RESEARCH ARTICLE

Effects of Reproductive and Social Variables on Fecal Glucocorticoid Levels in a Sample of Adult Male Ring-Tailed Lemurs (*Lemur catta*) at the Beza Mahafaly Reserve, Madagascar

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Glucocorticoids, a group of adrenal hormones, are secreted in response to stress. In male primates, variables such as breeding seasonality, dominance hierarchy stability, and aggressive and affiliative interactions can affect glucocorticoid levels. In this study, we examined interindividual differences in mean fecal glucocorticoid (fGC) levels among males in three groups of wild ring-tailed lemurs to better understand the physiological costs of group living for males in a female-dominant species that exhibits strict reproductive seasonality. Fecal and behavioral data samples were collected during one mating and two postmating seasons (2001 and 2003). The mean fGC levels were examined in relation to reproductive season, male rank, number of resident males, intermale and female–male agonism, and affiliative behavior with females. The mean fGC levels were not significantly elevated during mating season compared to the postmating period. During the mating season, male dominance hierarchies broke down and rank effects could not be tested; however, there was no relationship between male rank and fGC levels in the postmating periods. In 2001, males that resided in the group with the fewest males exhibited lower fGC levels during the postmating period. They also affiliated more with females than did males in the other groups. During the mating season of 2003, males engaged in more affiliative behaviors with females compared to the postmating season, but female–male agonism did not differ by season. However, rates of intermale agonism were significantly higher during mating compared to postmating periods, but such heightened agonism did not translate to a higher stress response. Thus, neither male–male competition for mates nor heightened

agonism between males during the breeding season affected male fGC levels. Fewer males residing in a group, however, did have some effect on male–female affiliation and male fGC levels outside of the mating period. Males that live in a group with only a few (two or three) males may experience less physiological stress than those that live in groups with more males. Am. J. Primatol. 67:5–23, 2005.   © 2005 Wiley-Liss, Inc.

Key words: fecal glucocorticoids; ring-tailed lemurs; males; reproductive seasonality; stress response

INTRODUCTION

In mammals, the stress response involves the release of adrenal glucocorticoids [Abbott et al., 2003; Balm, 1999]. Glucocorticoids function to increase the availability of glucose in the bloodstream and inhibit insulin from promoting glucose uptake and glycogen synthesis, and thus make energy reserves available in times of acute stress [Genuth, 1993; Sapolsky, 1982, 1983, 1992; Muller & Wrangham, 2004]. The stress response helps an individual adapt to an acute stressor, and while this is highly adaptive in the short term, the prolonged release of fecal glucocorticoids (fGCs) can cause numerous very serious negative physiological effects, including immunosuppression [Abbott et al., 2003; Sapolsky, 1992, 2002; Wingfield & Ramenofsky, 1999].

Thanks to refinements of noninvasive techniques for monitoring hormonal/behavioral interactions in wild primates [Whitten et al., 1998] over the past decade, numerous researchers have been able to examine relationships between social and environmental stressors and fGC levels in a number of naturally-occurring primate populations. Variables such as age, rank, dominance hierarchy stability, mating, seasonal reproduction, seasonal resource fluctuation, and feeding competition have been considered in relation to the stress response in several strepsirhine and haplorhine primate species, and we now have much greater insight into hormonal correlates of behavior and the immense variability that exists between taxa (see references below). In this paper we examine fGC levels in relation to some life-history and behavioral variables in adult male ring-tailed lemurs (*Lemur catta*) over one mating and two postmating seasons at the Beza Mahafaly Reserve, southwestern Madagascar.

In some seasonally breeding primates, corticoid levels and male mating behavior have been investigated in species that experience both short- and longer-term mating seasons. Prebreeding season elevations in cortisol levels have been noted in male squirrel monkeys and rhesus macaques [Bercovitch, 1992; Schiml et al., 1996], and elevated male cortisol levels have been associated with consortships in male Japanese macaques and tufted capuchins [Barrett et al., 2002; Lynch et al., 2002]. In muriquis, Strier et al. [1999, 2003] found that fGC levels were significantly higher in adult males after they completed their first copulation, and high levels were sustained just after they reached their peak in sexual activity.

In nonbreeding contexts, patterns of male glucocorticoid excretion vary across taxa in relation to rank, stability of the male dominance hierarchy, age, and seasonal access to food resources. In early studies of the stress response in rodents and primates, it was assumed that low rank correlated with high stress levels and accompanying high corticoid concentrations [Bronson & Eleftheriou, 1964; Louch & Higginbotham, 1967; Manogue, 1975; see review by Creel, 2001];

however, recent research across taxa has revealed that low rank and high corticoid levels are not necessarily linked, and in fact great variability exists. For example, while no correlation between these two variables has been found in tufted capuchins [Lynch et al., 2002], mountain gorillas [Robbins & Czekala, 1997], or long-tailed macaques [van Schaik et al., 1991], in other species dominant individuals have exhibited consistently higher corticoid levels compared to lower-ranking conspecifics [reviewed in Abbott et al., 2003].

Sapolsky [1983, 1989] argued that in groups with stable dominance hierarchies, high rank should be less stressful because of the predictability of the situation and the fact that the high-ranking animal has social control. This in turn should lead to overall lower corticoid concentrations. However, in species or groups in which an unstable dominance hierarchy exists, the position of high-ranking individuals could be threatened at any time, and thus corticoid levels in dominant individuals should be higher. In fact, this was found to be the case in wild savannah baboon groups [Sapolsky, 1983, 1989]. Muller and Wrangham [2004] argued that social dominance can result in physiological stress in species in which the dominant animal(s) exhibit high degrees of agonism, because of higher metabolic demands related to greater energy expenditure. Furthermore, they pointed out that increased levels of cortisol in high-ranking males could incur a cost to them in terms of reproductive benefits.

Adult male ring-tailed lemurs experience a number of the above-mentioned social and environmental variables. For example, the short mating season in this species occurs over a 3–4-week period annually, and each female is receptive for only 6–24 hr each year [Jolly, 1966; Sauther, 1991; van Horn & Resko, 1977]. The male dominance hierarchy that exists before the onset of mating breaks down during the mating season [Budnitz & Dainis, 1975; Gould, 1994; Jolly, 1966; Sauther, 1991; Sussman, 1991], and males engage in extreme physical combat over access to these briefly receptive females, often seriously wounding one another [Gould, 1994; Jolly, 1966; Sauther, 1991]. Rates of intermale agonism are higher at this time that at any other time during the annual cycle [Gould, 1994, 1997] (this study). At times, the highest-ranking male in the normal (premating season) male dominance hierarchy is able to sequester an estrous female and mate exclusively with her [Gould, 1994; Sauther, 1991] (Gould, personal observation). At other times, all males in the group (as well as extragroup males) will attempt to mate with a receptive female, sometimes attacking and pushing the mating male off of the female in order to mount.

Outside of the mating season, the male dominance hierarchy can also be unstable, and dyadic dominance relationships can sometimes be nontransitive [Gould, 1994, 1997; Sussman, 1992; Sauther & Gould, 2003; Sauther et al., 1999]; thus the position of highest-ranking male in a group can be precarious at virtually any time of the year.

Adult males also experience feeding and social dominance by adult females, and female–male agonism occurs daily [Gould, 1994, 1996; Jolly, 1966, 1984; Sauther, 1991; Sauther et al., 1999; Sussman, 1991, 1992]. Such agonism can be mild, such as low-level displacements from food resources, or more severe, such as chasing, cuffing, and pushing from trees. True female dominance is rare in mammals, and is suggested to have evolved in ring-tailed lemurs as a female strategy to minimize feeding competition from males in a situation where strict reproductive synchrony (birth and lactation) is tied to highly seasonal food resource availability [Jolly, 1984; Sauther, 1993, 1998].

Higher-ranking (central) males tend to engage in higher rates of social behavior with females than do lower-ranking or new immigrant (peripheral)

males [Gould, 1994, 1996; Sauther, 1992]. Such affiliation results in numerous benefits to males, such as greater predator protection, more grooming partners, greater ectoparasite control, and enhanced opportunity for thermoregulation during the cold season [Gould, 1996, 1997, 1999]; however, increased affiliation with females can also incur a cost to males because more contact time with females can result in higher levels of female–male aggression [Gould, 1996].

The number of resident males in a group can also be important with respect to stress levels. Ridley [1986] noted that in species with short mating seasons, one male cannot monopolize all females, and thus there is no benefit in excluding other males from living in a group. However, fewer males residing in a group may be less costly in terms of male mate competition during the short breeding period, and fewer males may also mean more opportunity to affiliate with females and thus experience the above-mentioned benefits [Gould, 1994, 1996; Sauther & Gould, 2003]. Conversely, smaller-bodied, sexually monomorphic primates (e.g., *Lemur catta*, with a mean weight of 2.2 kg) [Sussman, 1991] are vulnerable to predation [Gould, 1996; Sauther, 1989, 2002]. Therefore, there should be a balance between intergroup male mating competition and the critical number of resident animals needed to provide predator protection.

Considering the above-mentioned variables and conditions experienced by adult male ring-tailed lemurs, we explored the following questions:

1. Given the brevity of the annual mating season (3–4 weeks) and the extreme intermale competition over access to receptive females during this time, are there differences in the mean fGC levels of males between the mating and postmating periods?

2. Are there rank-related differences in mean fGC levels in adult males, and do the higher-ranking "central males" that affiliate more with adult females exhibit lower fGC levels than males on the periphery of the group?

3. Since fewer males in a group means less mating competition, less intermale feeding competition, and possibly more opportunities to affiliate with females, which can lead to a number of benefits (mentioned above), does the number of males in a group have any relation to the mean fGC levels?

4. Is there any relationship between the number of resident males in a group, affiliation rates with females both during and after the mating period, and female–male agonism in either period?

To answer these questions, we measured fGC levels in dried fecal samples collected from wild adult male *Lemur catta* in Madagascar. Cavigelli [1999] compared *Lemur catta* individual fGC measures to serum cortisol levels, and found that fecal and serum levels were significantly correlated. This supports the validity of extracting fGCs as a method for assessing physiological stress in this species. To answer the affiliative/agonistic behavior questions, we compared rates of affiliative behavior between males and females, and rates of female–male agonism during and after the mating season.

MATERIALS AND METHODS

Study Animals and Research Site

All adult males in three groups of ring-tailed lemurs that resided within the Beza Mahafaly Reserve were studied in June–July of 2001 (postmating season) and late April–June 2003 (mating and postmating). Mating season in 2003 occurred from 1–20 May. There were nine to 11 groups of *Lemur catta* living in the reserve [Gould et al., 2003; Sussman, 1991]. Beza Mahafaly Special Reserve is situated in southwestern Madagascar, 23° 30′ S. latitude and 44′ E. longitude.

TABLE I. Adult Group Composition in 2001 and 2003

Group	Adult males	Adult females
2001		
Red group	5	4
Green group	4	5
Lavender group	3	4
2003		
Red group	4	4
Green group	6	6
Lavender group	4 (though one male was absent much of the mating season)	4

TABLE II. Focal Male ID, Rank, and Age Class for 2001 Season

Male ID	Rank	Age-class
Red group		
r	1 (but subordinate to D)	Young prime
w	2	Young prime
x	3	Prime-old prime
e	4	Old
d	5 (but dominant to R)	Old
Green group		
g	1	Young prime
l	2	Young prime
y	3	Prime
f	4	Young natal male
Lavender group		
m	1	Unknown (unable to capture)
n	2	Young natal male
o	3	Prime

Parcel 1 of this reserve, where the study was conducted, consists of 80 ha of mixed vegetation: riverine forest in the eastern part of the reserve, near the Sakamena River, and more xerophytic forest toward the western boundary [Sussman & Rakotozafy, 1994]. The three study groups' home ranges were located in the eastern riverine forest part of the reserve. In 2001 there were 12 focal males, and in 2003 there were 14 males.

The adult group compositions for the two field seasons are presented in Table I. In Tables II and III the males' ID and their rank and age for each field season are presented.

None of the five males residing in Red group in 2001 were still members of the same group in 2003. Only one, an old male, remained in the reserve population, and he was found in Green group. Of the four Green group males in 2001, one was still living in the group in 2003, and one, a natal male, had immigrated to Lavender group by 2003. Of the three males found in Lavender group in 2001, one had immigrated to Green group; one, a natal male, had immigrated to another group within the reserve boundaries; and the third was not seen. The remainder of the 2003 males had immigrated into these groups from groups either within or outside the reserve.

TABLE III. Focal Male ID, Rank, and Age Class for 2003 Season (Mating and Post-mating)*

Male ID	Rank	Age-class
Red group		
a	1	Young prime
p	2	Young
l	3	Prime
n	4	Unknown (unable to capture)
Green group		
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)
y	3	Prime
f	4	Young

*Because intermale dominance hierarchy often breaks down during mating season, pre-mating ranks were used. These ranks were resumed after mating season had ended.

All males were fitted with collars and identification tags before data collection began. The focal males were immobilized by means of a Telinject blowpipe and tranquilized with .25–.30 cc. of Tiletamine (Telazol). While the animals were immobilized, a dental examination was conducted, and the relative age class of each focal male was determined according to a set of dental-wear criteria developed by Sauther et al. [2002]. The age classes used in this study were ''young adult,'' ''prime-aged,'' and ''old.''

The characteristics of *Lemur catta*, which have been discussed elsewhere [Jolly, 1966; 1984; Sauther et al., 1999; Sussman, 1977] and are important factors in the present study include female philopatry, marked female dominance in all feeding and social contexts, a short and discrete mating period of 3–4 weeks, and severe male–male competition over access to females during the mating period.

Behavioral Data

In the immediate postmating period of 2001 (beginning of June to mid-July), 349 continuous-time, focal-animal sessions [Altmann, 1974] of 15-min duration were conducted on all males (n=12) that resided in three *Lemur catta* groups in the eastern part of the reserve by L.G. and one research assistant. A total of 21–37 sessions were conducted for each focal animal (mean=29 sessions), and 530 sessions of the same duration were conducted in 2003 by L.G. and two assistants: 279 during the mating season (May 1–20) and 251 during postmating period (late May through early July). During the mating season 17 to 24 focal sessions were conducted for each focal male (mean=21 sessions), and during the postmating season 12 to 32 sessions (mean=18) were conducted. Focal males were individually identified by their plastic identification tag. Interobserver reliability in the behavioral data collection was >95%.

All behaviors and interactions with all conspecifics were recorded, and the start time of each behavior was noted during the focal-animal session. A male's rank in the intermale dominance hierarchy in his group was assessed by the direction of aggressive and submissive gestures, including both severe aggression (e.g., chasing, cuffing and tail waves/stink fights) and milder agonism (e.g., displacements and direction of submissive chattering). During the mating season, the male dominance hierarchy actually breaks down and lower-ranking males can dominant higher-ranking ones, so in this species one cannot actually test stable rank and fGC levels during the brief breeding period. Therefore, we used premating ranks.

Matings were recorded whenever possible; however, ring-tailed lemurs often mate at night, and we were only able to observe five of the 14 adult females in the groups mating.

For each focal male, we divided the total observed number of affiliative interactions with females and the total observed number of agonistic interactions with other males in each season (mating/postmating) by the number of focal-animal sessions conducted on him during those seasons to obtain a rate per session of affiliative behaviors with adult females and agonistic behaviors with other males.

Fecal Sample Collection and Analysis

A total of 10 to 12 fecal samples were collected from each focal male during each research season. During the 2003 mating season, five or six fecal samples were collected from 13 of the 14 focal males over the 3-week breeding period. For one male in Lavender group ("m"), only two fecal samples were collected during the mating season, as he had temporarily transferred to another group for most of the mating period and only returned to Lavender group at the end of the mating season. Therefore, he was not included in the mating-season analyses. During the postmating season, five or six fecal samples were collected for all 14 focal males.

Fecal samples were collected from focal animals primarily early in the morning, when the animals descended from the high canopy, or immediately after the midday rest period (only 19% were collected in the afternoon). No difference was found between fGC levels collected in the morning or afternoon (t-test, $P=0.58$). Within 3 hr of collection, the samples were placed in aluminum foil, flattened, and dried in a Coleman camp oven at 55–70°C (solar and tea candle heat) for 15 min to half an hour, depending on the amount of sunlight and ambient temperature, until they were thoroughly dried. The dried samples were then ground to a fine powder, packaged in an aluminum foil packet, and double zip-locked, following the protocol described in Whitten et al. [1998] and Brockman and Whitten [1996] for white sifakas at the same research site. This preparation method yields interpretable steroid profiles for 3 or more years [Whitten et al., 1998]. Once the samples were returned from the field, they were sent to the Wisconsin Primate Center for enzyme immunoassay analysis. The mean fGC levels (expressed as ng/gm of dried feces) were calculated for each focal male.

In the laboratory, the dried, mixed fecal samples were weighed (0.05–0.25 g, depending on the available amount) and extracted with 2.5 ml distilled water and 2.5 ml of ethanol according to the methods reported in Strier and Ziegler [1997]. The extracted samples were dried and resuspended in 1 ml 30% methanol for solid phase extraction. This additional extraction was used to further clean the sample, which is necessary to obtain parallelism and accuracy for this species. Solid phase extraction was performed with the use of 60 mg/3 ml polymeric

sorbent (Strata-X; Phenomenex, Torrance, CA). The procedure followed the recommended technique enclosed with the column, except that we used a 20% methanol wash to further purify the steroids. The samples were eluted in 1 ml of methanol, dried, and resuspended in the same volume of ethanol. The fGC values were determined by enzyme immunoassay (EIA) [Ziegler et al., 1995]. The samples were diluted by 25–50 and then added to the assay in 100-μl amounts. The assay was validated by parallelism and accuracy. No difference was found in the slope of serially diluted pooled *Lemur catta* fecal samples and standards over the range of the curve (t=1.16, P>0.05, df=32, n=9). We determined the accuracy of the assay by adding a standard amount of lemur fecal pool to each standard curve point (3–1,000 pg). The mean percentage of observed vs. expected concentration was 125.02% + 3.92%. The intra- and interassay coefficients of variation for the *Lemur catta* fecal pool were respectively 2.5 and 17.4 for the low pool, and 2.7 and 14.8 for the high pool.

Data Analysis

When all focal males were compared together (n=13) in the 2003 sample to determine whether differences occurred in fGC levels, male–female affiliation, and intermale agonism between mating and nonmating periods, paired t-tests were used. When between-group differences were being tested, non-parametric analyses of variance (ANOVAs) were used, because the sample sizes (n=3–6) of each group were too small to satisfy the assumptions of parametric statistical tests.

RESULTS

fGCs and Mating vs. Postmating Periods, 2003

No significant difference was found in mean fGC levels between mating and postmating periods for all males in the sample in 2003 (paired t-test, P=0.62, df=12; Fig. 1).

Number of Males in Group

In 2003, the number of males in the group during the mating season (Lavender group, n=3; Red group, n=4; Green group, n=6) did not appear to influence the mean fGC levels (Kruskall-Wallis one-way ANOVA, P=0.83, df=2; Fig. 2), nor was there a difference during the postmating period, when male "m," who had been absent for much of the mating season, returned to Lavender group, increasing the number of males to 4 (Kruskall-Wallis one-way ANOVA, P=0.77, df=2) in 2003 (Fig. 3).

However, when the males in the three groups in 2001 (postmating period) were compared, there was a difference (Kruskall-Wallis one-way ANOVA, P=0.029, df=2; Fig. 4). More specifically, males residing in the group with the largest number of males (Red group, n=5) exhibited significantly higher mean fGC levels than males living in Lavender, the group with the just three males (Mann-Whitney U-test, U=0, P=0.025) and higher levels compared to the four males in Green group (Mann-Whitney, U=3, P=0.08). There was no difference in mean fGC levels when Green and Lavender group males were compared (Mann-Whitney, U=2, P=0.15).
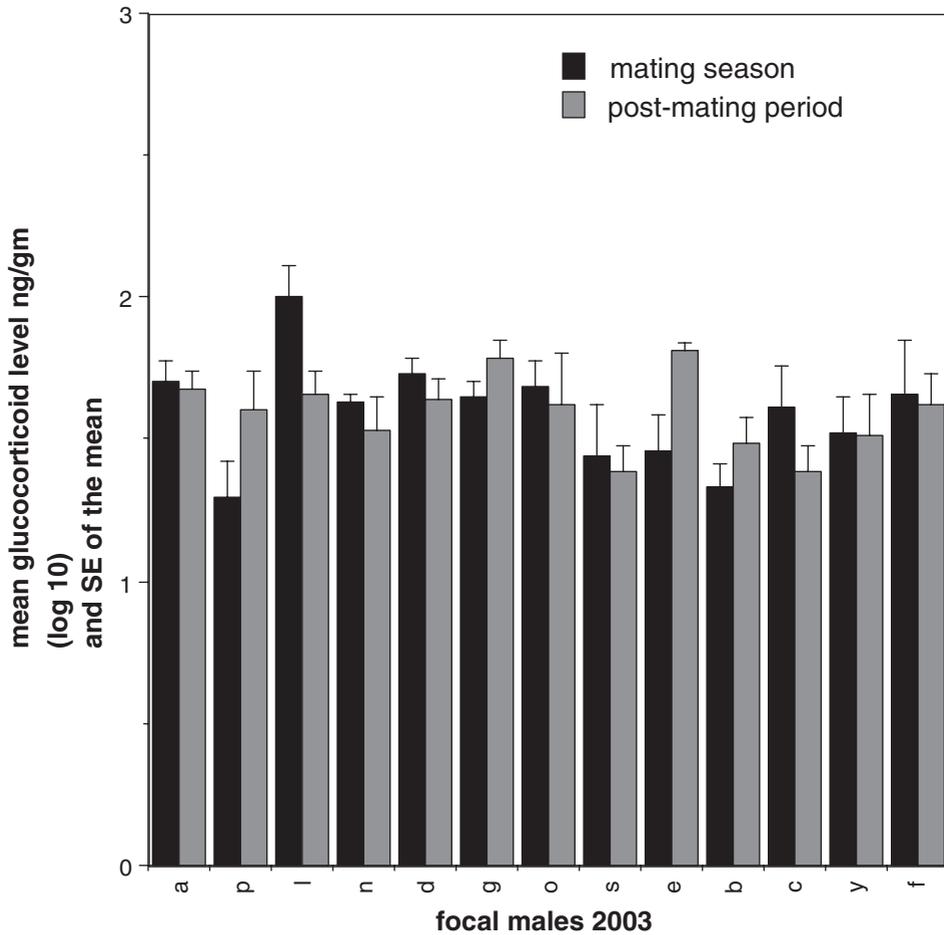
Fig. 1. Comparison of mean fGC levels of focal males in the mating and postmating periods of 2003. The fGC levels are expressed as nanogram per gram of dried feces, and log-transformed values.

Male Dominance Rank

In both years of the study, no difference was found in mean fGC levels and male rank when the top-ranking males of each group (n=3) were compared with all other males in the groups (Mann-Whitney U-test, $P=0.92$ in 2001; $P=0.75$ in 2003; Figs. 3 and 4).

Affiliation and Agonism

In 2001 the three males in Lavender group engaged in affiliative behavior with females more frequently than did males in the other two groups (Kruskall-Wallis one-way ANOVA $P=0.05$, df=2; Fig. 5), and their fGC levels were, on the whole, lower (Fig. 6). There was no significant difference between the groups in terms of the frequency of agonism exhibited by females toward males (Kruskall-Wallis one-way ANOVA $P=0.47$, df=2). The greatest variability in
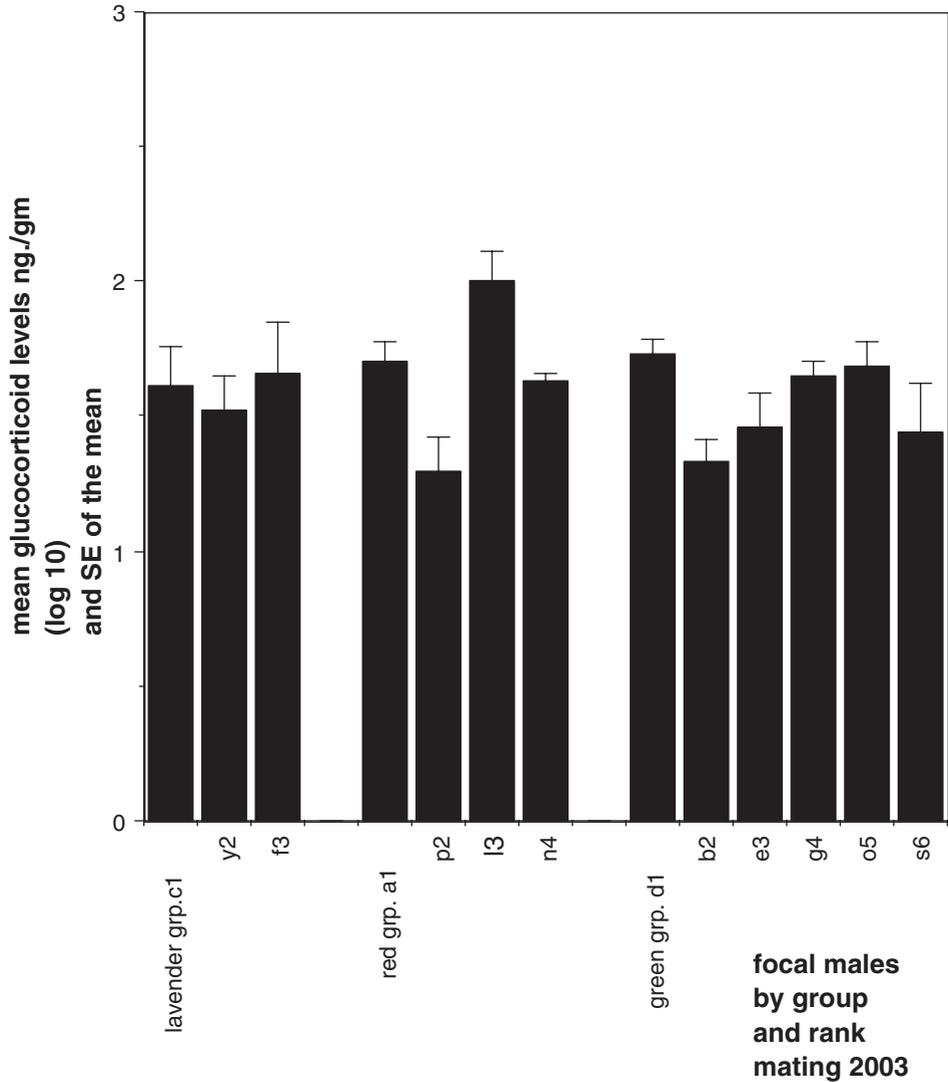
Fig. 2. Focal males by group, rank (X-axis), and mean fGC levels (Y-axis) during the mating season for the three focal groups studied in 2003. Males are organized by highest-ranking male on the left-hand side of each group, followed by other males in their rank order. Since male dominance hierarchy breaks down during the mating season, immediate pre- and postmating ranks are used.

female–male agonism was found in Red group, the group with the highest number of males (n=5).

In 2003 males engaged in significantly more affiliative behavior with females during the mating season compared to the postmating season (paired t-test, $P=0.04$, df=12; Fig. 6), but there was no significant difference in female–male agonism between the mating and postmating periods (paired t-test, $P=0.10$, df=12). Furthermore, there was no relationship between female–male agonism and the number of males in a group in either period (Kruskall-Wallis one-way ANOVA, $P=0.28$, df=2 for mating season; $P=0.22$ for postmating season).
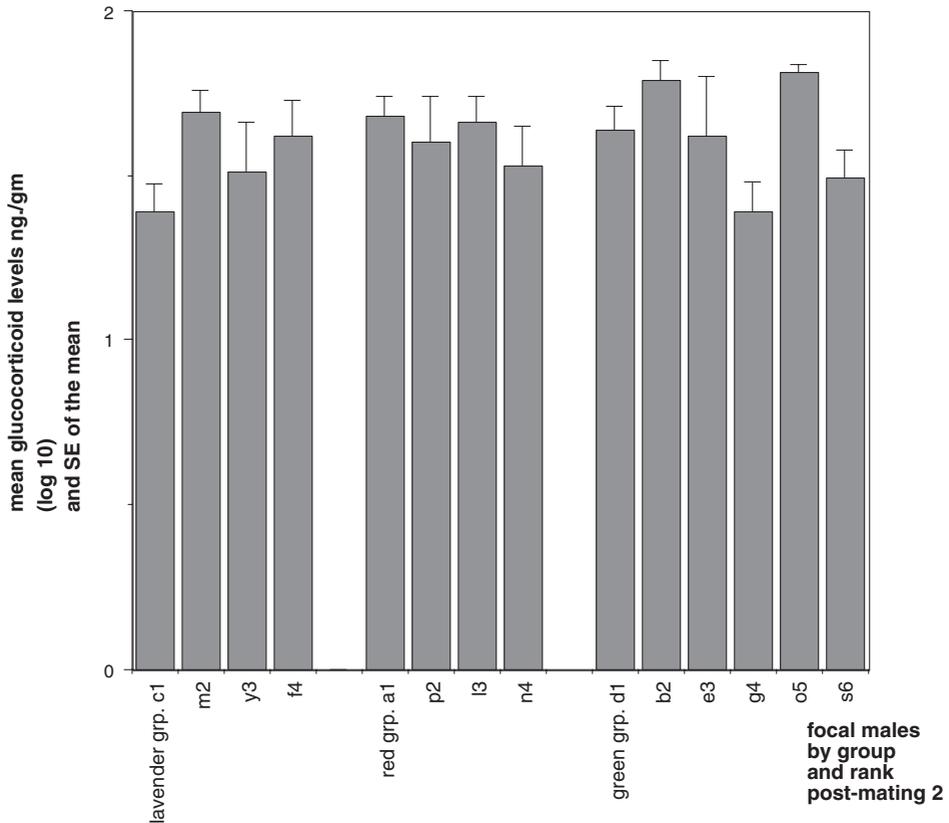
Fig. 3. Focal males by group, rank, and mean fGC levels during the postmating period for the three focal group studied in 2003. Males are organized by highest-ranking male on the left-hand side of each group, followed by other males in their rank order.

There was a significant difference in male–male agonism when the 2003 mating and postmating periods (paired t-test, $P=0.019$, df=12; Fig. 7) were compared, and males living in Green group, the group with the largest number of males, engaged in significantly more agonism with each other during the mating season (Kruskall=Wallis one-way ANOVA, $P=0.04$, df=2). However, no correlation was found between rates of intermale agonism in any group and the mean fGC levels during the mating period (Spearman's rho=$-.02$, $P=0.94$, n=13). Furthermore, there was no difference in the rates of intermale agonism and the number of males in the group during the postmating period (Kruskall-Wallis one-way ANOVA, $P=0.17$, df=2).

DISCUSSION

Reproductive Seasonality and Stress Response in Adult Males

One might expect that the mating season situation in *Lemur catta* would lead to an increase in the stress response for adult males, considering the high degree of male–male agonism, the potential for injury, and the scramble to attain mating success. Yet in this study there was no significant difference in mean fGC levels
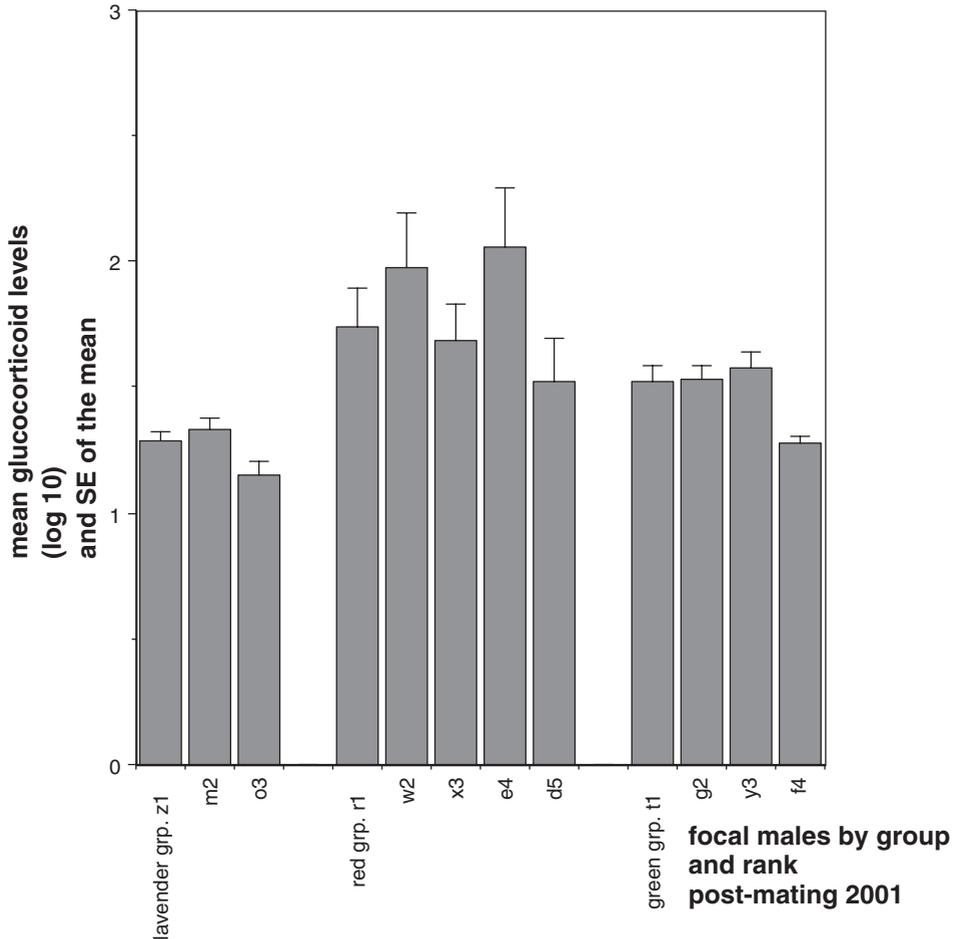
Fig. 4. Focal males by group, rank, and mean fGC levels during the postmating period for the three focal groups studied in 2001.

between the mating and nonmating periods. This may seem puzzling; however, Wingfield and Ramenofsky [1999] argued that the notion of ''reproductive stress'' may be inaccurate because such events occur on a predictable schedule and an organism will be able to make the necessary physiological preparations. They added that although events such as reproduction and migration are energetically demanding, they are not necessarily stressful.

In comparison, Cavigelli [1999], who examined fGC levels in female *Lemur catta* during gestation and lactation seasons at the same site, found that although female fGC levels were higher in late gestation and late dry season (which she attributed to changes in female physiological state associated with imminent lactation and elevated feeding effort when food is most scarce), there was no correlation between female fGC levels and predation threat, food accessibility, or interfemale feeding agonism during the lactation/infant rearing period, a time when one might predict that females would be more stressed. She too suggests that in a situation of regular environmental fluctuation, animals may be able to
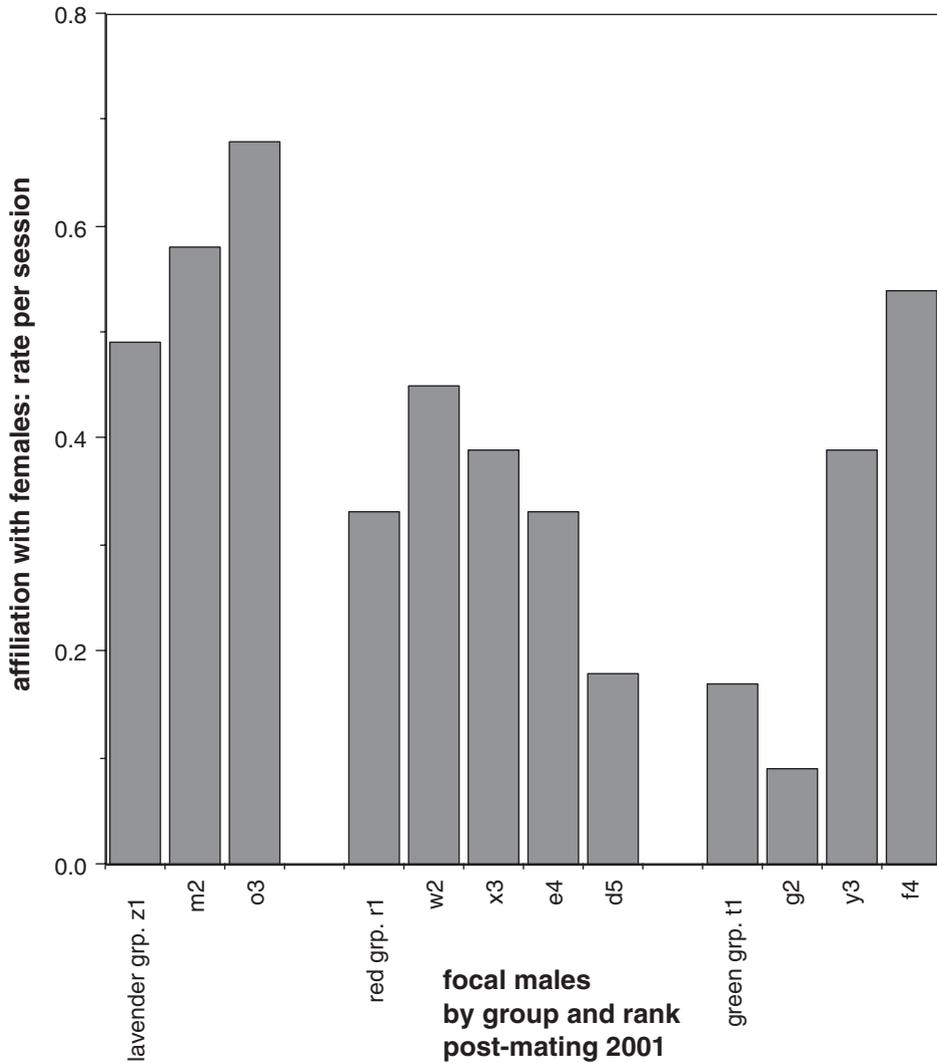
Fig. 5. Male affiative behavior with females during the 2001 field season. Rates per 15-min focal animal session of affiliative behavior between each male and the females in his group are presented. As in Figs. 2–4, males are organized by group and rank on the X-axis.

physiologically prepare for such change. Thus, even though *Lemur catta* of both sexes experience marked environmental and behavioral/reproductive variability throughout the year, since it occurs on a very predictable basis, these fluctuations may not be perceived as stressful events.

However, the number of males residing in a group may, under certain circumstances, be a factor in male stress levels. In 2001, males that resided in the group with the highest number of males (red group) exhibited higher fGC levels than males in the other two study groups. In a group with more males, there can potentially be higher between-male competition for all desirable resources, such as food, water, best resting places, and grooming partners, and such competition
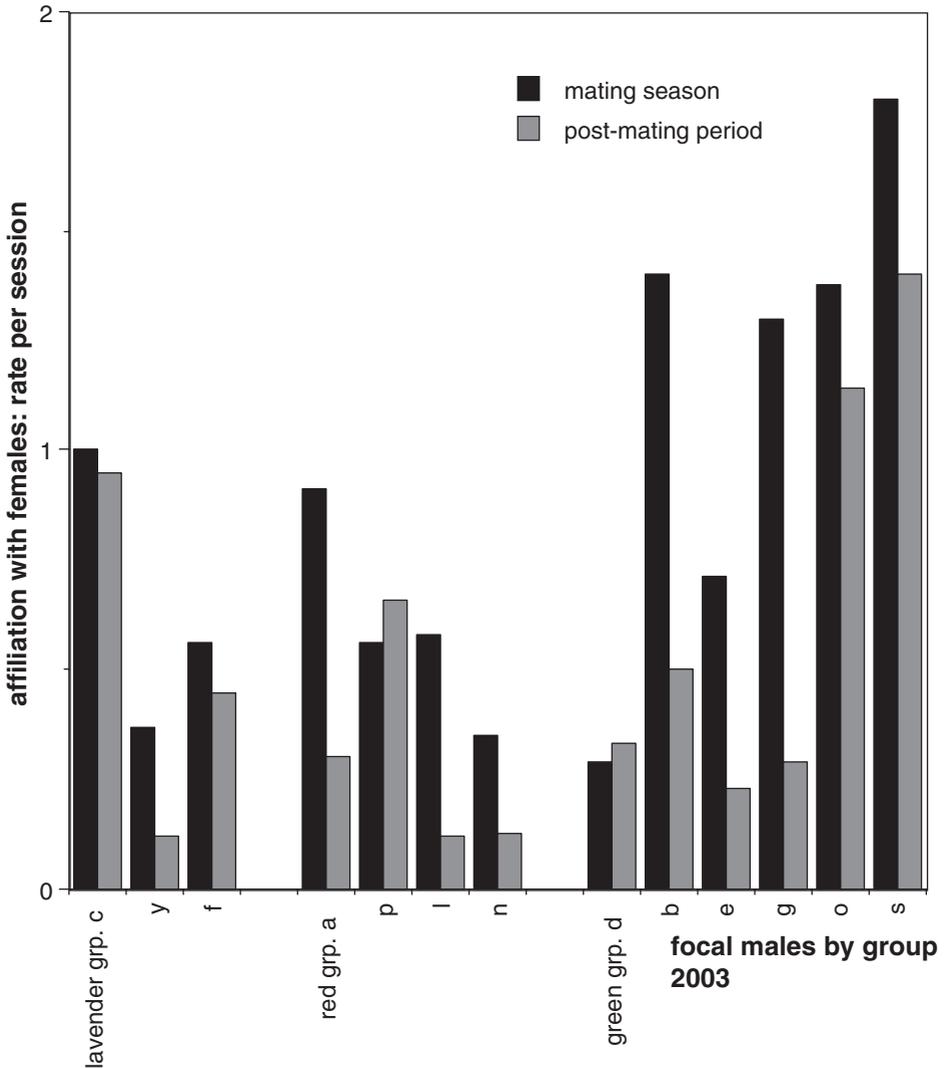
Fig. 6. Comparison of rates (per 15-min focal animal session) of male affiliative behavior with females in mating season vs. the postmating period of 2003. Males are organized by group and rank on the X-axis.

may affect individual stress levels at any time of the year. However, in 2003 the group with the highest number of males did not exhibit higher mean fGC levels in the postmating period, and thus factors such as the actual combination of males in a group and their relationships to each other may result in marked variability from 1 year to the next.

Rank

Dominance hierarchy stability can play an important role in stress levels. Sapolsky [1989, 1992] noted that with unstable hierarchies, dominant animals
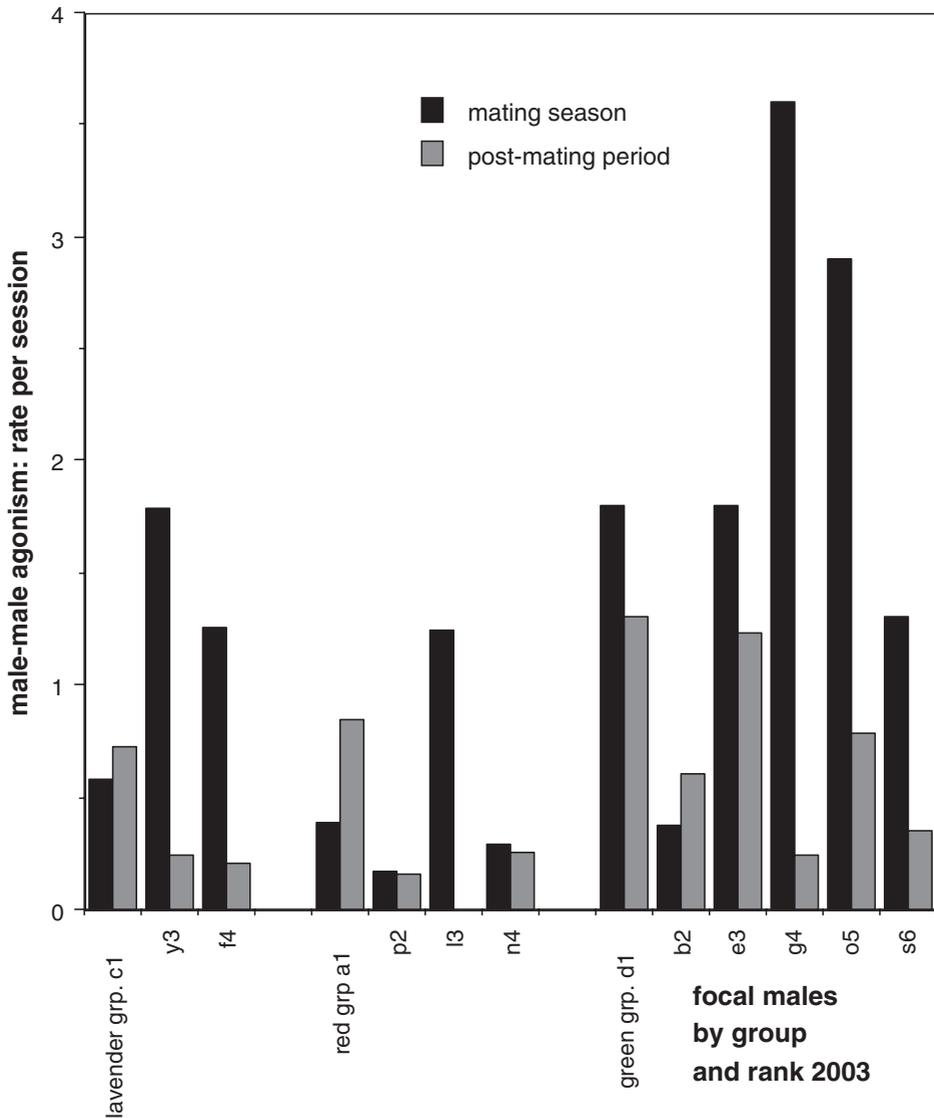
Fig. 7. Comparison of rates (per 15-min focal animal session) of agonistic behavior between each focal male and the other males in his group in the mating and postmating periods of 2003. Males are organized by group and rank on the X-axis.

exhibit a far higher stress response because their capacity for social control is threatened. The male dominance hierarchy in ring-tailed lemurs is often unstable, even outside of the mating season, and both rank reversals and nontransitive dominance relationships between males are common [Budnitz & Dainis, 1975; Gould, 1994, 1997; Taylor, 1986]. In 2001, a nontransitive dominance relationship in Red group, the group with the highest number of males (n=5) was noted between the top- and bottom-ranking males (r1 and d5). The lowest-ranking male (d5) was sometimes able to supplant male r1 and elicit

submissive chatter, yet he was subordinate to the other three males in the group. However, the males that exhibited the highest fGC levels in that group (ranked second and fourth, respectively) did not change rank throughout the course of the study. Nonetheless, the nontransitive dominance relationships in the group may have been a social stressor experienced by all males, which may explain the higher overall fGC levels found among the males in Red group. Furthermore, 2 years later none of these males resided in Red group, so social instability may relate to both higher stress levels and dispersal. In 2003 none of the males in any of the three groups exhibited significantly higher fGC levels in relation to each other in the postmating period.

Affiliation and Aggression: Critical Number of Males

Opportunities for social contact, grooming, and reconciliation have been cited as extremely important variables in understanding interspecific differences between primate species and reactions to acute stressors [Abbott et al., 2003]. Adult male ring-tailed lemurs at Beza Mahafaly form affiliative relationships with both adult females and other adult males outside of the mating season, but these are usually not long term, and a male may have many ''preferred partnerships'' throughout an annual cycle [Gould, 1994, 1996, 1997].

It has been suggested that affiliation with females benefits males in terms of access to the female core of the group, which can lead to enhanced predator protection and greater opportunities for social contact and grooming, and possibly enhanced mating opportunities [Sauther, 1992; Gould, 1994; 1996; Sauther & Gould, 2003]. Living in a group with few males may be even more beneficial, and there may in fact be a critical number of males in a group at which stress levels begin to rise. In 2001, the males residing in the group with only three males had lower fGC levels than males in the other groups, and they also affiliated more with the females in their groups. In 2003, no intergroup differences in mean fGC levels were found, but all groups contained at least four males. Furthermore, in two previous year-long studies at Beza Mahafaly in 1988 and 1992, Sauther and Gould [2003] found that males living in groups with just two males affiliated more frequently with females than males in groups containing more males. Such affiliation may be particularly important during the brief mating season, since Sauther and Gould [2003] noted that females tend to choose resident males first as mating partners. Thus, for a male ring-tailed lemur, living in a group with few males (three or fewer) may be beneficial in terms of lower stress levels, greater potential for mating success, and affiliation with females, and possibly less intermale competition for food resources. In further support of this argument, Pride [2005] reported that at Berenty Reserve, a field site where groups are on average larger than at Beza Mahafaly [Gould et al., 2003; Jolly et al., 2002; Koyama et al., 2002], male fGC levels increased just before and during the mating season as the group size increased. Also at Berenty, most migrating males transfer into groups with fewer males [Jones, 1983], and at Beza Mahafaly there is a greater tendency for males to leave groups with high male/female sex ratios compared to groups with lower ratios [Sussman, 1992].

CONCLUSIONS

In this study, contrary to that which was expected, marked male–male mating competition did not result in a greater stress response for adult male ring-tailed lemurs at Beza Mahafaly Reserve, though the number of males residing in a

group may be a factor in physiological stress. Wingfield and Ramenofsky [1999] noted the important distinction between life-history stages (LHS), such as migration, breeding, and nonbreeding, and emergency life-history stages (ELHS), which are triggered by events such as crowding, limited resources, increased predation pressure, and habitat destruction. However, since some researchers (see Introduction) have found elevated fGC levels in relation to mating in some male primate species, we must recognize that while reproductive behavior may not be considered an ELHS, there is great variability across taxa in terms of male mating competition and the accompanying stress response.

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