RESEARCH ARTICLE

Variation in Fecal Testosterone Levels, Inter-Male Aggression, Dominance Rank and Age During Mating and Post-Mating Periods in Wild Adult Male Ring-Tailed Lemurs (*Lemur catta*)

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In primate species exhibiting seasonal reproduction, patterns of testosterone excretion in adult males are variable: in some species, peaks correlate with female receptivity periods and heightened male–male aggression over access to estrous females, in others, neither heightened aggression nor marked elevations in testosterone have been noted. In this study, we examined mean fecal testosterone (fT) levels and intermale aggression in wild adult male ring-tailed lemurs residing in three groups at Beza Mahafaly Reserve, Madagascar. Results obtained from mating and post-mating season 2003 were compared to test Wingfield et al. [1990. Am Nat 136:829–846] ''challenge hypothesis'', which predicts a strong positive relationship between male testosterone levels and male–male competition for access to receptive females during breeding season. fT levels and rates of intermale aggression were significantly higher during mating season compared to the post-mating period. Mean fT levels and aggression rates were also higher in the first half of the mating season compared with the second half. Number of males in a group affected rates of intermale agonism, but not mean fT levels. The highest-ranking males in two of the groups exhibited higher mean fT levels than did lower-ranking males, and young males exhibited lower fT levels compared to prime-aged and old males. In the post-mating period, mean male fT levels did not differ between groups, nor were there rank or age effects. Thus, although male testosterone levels rose in relation to mating and heightened male–male aggression, fT levels fell to baseline breeding levels shortly after the early mating period, and to baseline non-breeding levels immediately after mating season had ended, offsetting the high cost

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of maintaining both high testosterone and high levels of male–male aggression in the early breeding period. Am. J. Primatol. 69:1325–1339, 2007.   © 2007 Wiley-Liss, Inc.

INTRODUCTION

The challenge hypothesis [Wingfield et al., 1990] predicts a direct relationship between male testosterone levels (T), mating systems, and reproductive strategies. Wingfield et al. [1990] note that in some avian species, levels of T must rise above a certain minimum for sexual behavior to be expressed. As T levels increase from a non-breeding to a breeding baseline, sexual behavior increases markedly, but any increase in T beyond the breeding baseline can result in male–male aggression over access to estrous females. Wingfield et al. further suggest that reproductive aggression related to an increase in T should be strongest during periods of social instability, including situations involving challenges by conspecific males for access to estrous females. An increase in male–male agonism during reproductive periods may, in turn, stimulate T production, resulting in a 'feedback loop' [Wingfield et al., 1990, p 833]. Conversely, the authors suggest that once the intermale 'challenge' ceases, either due to withdrawal of the rival male(s) or the end of female receptivity, the stimulation for maintaining high levels of T ceases and circulating T concentrations decline. Thus, T levels should be positively related to the degree of intermale aggression occurring over mating competition. The challenge hypothesis was initially applied to birds, and males in polygynous species were found to exhibit higher T concentrations for longer periods in the breeding season than did males in monogamous species [Wingfield et al., 1987, 1990].

With recently refined non-invasive hormonal monitoring techniques [Hodges & Heistermann, 2003; Whitten et al., 1998], primate field researchers are now able to examine relationships between T, aggression, mating behavior, and social organization in naturally occurring populations of primates to determine if the challenge hypothesis applies. As a result, variation in adult male T levels has been investigated in a number of prosimian and anthropoid species in the wild, and we are now gaining a clearer picture of the variables that can affect male T levels, as well as strategies that are used by males to mitigate the cost of maintaining high T levels in social and reproductive situations [Barrett et al., 2002; Brockman et al., 1998, 2001; Cristobal-Azkarate et al., 2006; Huck et al., 2005; Kraus et al., 1999; Lynch et al., 2002; Marshall & Hohmann, 2005; Muehlenbein et al., 2004; Muller & Wrangham, 2004; Ostner et al., 2002; Sannen et al., 2003; Strier et al., 1999].

In seasonally breeding polygynous primate groups in the wild, patterns of testosterone excretion in adult males are highly variable. In male Japanese macaques, and red-fronted brown lemurs, fecal testosterone (f T) levels are higher either at the onset, or during mating periods than at other times, and in tufted capuchins male f T levels rise during the peak of female estrus synchrony after the birth season [Barrett et al., 2002; Lynch et al., 2002; Ostner et al., 2002]. In Verreaux's sifaka, male f T peaks 1 month before the breeding season and remains relatively constant for a 3-month period encompassing mating and male transfer [Brockman et al., 1998]. Conversely, in male muriquis, only a slight increase in f T occurs at the onset of mating season, and no overall difference is found between mating and non-mating periods [Strier et al., 1999].

Rank and the stability of the male dominance hierarchy within a group also have variable effects on testosterone levels among males. In wild bonobos, chimpanzees, and Verreaux's sifaka, dominant males exhibit higher T levels than do lower-ranking individuals [Marshall & Hohmann, 2005; Kraus et al., 1999; Muehlenbein et al., 2004; Muller & Wrangham, 2004; Sannen et al., 2003]. In Verreaux's sifaka and olive baboons, high-ranking males have been found to exhibit higher T levels during socially stable periods [Brockman et al., 1998; Sapolsky, 1983], although in the baboons, T levels were higher only during stressful situations occurring during such stable periods [Sapolsky, 1983]. In contrast, in Japanese macaques, tufted capuchins, and red-fronted brown lemurs, no relationship has been found between male rank and fT levels [Barrett et al., 2002; Lynch et al., 2002; Ostner et al., 2002].

Ring-tailed lemurs (*Lemur catta*) exhibit extreme reproductive seasonality, with mating occurring only during a 3–4 week period annually, and each female is receptive for only 6–24 hr each year [Jolly, 1966; Sauther, 1991; van Horn and Resko, 1977]. The brevity of both the mating period and female receptivity results in marked male–male competition over access to estrous females, involving both ritual (stink-fighting, tail marking and waving) and actual aggression (physical fighting) [Cavigelli & Pereira, 2000; Gould, 1994, 1997; Jolly, 1966; Koyama, 1988; Sauther, 1991; Taylor & Sussman, 1985]. In semi-free ranging *L. catta* at the Duke University Primate Center, Cavigelli and Pereira [2000] found that rates of aggression in adult males during the stable pre-mating period were not correlated with testosterone levels, but during the mating season they were positively and significantly correlated, particularly on days of female receptivity.

We were interested in discovering if and to what extent the challenge hypothesis can be applied to male *L. catta* in the wild during the brief mating period. We investigated relationships between male fT levels and rates if intermale agonism, as well as individual mean fT levels and rank, age, and number of males in a group, and how the costs of maintaining high, or above baseline levels of testosterone during mating season are mitigated [as per Wingfield et al., 2001]. We examined and compared individual mean fT levels with the above-mentioned variables during the mating and post-mating periods in 13 adult male ring-tailed lemurs at the Beza Mahafaly Special Reserve, southwestern Madagascar, in 2003. The following predictions were tested:

(1) Because of the short mating season and marked intermale mating competition occurring at this time, mean fT levels in males should be higher during the mating season compared to the post-mating period;
(2) Individual females within a *Lemur catta* group become receptive at different times during the 3–4 week mating period [Koyama, 1988; Sauther, 1991] thus, male mating competition occurs throughout the mating season. Therefore, male fT levels should remain relatively constant during this period, since intermale aggression can occur at any time while individual females become receptive;
(3) Rates of intermale aggression should be significantly higher during the mating period, compared with post-mating, if mean fT rates are higher; and
(4) There should be a positive relationship between the number of resident males in a group and rate of male–male aggression during the mating season, since more males in a group potentially means greater competition over

access to estrous females. We also investigated whether or not there were differences in mean fT levels during both mating and post-mating periods in relation to rank and age of the male;

(5) Since the male-dominance hierarchy within a ring-tailed lemur group has been noted to break down during mating season [Budnitz & Dainis, 1975; Gould, 1994; Jolly, 1966; Sauther, 1991; Sussman, 1991], we predicted that no significant difference should be found between the pre-mating rank of a male and fT level during mating season, since higher-ranking males do not necessarily out-compete lower ranking males for access to receptive females [Gould, 1994; Gould et al., 2005].

MATERIALS AND METHODS

Study Site and Study Animals

Fecal samples and focal animal data [Altmann, 1974] were collected on adult males residing in three groups of ring-tailed lemurs at the Beza Mahafaly Special Reserve, Madagascar, during the mating season of 2003 (May 1–20), and the post-mating period (late May to end of June). Between nine and 11 groups of ring-tailed lemurs inhabit the 80 ha parcel (Parcel 1) of this protected area in southwestern Madagascar (23°–30′S. latitude and 44′E. longitude). Parcel 1 is characterized by mixed vegetation, including a strip of high-canopy gallery forest in the east, nearest the Sakamena River, grading to lower canopy deciduous and then xerophytic forest as one moves toward the western boundary of the reserve [Sussman & Rakotozafy, 1994]. Home ranges of the three study groups were located in the gallery forest area, averaged 17 ha, and overlapped extensively [Gould et al., 2003; Sussman, 1991].

L. catta exhibits female dominance, female philopatry and male dispersal, and male membership in a group usually changes from 1 year to the next [Gould et al., 2003; Gould, 2006; Jolly, 1966, 1984; Jones, 1983; Sussman, 1991, 1992]. In 2003, there were 14 males in the three study groups; however, one male was absent for much of the first half of the mating season, and was therefore excluded from the analysis. Group composition, and rank and age-class information on the focal males is presented in Tables I and II.

Methods

Focal animal identification and age determination

Before data collection, the focal males were temporarily immobilized using a Telinject blowpipe and 0.25–0.30 cc of Tiletamine (Telazol) and fitted with identification collars and plastic numbered tags. Dosage of Telazol used reflects previous immobilization protocol on this population of 0.10 cc per kilo of body weight [Gould et al., 2003] as well as protocol used for *Propithecus verreauxi* at the same site [Richard et al., 2002]. Immobilization, collaring and all data collection described herein complied with protocols approved by the University of Victoria's Animal Care Committee and adhered to the legal requirements of the Département des Eaux et Forêt and ANGAP, Madagascar.

While immobilized, the males were given a physical and dental examination, and relative age-class (young adult, prime-aged and old) of each male was determined following a set of dental-wear and morphological criteria developed by Sauther et al. [2002]. Approximate ages in years, related to dental and morphological criteria outlined in Sussman [1992], Sauther et al. [2002], and Gould [1994] are presented in Table II.

TABLE I. Group composition, focal male ID, rank, and age class for 2003 season (mating and post-mating)

Male ID	Rank	Age-class
Red group 2003		
a	1	Young prime
p	2	Young
l	3	Prime
n	4	Unknown (unable to capture)
Green group 2003		
d	1	Old
b	2	Unknown (unable to capture)
e	3	Young prime
g	4	Prime
o	5	Prime
s	6	Young natal male
Lavender group		
c	1	Prime
m	2	Unknown (unable to capture) Not included in study as he was absent for early mating season
y	3	Prime
f	4	Young

Because the intermale dominance hierarchy within a group often breaks down during mating season, pre-mating ranks were used. These ranks resumed after mating season had ended. Male 'm' in Lavender group disappeared for much of the mating season, and was therefore not included in the analysis. Red group contained four adult males and four adult females, Green group six adult males and six females, and Lavender group four males and four females in the 2003 mating/post-mating seasons.

TABLE II. Age classes of focal males and approximate corresponding ages [from Gould, 1994; Sussman, 1992; Sauther et al., 2002]

Age-class	Approximate age in years
Young adult	3–4 years of age (onset of sexual maturity)
Young prime	Approximately 4–6 years of age
Prime	Approximately 7–12 years of age
Old	Over 12 years of age

Behavioral data collection

During the mating and post-mating periods, a total of 132.5 hr of continuous-time focal animal data [Altmann, 1974] were collected on all males in the study groups by L.G. and two research assistants. Specifically, 530 data sessions of 15-min duration were collected: 279 (May 1–20) in mating season and 251 in the post-mating period (May 23–June 6). We collected between 17 and 24 focal sessions on each male in mating season (mean = 21) and between 12 and 32 sessions on each male in the post-mating period (mean = 21 sessions). Mating season was further divided into early (May 2–13) and late (May 15–20) periods, to examine whether or not fT levels remain high throughout the entire mating season.

Male rank was determined by the direction and outcomes of aggressive and submissive interactions, including both severe aggression (e.g. chasing, cuffing, pushing, jump-fighting and tail waves or ''stink fights'' wherein a male draws his tail between the scent glands on his wrist and then waves the pheromone impregnated tail over his head at the opponent male) [Jolly, 1966], and milder agonism (e.g. displacements and direction of submissive chattering). Rates of aggression per hour were calculated for each focal male with all other animals in his group, as well as with extra-group males during the mating season.

Fecal sample collection and fT analysis

Ten to 12 fecal samples were collected from each focal male during the data collection periods (5–6 samples during mating season and 5–6 post-mating for each focal male). Samples were obtained in either early morning before the group began daily travel, or immediately after the midday rest period. Samples were prepared (dried and packaged) following the method described by Brockman and Whitten [1996]. As fecal samples were collected, they were immediately packaged in aluminum foil and sealed. Samples were flattened and dried within 3 hr of collection, by placing in a Coleman camp oven at 55–70°C (solar and tea candle heat) for between 15 and 30 min depending upon amount of direct sunlight on the metallic surface of the oven and ambient temperature. When thoroughly dried, samples were ground to a fine powder, re-packaged in aluminum foil packets, and double zip-locked, following the protocol presented in Brockman and Whitten [1996] and Whitten et al. [1998]. This method of fecal sample preparation yields stable, interpretable steroid profiles for 3 years or more [Whitten et al., 1998]. Once back from the field, LG sent the samples to the Wisconsin Primate Center for quantitation of testosterone. Testosterone levels in ring-tailed lemur fecal samples have been shown to reflect circulating T levels [Cavigelli & Pereira, 2000].

Testosterone determination and validation

Mixed fecal samples were weighed (0.05–0.25 g), and extracted with 2.5 ml distilled water and 2.5 ml of ethanol as reported for this species [Gould et al., 2005]. This method recovers over 90% of testosterone. One ml of the fecal supernatent was re-extracted with 5 ml ethyl acetate, dried and resuspended in 1 ml ethanol. Of this, 200 μl was dried and resuspended in iso-octane:ethyl acetate (94:4) for celite column chromatography to separate testosterone from other androgens. The chromatography used System I technique as described in Abraham et al. [1972] with the modifications made by Ziegler et al. [1996]. Eluted testosterone was dried and resuspended. In 200 μl ethanol and 75 μl was taken for a testosterone enzyme immunoassay by the method reported in Ginther et al. [2001]). The testosterone antibody (AB156, supplied by C. Monro, UC-Davis) crossreacts over 90% with DHT and therefore requires chromatographic separation. Samples are diluted with 300 μl of testosterone-horseradish peroxidase (HRP) and plated as 100 μl in duplicate. Serially diluted pooled lemur samples were parallel to the standards for testosterone ($t = 1.82$, $df = 30$, $P > 0.05$). Accuracy for testosterone was measured at 95.8 ± 2.6, $n = 8$. Recovery for the entire procedure was 80%. Results are reported as fT ng/gm dry weight for each male.

Data analysis

fT levels were averaged for each male per condition (mating and non-mating periods, and early/late mating season). Individual rates of aggression were calculated as a rate per hour, by tallying the number of aggressive events

recorded for each male in each period (mating and post-mating) and dividing the total by the number of hours collected on that male for that particular period. Rates of intermale aggression between early and late mating season were calculated in the same manner.

When all focal males ($N = 13$) were compared to determine differences in (1) mean fT levels, and (2) intermale aggression between mating and post-mating seasons as well as differences in early versus late mating periods, paired *t*-tests were used. To test for differences between the highest-ranking male versus lower-ranking males in each group, the test for comparison of a single observation with the mean of a sample [Sokal & Rohlf, 1995] was applied. For determining between-group differences in mean fT and male–male aggression, as well as age differences in fT, non-parametric analysis of variance tests were used, as the sample sizes (N's of between 3 and 6 for each group) were too small to test the assumptions of parametric statistical tests.

RESULTS

Mating versus post-mating periods and fT levels

Mean fT levels were significantly higher during the mating season compared with the post-mating period (paired sample *t*-test, $t = 3.58$, $P = 0.004$, $df = 12$), Figure 1, mating season) and mean fT levels were significantly higher in the first half of the mating season compared with the latter half (paired sample *t*-test, $t = 3.0$, $P = 0.01$, $df = 12$), Figure 2.

No difference was found in mean fT levels in the late (second half) of the mating season compared with the post-mating period (paired sample *t*-test, $t = 0.69$, $P = 0.49$, $df = 12$), but the difference between early mating season mean fT and post-mating period mean fT was highly significant (paired sample *t*-test, $t = 3.7$, $P = 0.003$, $df = 12$).

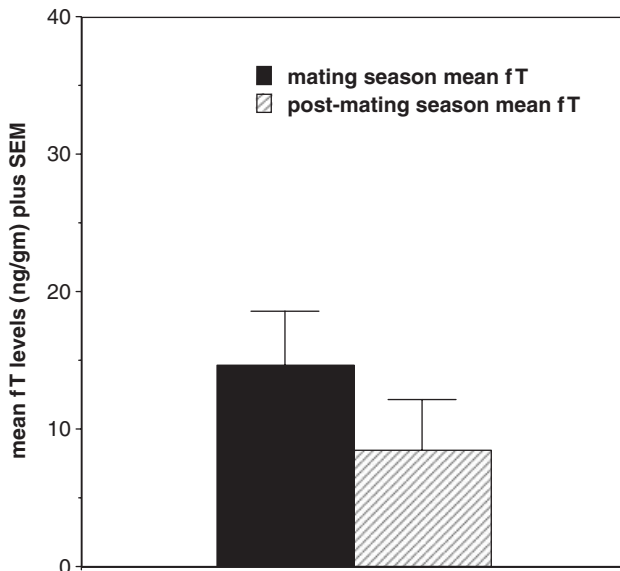

Fig. 1. Comparison of mating season and post-mating period mean fT levels in the focal males ($N = 13$) in 2003.
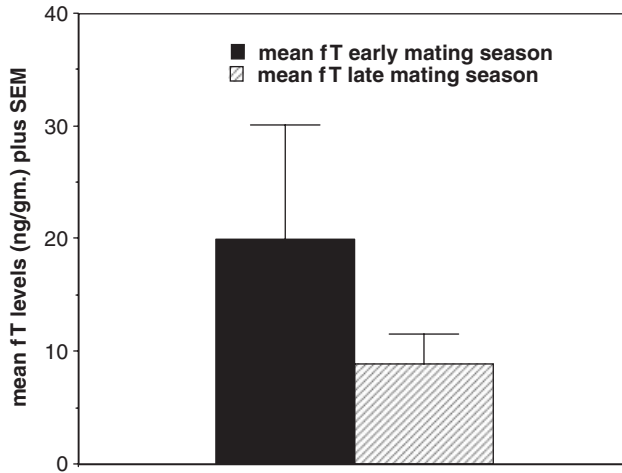
Fig. 2. Differences in early (first half) versus late (second half) mating season mean f T levels in the focal males.

Focal males were significantly more aggressive during the mating season compared with the post-mating period (paired t-test, $t = 3.24$, $P = 0.01$, $df = 12$ Fig. 3), and they engaged in significantly higher rates of aggression in the early versus late mating periods ($t = 2.38$, $P = 0.03$, $df = 12$).

Number of males in a group, agonism, and f T levels

The males in Green group, the group with the highest number of males ($N = 6$), exhibited significantly higher rates of aggression during the breeding season than did males in the other two groups (Kruskal–Wallis test, $P = 0.04$, $df = 2$), but there was no between-group difference in mean f T levels (Kruskal–Wallis test, $P = 0.53$, $df = 2$, Fig. 4).

Rank and f T levels

When examining mean f T levels over the entire mating season, the males that were top-ranking before the mating season began in two of the three groups (Green and Lavender), exhibited significantly higher f T levels compared to the other males in their respective groups (comparison of single sample against the mean t-test [Sokal & Rohlf, 1995] Male 'D' in Green group $t = 2.7$, $df = 5$, $P < 0.05$; Male 'C' in Lavender group, $t = 4.45$, $df = 2$, $P < 0.05$) Fig. 4. However, in Red group, it was the third-ranking male who exhibited the highest mean f T level, not just in his group, but for the entire sample. The top-ranking males did not, however, exhibit higher rates of intermale agonism during the mating season (Fig. 4).

Age and f T

Age of the male affected f T excretion as well as rate of agonism during the mating season, as the three young males in the sample (natal or having dispersed for the first time) exhibited both significantly lower f T levels and lower rates of male–male agonism during mating season compared with the older males (f T-Mann–Whitney U-test, $P = 0.018$, agonism Mann–Whitney $U = -$test,
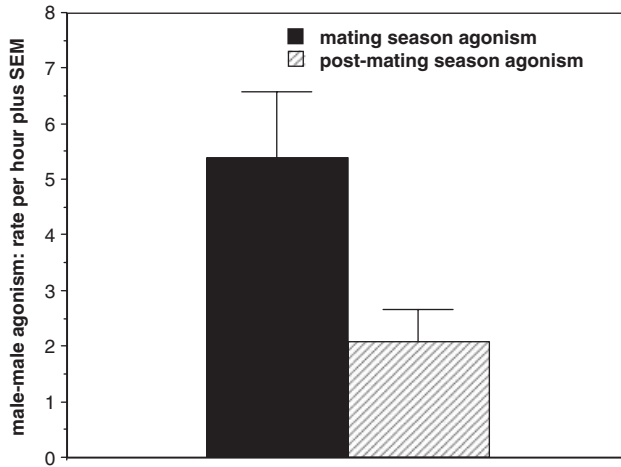
Fig. 3. Comparison of mean hourly rate of male–male agonism in the mating versus post-mating periods in the focal males.

$P = 0.042$, Fig. 4). No difference was found for either variable in the post-mating period (fT, $P = 0.31$ and intermale agonism $P = 0.09$). As we were not able to observe every instance of mating/female receptivity throughout the mating season, we do not know if the two young non-natal males mated in their respective groups or if any of the three mated as extra-group males.

DISCUSSION

L. catta is a species that fits the predictions of the challenge hypothesis well in both captivity [Cavigelli & Pereira, 2000] and in the wild. In this study, both aggression between males and fT levels are much higher in the brief mating season compared with the immediate post-mating period. The males in our sample also follow Wingfield et al. [1990] argument that in seasonally breeding animals, a peak in testosterone should occur during the onset of mating season, when male–male competition is high, as we found both higher fT levels and higher rates of male–male aggression in the first half of the mating period. This 'high testosterone/high agonism' pattern in the mating season is also seen in Japanese macaques [Barrett et al., 2002], but seems to be variable in lemurs, as Ostner et al. [2002] found higher fT and agonism during mating season in some but not all red-fronted lemur groups studied at Kirindy reserve in western Madagascar, and Brockman et al. [1998] reported fT levels peaking 1 month before the onset of mating season in Verreaux's sifaka at Beza Mahafaly Reserve, and remaining high for 3 months. In Brockman et al.'s sample, however, intermale aggression was observed primarily during the 3-week mating period.

Number of Males in Group, fT and Agonism

Ring-tailed lemur females exhibit very short receptive periods, ranging from a just few hours to 24 hr [Jolly, 1966; Sauther, 1991; van Horn & Resko, 1977] and the entire mating season occurs in a 3–4 week period. Because the mating period in *L. catta* is so brief each year, male–male competition for access to receptive females in very high, but only for the duration of the mating season [Budnitz & Dainis, 1975; Gould et al., 2005; Jolly, 1966; Koyama, 1988; Sauther, 1991]. In this study, intermale aggression declined markedly and immediately once mating
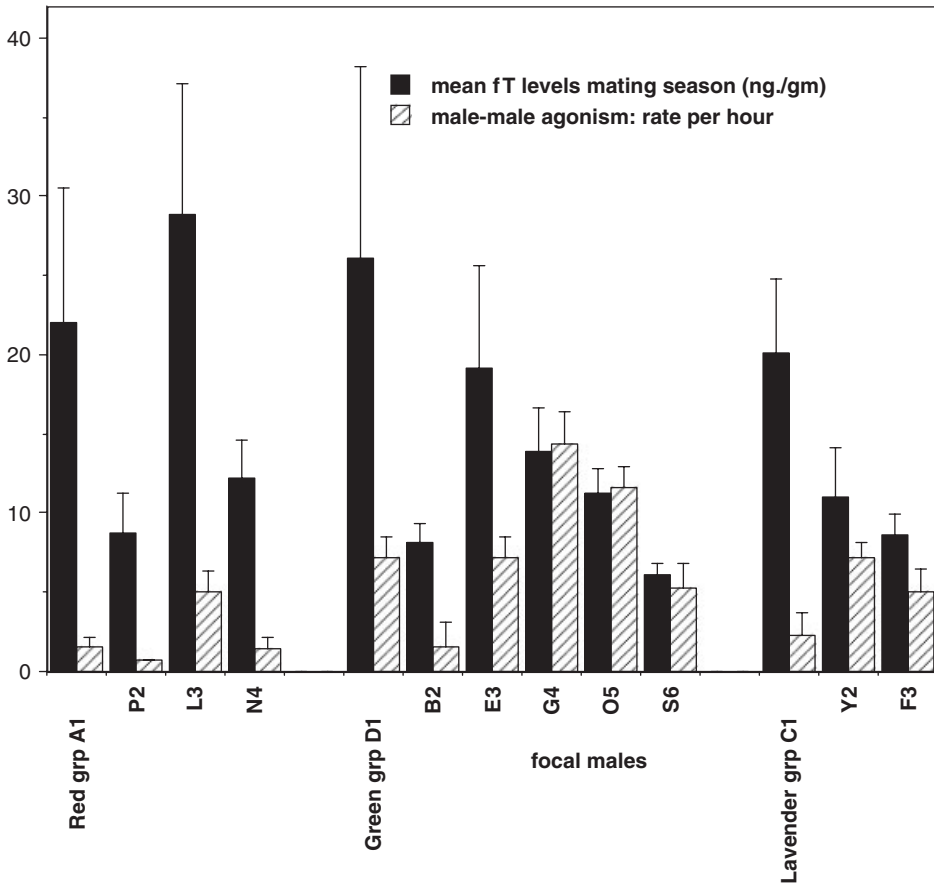
Fig. 4. Mean f T and hourly rate of male–male agonism for each focal male, by group, during the mating season of 2003. Males are presented of within-group dominance rank before the mating season, e.g. males A1, D1, and C1 were the top-ranking males in their respective groups before the mating season. The male dominance hierarchy remained consistent once the mating period had ended. Males P2 and F3 were young non-natal males, and male S6 was a natal male.

season had ended. Therefore, it stands to reason that the group with more males (Green group which contained six males, as compared to three and four males in the other two groups) would exhibit higher rates of agonism, as male-mating competition would be greater in a group containing more males, yet the mean f T levels of the males in Green group were not higher than in the other groups. Potentially, there may be an upper limit that is reached in f T levels for all males in a population [sensu Wingfield et al., 1990], wherein f T rises above the baseline breeding level regardless of number of males in a group, or, conversely, inter-group differences in mean f T may only be evident if comparing very large groups containing many males with much smaller groups with far fewer males, and the difference between numbers of males in our focal groups may not be great enough for marked differences in f T to be evident.

Inter and Intra-Individual Variation in f T During Mating Season

Cavigelli and Pereira [2000] found marked individual variation in male f T excretion 2 days before a female's receptivity, the actual day of receptivity and the

following day. In our sample of males, marked intra-individual variation in fT existed throughout the entire mating period, likely because in this species, females in a group become receptive at different times over the 3–4 week mating period, and no two females are receptive on the same day [Sauther, 1991]. Furthermore, extra group males (from other, usually adjacent groups) often appear with a group on the day of a female's receptivity and engage in both inter-male agonism and copulations with the estrous female [Gould, 1994; Sauther, 1991]. Therefore, although we see an overall increase in both rates of agonism and fT levels between mating and post-mating periods, variation on individual days of female receptivity may be a stronger predictor of T excretion than inter-male agonism, although it is clear that the three variables are strongly related. We were not able to observe days of receptivity for all females in the three groups, however, therefore it was not possible in this study to determine if a pattern occurred with respect to days of female receptivity and fT levels in males.

Rank and fT

In *L. catta*, the male dominance hierarchy in a group can break down during the mating period, and subordinate males can sometimes dominate higher-ranked males at this time [Budnitz & Dainis, 1975; Gould, 1994; Jolly, 1966; Sauther, 1991; Sussman, 1991]. However, the highest or high-ranking males in the pre-mating season hierarchy are often the first to mate with a receptive female in their group, and such males have also been observed sequestering a female and 'mate-guarding' just before, during, and after her receptive period [Gould, 1994; Parga, 2003; Sauther, 1991]. In our study, the male dominance hierarchy that existed before mating season resumed without change afterwards, even though during periods of actual female receptivity, lower-ranking males challenged higher-ranking ones for access to the receptive female. Although lower-ranking males have been observed monitoring females or attempting to mate-guard [L. Gould, personal obsservation, Sauther, 1991] the highest-ranked male tends to be either the only one to mate-guard in a group, or he is able to sequester a female for a longer period of time than other males in the group [L. Gould personal observation, Parga, 2003; Sauther, 1991]. Such behavior by high-ranking males may be a result of, or enhanced by, an increased fT level throughout the breeding period, as two of the three highest-ranking males in the groups did exhibit higher fT levels during this time. A relationship between high rank and high fT levels in the breeding season has also been found in Verreaux's sifaka [Brockman et al., 1998; Kraus et al., 1999], but not in red-fronted lemur groups studied by Ostner et al. [2002]. However, in the sifaka, the fT levels of the dominant males remained high outside of the mating season, whereas in our study, fT levels of all males dropped sharply once mating activity ceased.

Age, fT and Mating in Young Adult Males

As might be expected, the three younger males in the sample (two natal males and one 4-year-old, who had immigrated into an adjacent group the previous dispersal season), exhibited significantly lower fT levels that the older males in the sample during the mating season. A similar trend in multimale species has been noted in young bonobo males [Marshall & Hohmann, 2005]; subadult Verreaux's sifaka [Brockman et al., 1998]; and subadult wedge-capped capuchins [Lynch et al., 2002]. In our study, natal and young immigrant males were occasionally observed engaging in stink-fights during the mating season, but these individuals were not observed actually mating. Sauther [1991] reports

a similar pattern from a previous study at Beza Mahafaly wherein agonistic behavior (chasing extra-group males) exhibited by young natal males during mating season was not accompanied by mating. However, as it was impossible to monitor every instance of both mating and female receptivity in all three groups during the mating season, and since copulations do occur at night in this species [Pereira & Weiss, 1991; Sauther, 1991], we do not know if the youngest males, including the natal male, mated, either within their groups (in the case of the young non-natal males), or as extra-group males in the case of all three. *L. catta* males usually disperse for the first time between 3 and 5 years of age [Sussman, 1992]. In the wild, it seems likely that an increase in f T levels begins between the second and third year of life, and may be accompanied by the onset of male mating agonism.

Avoiding the Cost of Maintaining High f T Levels

Fecal testosterone levels dropped dramatically and quickly once the mating season had ended. Wingfield et al. [2001] note that maintaining prolonged high levels of circulating testosterone is costly, and can result in increased risk of injury, loss of fat stores, compromised immune system function and even an increase in oncogenic effects, all of which can potentially have a serious effect on lifetime fitness. If maintaining high levels of f T and aggression during mating season are important aspects of male mating success in *L. catta*, then a fall to baseline non-breeding f T levels and a marked decrease in inter-male aggression once females are no longer receptive could function as an important physiological pattern which has evolved to offset the cost of high testosterone production and potential loss of fitness during the brief mating period. Furthermore, mean levels of fecal glucocorticoid, an adrenal hormone associated with physiological stress, were not significantly higher in the focal males during the mating season compared to post-mating [Gould et al., 2005], and individual glucocorticoid levels varied dramatically from one day to the next during the mating period. Thus, adjusting glucocorticoid levels during and markedly decreasing f T levels immediately after mating season may be of great importance in the maintenance of male health in this species. This pattern could be of particular importance in *L. catta* because mating season occurs at or shortly before the onset of the dry season, when food resources become increasingly scarce in south and southwestern Madagascar, the geographical range of this species [Sauther, 1992, 1993; Sauther et al., 1999]. In Verreaux's sifaka at the same site, mating season occurs for a 3–4 week period between January and March, depending upon the group [Brockman et al., 1998]. Mid-to-late rainy season also occurs during these months, therefore Verreaux's sifaka are not as affected by marked changes in seasonal food resource availability just after the mating period as are sympatric ring-tailed lemurs.

Directions for Future Research with Strict Seasonally Breeding Primates

With its emphasis on increasing testosterone levels in relation to male mate competition during seasonal breeding periods, the predictions of Wingfield et al. [1990] challenge hypothesis should theoretically fit well with seasonally reproducing, polygynous primates. However, it is clear from the studies conducted thus far on primate species that experience discrete reproductive seasonality, that patterns of testosterone excretion in relation to mating are variable, and so are the behavioral responses observed during these short

breeding periods [Brockman et al., 1998, 2001; Kraus et al., 1999; Lynch et al., 2002; Ostner et al., 2002 and this paper]. Brockman et al. [1998, 2001] and Kraus et al. [1999] note that male fT levels in Verreaux's sifaka do not decrease immediately after mating season, and in both Verreaux's sifaka and red-fronted lemurs, there is a relationship between high levels of male fT and male dispersal during the birth season [Brockman et al., 1998, 2001; Ostner et al., 2002]. The onset of male dispersal in *L. catta* correlates with the birth season, can continue for 5 or 6 months [Gould, 1994, 2006; Jones, 1983; Sussman, 1992], and is accompanied by high rates of agonistic behavior between resident and dispersing males [Gould, 1994, 2006; Jones, 1983]. In fact during a year-long study of males at Beza Mahafaly [Gould, 1994, 1996, 1997], rates of inter-male agonism were as high during the migration period as they were in the mating season (L. Gould, unpublished data). Data on male fT levels over the course of the migration period are needed to determine whether male *L. catta* follow the increased fT patterns seen in Verreaux's sifaka and red-fronted lemurs during male dispersal. If so, the period between mating and dispersal (June to end of September at Beza Mahafaly) with accompanying low rates of male agonism and fT levels may be a physiological recovery period for *L. catta* males between the demands of mating (and male mate competition) and migration.

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