 | 7(7) |
| ST | 43 | −0.505 | Medium | 769 | 35(39) | 329 | 9(12) |
| SY | 34 | −0.641 | Low | 657 | 35(38) | 425 | 17(22) |
| YB | 25 | −0.800 | Low | 605 | 42(45) | 448 | 18(24) |
| LK | 16 | −0.853 | Low | 494 | 45(56) | 279 | 32(40) |

Sample sizes are the total number of daily testosterone values, followed by the number of urine samples used to calculate those values (in parentheses).

**Table 4.** Pairwise comparisons of mean morning testosterone levels for the alpha and all other males

| Dyad | | $Z_{fp}$ | $P$ | $N$ |
|---|---|---|---|---|
| MS | AJ | 1.3456 | 0.178 | 30(32) |
| MS | TU | 6.0670 | <0.0001 | 20(20) |
| MS | BB | 7.2188 | <0.0001 | 12(12) |
| MS | SL | 6.2648 | <0.0001 | 7(7) |
| MS | LB | 3.9249 | <0.0001 | 36(49) |
| MS | BF | 3.0410 | 0.002 | 13(14) |
| MS | ST | 1.0899 | 0.276 | 35(39) |
| MS | SY | 3.3556 | 0.0008 | 35(38) |
| MS | YB | 3.4403 | 0.0006 | 42(45) |
| MS | LK | 6.0615 | <0.0001 | 32(40) |

$Z_{fp}$ values greater than 2.79 were significant using 0.05 as the limit for experiment-wise type I error. Sample sizes are the total number of daily testosterone values, followed by the number of urine samples used to calculate those values (in parentheses).

Individual rates of aggression were not closely correlated with measures of urinary testosterone excretion. This was true of both low-level (morning: $r_9 = 0.48$, $P = 0.13$; afternoon: $r_9 = 0.21$, NS) and high-level aggression (morning: $r_9 = 0.60$, $P = 0.05$; afternoon: $r_9 = 0.05$, NS).

## DISCUSSION

### Testosterone and Reproductive Aggression

As expected, urinary testosterone levels in the adult males increased significantly in the presence of maximally tumescent parous females. This testosterone rise could in theory have been caused by increased sexual behaviour, by the presence of more males (leading to more aggression), or by increased aggression related to sexual competition.

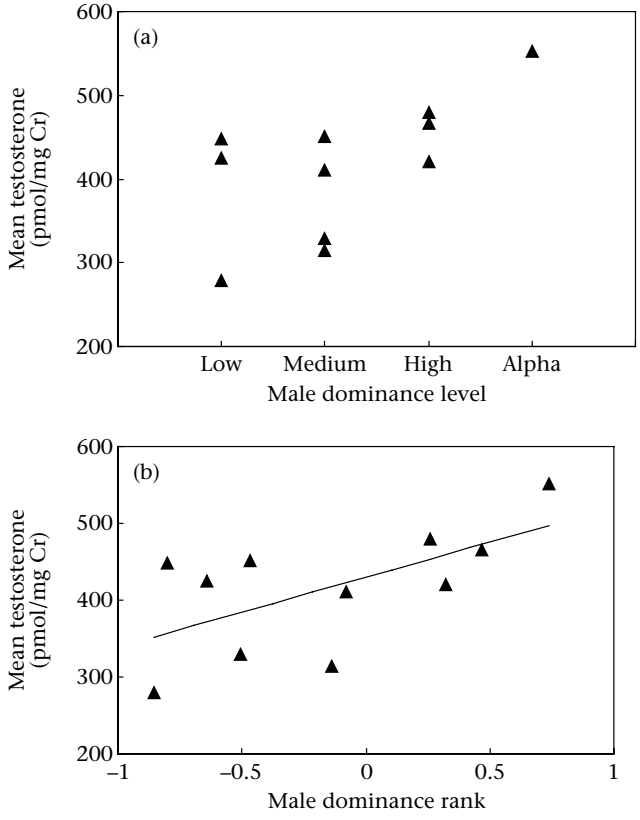


**Figure 5.** Afternoon urinary testosterone excretion in males and (a) male dominance level and (b) male rank.

The hypothesis that increased sexual behaviour alone leads to increased male testosterone was not supported, because testosterone rose only in response to parous females (when reproductive aggression was intense), and not in the presence of nulliparous females (when there was little or no reproductive aggression). Thus, testosterone levels were correlated more closely with aggressive than with sexual behaviour, as predicted by the challenge hypothesis.

Parties containing maximally swollen females tend to contain more males (Wrangham 2000; Mitani et al. 2002). This raises the possibility that it was the number of males rather than the intensity of sexual competition that influenced testosterone levels. However, individual rates of aggression did not increase with increasing party size (Muller 2002). Hence, the increased rates of aggression described above could not be accounted for simply by the presence of more males.

By contrast, we found clear increases in the rate and intensity of aggression when males were in parties with maximally tumescent parous females. Because we were not always able to observe cycling females throughout the entire period of maximal swelling, it was sometimes impossible to distinguish the periovulatory period from the prior phase of swelling. As a result, we weighted all days of maximal tumescence equally. But in a detailed analysis of a single complete cycle, rates of aggression differed between the initial days of maximal swelling and those of the periovulatory period as expected, and as previously found elsewhere (Tutin & McGinnis 1981; Watts 1998). Thus, it seems likely that if we had considered only days in the periovulatory period, individual increases in male aggression would have been more pronounced.

By showing that oestrous-period rises in testosterone were associated more closely with aggression than with copulation, our results conform to the challenge hypothesis. But they also show that the challenge hypothesis applies differently to chimpanzees than to seasonally breeding birds. Polygynous male birds maintain testosterone levels near the physiological maximum throughout the breeding season, and therefore show weak or nonexistent testosterone responses to aggressive interactions within the breeding season (Wingfield et al. 1990). Chimpanzees, by contrast, do not have a breeding season, although conceptions in Kanyawara show an annual peak (Sherry 2002). As a result, male chimpanzees appear to maintain levels of testosterone sufficient to support copulation throughout the year (i.e. the equivalent of baseline breeding-season levels in birds). This is what happens in birds living in highly unpredictable environments, where signals such as photoperiod and temperature are not reliable indicators of food abundance, and the breeding season does not occur at the same time every year (Wingfield et al. 2000).

Chimpanzees might therefore have been expected, like polygynous birds, to persistently maintain such high levels

of testosterone that testosterone would not increase in aggressive contexts. However, we found evidence for a relatively pronounced testosterone response to male–male competition over oestrous females. The rarity with which males encounter cycling parous females probably accounts for this pattern. In the wild, a female chimpanzee may not have her first infant until she is 13–15 years old. Interbirth intervals average 5–7 years (reviewed in Knott 2001). Finally, at Kanyawara, parous females average only five cycles per birth (Wrangham 2002). As a result, cycling parous females are temporally rare. In the present study they were present on only about 13% of observation days. The actual frequency was probably lower, since it was easier to find and follow chimpanzees when they were assembled in large parties with oestrous females. Because there can be significant physiological costs associated with increased androgen production, including increased energetic costs and immunosuppression (Wingfield et al. 1997), it might pay individuals to maintain lower testosterone levels and respond more to challenges, as occurs in monogamous birds (Wingfield et al. 1990). Our data suggest that this is the chimpanzee strategy.

### Testosterone, Rank and Dominance Stability

Because high-ranking males tend to display more aggression than low-ranking males, we expected a positive correlation between male rank and testosterone output. This prediction was only partially supported, because the result differed by time of day. For morning samples, the correlation across all adult males was weak and statistically nonsignificant, whereas for afternoon samples, the correlation was positive and significant. The highest-ranking male, however, showed the highest levels of urinary testosterone regardless of time of day, a pattern similar to that seen in African hunting dogs (Creel et al. 1997).

In humans, evening levels of testosterone show stronger correlations with behavioural measures than do morning levels (e.g. Worthman & Konner 1987; Berg & Wynne-Edwards 2001; Gray et al. 2002). This pattern may be widespread because morning testosterone levels reflect physiology during sleep, whereas evening samples are influenced by the cumulative outcomes of diurnal social interactions.

The afternoon correlation between male rank and testosterone could in theory be a consequence of an unstable hierarchy (cf. Sapolsky 1993). However, the dominance hierarchy at Kanyawara was stable throughout the study period (i.e. there were no rank reversals and the rate of reversals in decided agonistic bouts was less than 3%). Our data therefore suggest that among chimpanzees testosterone correlates with male rank regardless of the stability of the hierarchy. This result supports the proposal that the relationship between testosterone and rank depends on the relationship between rank and aggression (Whitten 2000).

The positive correlation between rank and aggression in stable chimpanzee hierarchies may be accounted for by the fission–fusion nature of chimpanzee society. Chimpanzee males frequently separate into subgroups that may not meet again for hours, days or weeks. Dominant males are consequently at risk from opportunistic coalitions formed by lower-ranked individuals and must continually assert their dominance through agonistic display. Elevated levels of testosterone in high-ranking males may therefore be a response to the difficulty of predicting challenges from rivals or they may be a corollary of the higher rates of aggression that these males experience during the day relative to low-ranking males. More detailed observations of individual variation in rates of aggression and testosterone levels will be able to differentiate these alternatives.

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