Female dominance status and fecal corticoids in a cooperative breeder with low reproductive skew: ring-tailed lemurs (*Lemur catta*)

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Abstract

Many studies have shown that low dominance status within a social group is associated with elevated glucocorticoid hormone production, a common index of physiological stress. However, the reverse may be true among cooperatively breeding female mammals with high reproductive skew; that is, high dominance status is associated with elevated glucocorticoid levels. Elevated glucocorticoid levels in these dominant females may be a product of their being the only breeder within a group or may result from other challenges associated with high status. To test this difference, we studied fecal corticoid levels in cooperative breeding females with low reproductive skew (i.e., where reproduction is not limited to dominant group members): ring-tailed lemurs (*Lemur catta*). We collected behavioral and fecal corticoid data from 39 ring-tailed lemur females from eight groups across three sites. In seven of the eight groups, either one or both of the two most dominant females (ranks 1 and 2) exhibited the highest fecal corticoid levels in the groups. The best predictor of corticoid levels in high-ranking females was the proportion of aggressive agonistic interactions they initiated. For the lower-ranking females the best predictors of elevated corticoid levels were being the recipient of aggressive attacks and being relatively close to one's nearest neighbors. These results differ from many studies of caged male mammals where subordinate individuals often exhibit the highest glucocorticoid levels of a group. Furthermore, the results indicate that reproduction itself is not the primary reason for higher glucocorticoid levels among dominant cooperative-breeding females, but that some other factor must account for these elevated levels.
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The physiological stress response is associated with increased catabolic activity that enables organisms to respond to challenging conditions. Individual differences in physiological stress, specifically glucocorticoid levels, often relate to an individual's dominance status within a social group (e.g., Bronson and Eleftheriou, 1964; Christian and Davis, 1964; Coe et al., 1979; Creel et al., 1997; Saltzman et al., 1994; Sapolsky, 1982). The majority of studies on physiological stress and dominance have been conducted with captive male mammals and most often in these studies it is the subordinate males that maintain the highest glucocorti-

coid levels. These results are usually taken as an indication that low status is a stressful position for group-living animals. However, recent findings from group-living female mammals and with free-ranging populations are beginning to show a different pattern of results, with high-ranking females exhibiting elevated glucocorticoid levels (e.g., African wild dogs and dwarf mongooses: Creel et al., 1996; ring-tailed lemurs: Cavigelli, 1999).

Three recent studies with female mammals have reliably shown dominant females to have higher glucocorticoid levels than subordinates (common marmosets: Saltzman et al., 1994; African wild dogs and dwarf mongooses: Creel et al., 1996, 1997). Several other studies have shown the male-typical pattern in which low-ranking females maintained the highest levels of glucocorticoids (e.g., cynomolgus mon-

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keys: Shively et al., 1997). Still other studies have shown no clear relationship between female dominance status and baseline glucocorticoid levels (e.g., black tufted-ear marmosets: Smith and French, 1997; cynomolgus monkeys: Stavisky et al., 2001). The major difference between the first three studies in which dominant females had higher corticoid levels and the rest is that they were conducted with cooperative breeding species with high reproductive skew where the dominant female is usually the only one to reproduce within the group. It is primarily among these species (cooperative breeders with high reproductive skew) that dominant females are prone to have elevated glucocorticoid levels relative to group mates (reviewed in Creel, 2001). In fact, elevated glucocorticoid levels in these dominant female mammals may result from their being the sole breeders within their group. The energy-intensive processes involved in reproduction activate catabolic processes associated with hypothalamic–pituitary–adrenal (HPA) axis activation (cf. Saltzman et al., 1998). In particular, ovulation, pregnancy, and lactation are all associated with elevated glucocorticoid levels (rabbits: Kriesten and Murawski, 1988; humans: Allolio et al., 1990; Lockwood et al., 1996; black tufted-ear marmosets: Smith and French, 1997; common marmosets: Saltzman et al., 1998; ring-tailed lemurs: Cavigelli, 1999; spotted hyenas: Goymann et al., 2001; cf. humans: Altemus et al., 1995). This raises the question: Are glucocorticoid levels in cooperative breeding dominant females high mainly because the process of reproduction leads to increased adrenal activity, or are there challenges, other than reproduction, inherent to high dominance status in these females?

Because only a handful of studies have examined the relationship between dominance and glucocorticoids in female mammals, the interplay among reproduction, dominance status, and stress hormones is not yet clear (Goymann et al., 2001; Saltzman et al., 1998, 2000). One study conducted with female ring-tailed lemurs, a species classified as a cooperative breeder with low reproductive skew (i.e., reproduction is not limited to dominant females; Gould, 1992; Lewis and Pusey, 1997; Pereira and Izard, 1989), suggests that reproduction alone may not explain high corticoid levels in dominant females. In this study of two groups of ring-tailed lemurs, all females reproduced but the dominant females still had higher fecal corticoid levels than subordinates (Cavigelli, 1999). These results suggest that apart from reproduction, high dominance status in cooperative breeding species may be a position associated with elevated HPA axis activity (cf. Smith and French, 1997).

To disentangle the relationship among dominance status, reproduction, and glucocorticoid levels in female mammals, we collected behavioral and fecal corticoid data from eight groups of ring-tailed lemurs across three different sites: two sites in their natural habitat in Madagascar and a third site in the forest enclosures at the Duke University Primate Center (DUPC). By collecting data from free-ranging animals, we were able to assess the costs, benefits, and challenges nor-mally associated with dominance positions in the natural habitat and avoid confounding by-products associated with rank in confined cage conditions (Creel et al., 1997; Sapolsky, 1993) with restricted escape potential and/or human-imposed social groupings. We measured corticoid levels noninvasively by fecal extraction to avoid altering the animals' normal behavioral patterns and stress physiology. This is particularly important in studying HPA axis function since blood sampling, the traditional method of measuring glucocorticoid levels, can significantly alter HPA axis activity.

To better understand any potential relationship between corticoids and dominance, we also examined the relationship between individual female characteristics and corticoid levels. The goal was to determine if there is a behavior or set of behaviors that relates to dominance status and that is more predictive of HPA axis function than dominance status per se. For example, Sapolsky and colleagues (Ray and Sapolsky, 1992; Sapolsky and Ray, 1989; Virgin and Sapolsky, 1997) have identified several such behavioral tendencies in male olive baboons that are better predictors of basal glucocorticoid levels than dominance status alone (e.g., likelihood of initiating a fight, rate of grooming, and displacement of aggression). Thus, in addition to rank, we compared several individual characteristic (i.e., age, lactational status, fecal weight, and number) and several behavioral traits (i.e., aggression initiated, aggression received, and nearest neighbor distance) to individual corticoid levels to determine if there were specific characteristics associated with elevated corticoid levels both within and among dominance rank positions.

Methods

Study species

Ring-tailed lemurs are diurnal prosimian primates that live in multi-male multi-female groups in which females are philopatric and males disperse. They are highly seasonal breeders that live in arid environments with distinct wet and dry seasons in southern Madagascar (Jolly, 1966; Sussman, 1991). The dry season can last 5–6 months with little or no rain, during which time females gestate and then give birth during a 1- to 3-week window at the transition from the end of the dry season to the beginning of the wet season (Sauther, 1993). They rely on a few key resources during this precarious transition period from dry to wet, from gestation to lactation (Sauther, 1998). Eighty percent of females in a troop breed in any given year and on average 50% of each year's offspring will die within the first year of life (Koyama et al., 2001; Sussman, 1991), and this death rate can be greatly increased during drought years (Gould et al., 1999). These environmental and reproductive parameters suggest these females are living on the edge where competition for food resources among females is important for

Table 1
Comparison of social groups

Study site[a]	Group name	Dates samples collected	Hours of behavioral data	No. of adult females (adult males, subadults)	Mean adult female age (years)	Mean no. of nursing offspring per adult female	Fecal corticoid geometric mean (ng/g)	Group relative aggression[b]	Forest type
Berenty	A1	Sep–Oct '97	64	5 (5, 9)	7.8	0.4	16.3	0.34	Gallery
	A2	Sep–Oct '97	64	5 (3, 3)	7.0	0.6	16.4	0.26	Gallery
	A3	Sep–Oct '97	96	3 (0, 2)	6.3	0.7	22.3	0.54	Gallery
	Naturaliste	Sep–Oct '97	50	6 (7, 7)	5.7	0.5	19.4	0.78	Second growth
Beza Mahafaly	Green	Sep–Oct '95	150	5 (3, 11)	8.0	1.0	11.3	0.30	Riverine gallery
	Yellow Prime	Sep–Oct '95	112	5 (4, 12)	7.0	1.0	24.1	0.67	Xerophytic
DUPC	Lc1	July–Aug '97	32	5 (9, 8)	7.9	1.0	21.7	0.65	Temperate
	Lc2	July–Aug '97	32	5 (6, 5)	8.7	0.4	18.9	0.49	Temperate

[a] Berenty, Berenty Special Reserve, southeastern Madagascar; Beza Mahafaly, Beza Mahafaly Special Reserve, southwestern Madagascar; DUPC, Duke University Primate Center, forest enclosures, North Carolina, USA.

[b] Relative Aggression, proportion of all within-group agonistic (aggressive and nonaggressive) interactions that were aggressive (see text for definition).

offspring survival (Sauther, 1998). Within these stringent reproductive parameters, female agonistic interactions are relatively frequent compared to other primate species, both within and between groups, and even among females of the same matriline (Hood and Jolly, 1995; Jolly, 1998; Jolly et al., 1993; Kappeler, 1993; Sauther and Sussman, 1993; Vick and Pereira, 1989). Perhaps as a means of negotiating this highly agonistic social system, females within groups commonly form small cliques or dyads, usually consisting of a female and her adult daughter(s) or sisters (Jolly, 1998; Nakamichi and Koyama, 1997; Pereira, 1995; Taylor and Sussman, 1985). For further information on ring-tailed lemur socioecology, a comprehensive review has been published by Sauther et al. (1999).

Study population

We studied 39 adult females across three study sites, two sites in their natural habitat in southern Madagascar (Berenty Private Reserve—"Berenty"—and Beza Mahafaly Special Reserve— "Beza") and one site in the United States where semi-free-ranging groups have been maintained for over 12 years ("DUPC"; Table 1). The females came from eight social groups across these three sites: four groups from Berenty ("A1," "A2," "A3," and "Naturaliste"), two groups from Beza ("Green" and "Yellow Prime"), and two groups from the forest enclosures at the DUPC ("Lc1" and "Lc2"). Of the three sites, Beza and Berenty are the driest, with average yearly rainfall approximately 500 mm (Koyama et al., 2001; Sauther, 1992). The DUPC receives significantly more rainfall in any given year, at approximately 1200 mm (NOAA records for nearby RDU airport). Banana feeding by tourists visiting the A1, A2, and A3 groups at Berenty was curtailed the year prior to this study (Jolly et al., 2002). The Naturaliste troop at Berenty and the groups at Beza have never received supplemental food. At the DUPC, the lemurs were fed daily rations of Purina monkey chow to complement food foraged from the forest enclosure (young leaves, buds, flowers, etc.). These DUPC rations were decreased 7 years prior to this study, resulting in naturalistic foraging activities and behavioral activity budgets similar to those observed in the natural habitat (Cavigelli, 1998). Three years prior to this study, the Berenty and Beza groups experienced a drought; prior to this study the lemur populations were growing at these sites (Gould et al., 1999; Jolly et al., 2002). The A3 group was newly formed and was actively establishing their home range within the reserve (Dubovick, unpublished data) and both the Beza groups fissioned within 6 months after this study (Cavigelli, 1998; Gould et al., 1999), suggesting some social instability in these groups. More information on each study site can be found in other detailed reports (Berenty: Jolly, 1966; Jolly et al., 2002; Beza: Sauther and Sussman, 1993; Sussman, 1991; DUPC: Pereira and Izard, 1989; Taylor and Sussman, 1985).

Behavioral data were collected over a period of at least 6 weeks and fecal samples were collected from a 2- to 3-week period near the end of the behavioral data collection. Data were collected during the lactation season—a period that has been proposed as one of the most nutritionally demanding for females—they have just given birth and are lactating at the beginning of the rainy season and sometimes in advance of the rains (Sauther, 1993, 1998). Dates of data collection for each group are listed in Table 1. For the Madagascar groups (Berenty and Beza) behavioral data were collected throughout the day; for the DUPC groups behavioral data were collected between 1100 and 1300 h, coinciding with the daily provisioning time. Thus, the measure of relative aggression within the DUPC groups is probably high due to the competitive feeding context in which they were observed. Group composition varied; however, the majority of groups contained five adult females (Table 1). All methods were approved by the Institutional Animal Use and Care Committee at Duke University.

Dominance status

Dominance status (rank) was determined for each female by tabulating all aggressive and nonaggressive agonistic interactions among females into a matrix, with "winners" plotted along rows and "losers" plotted along columns. Within any interaction, the "winner" was defined as the female that approached another female without showing any submissive signals and the "loser" was defined as the female that responded to an approaching female with a clear submissive signal, most usually the "spat" vocalization (Jolly, 1966). Aggressive behavior recorded included: "charges," "chases," "lunges," "bites," "nips," and "cuffs." Nonaggressive agonistic acts included: "stares," "approaches," and "touches." Nonaggressive interactions were included in dominance analyses only when they successfully elicited a submissive behavior from the "recipient." Submissive behavior included: "spat," "crouch," "depart," "flee," and "jump away." Definitions for all acts were taken from published ethograms for ring-tailed lemurs (Jolly, 1966; Pereira and Kappeler, 1997). Ranks were determined for each female by reordering the matrix such that all agonistic interactions were above the diagonal. This system for determining dominance ranks is commonly used by primatologists and other animal behaviorists (e.g., Hausfater, 1975; Rowell, 1974), and it produces clear results and rankings in species that form transitive dominance hierarchies. Ring-tailed lemurs do not necessarily form linear transitive hierarchies—i.e., predominantly low-ranking females that can elicit submissive behavior from predominantly high-ranking females in their group (Jolly, 1966; Nakamichi and Koyama, 1997; Pereira, 1993; Pereira and Kappeler, 1997). However, we found no evidence of intransitive dominance hierarchies in the eight groups in this study. Furthermore, there was little evidence of rank instability—i.e., dominance rank reversals, undecided dominance positions, or reciprocal exchange of aggression between individuals. The one exception was in the social group that contained six adult females (Naturaliste): the rank for two mid-ranking females was not clear. These two females were each given a rank of "3" and the next lowest female in the hierarchy was given a rank of "4."

Reproductive state

All groups were observed shortly after the annual birth season, such that 25 of the 39 females were lactating for one or two infants. For the Beza and Berenty groups, fecal samples were collected within 1 month of birth, and for the DUPC groups samples were collected approximately 4 months from birth. For all groups, some females were never seen carrying or feeding an infant and presumably did not lactate or ceased lactation early after the birthing season. To account for these different reproductive states among the females in this study, each female was classified into one of three reproductive states: "nonlactation" ($n = 14$), "early

lactation" (first month of lactation, $n = 20$), or "late lactation" (last month of lactation, $n = 5$). To test for differential effects of early and late lactation (1 month postpartum vs 4 months postpartum) on fecal corticoid levels, an additional set of samples collected during late lactation from the Beza females was compared to their early lactation corticoid values. No females were known to be pregnant during this study.

Fecal corticoid analysis

The use of fecal corticoid extraction and analysis to estimate circulating cortisol levels in this species has been validated in a previous study showing a positive linear relationship between individual fecal and serum levels (Cavigelli, 1999). In circulation, a significant portion of glucocorticoid hormone molecules is bound to corticosteroid-binding globulin (CBG), a protein synthesized primarily by the liver. CBG limits glucocorticoid binding to receptors on cells, thus making the bound fraction relatively inactive (Mendel, 1989). By measuring fecal corticoids in feces we are most likely measuring the "biologically active" portion of circulating glucocorticoids (i.e., the unbound or free fraction).

For the Madagascar groups, fecal samples were immediately collected into vials containing 15 ml of 0.3% sodium azide in 100% ethanol. For the DUPC groups, samples were collected into Whirl-Pak bags (Nasco, Fort Atkinson, WI) and stored at −20°C within 3 h of collection. For each female, a mean (± SD) of 6.0 (± 3.0) samples were analyzed. All samples were analyzed within 6 months of collection.

Fecal corticoids were extracted from feces using the method developed by Wasser and colleagues (1994). The assay involved modifications to a commercially available human serum cortisol RIA kit. Extraction and assay methods are described in Cavigelli (1999). The kit was sensitive to 0.1 μg/dl and the cortisol antibody was known to cross-react 35% with corticosterone, 30% with 21-desoxycortisol, 17.5% with 11-desoxycortisol, 2.9% with progesterone, and less than 0.01% with androstenedione, androsterone, cholesterol, cortisone, DHEA, dihydrotestosterone, α- and β-estradiol, estriol, estrone, and testosterone. The mean (± SD) intraassay coefficient of variance was 10.39 ± 8.61% ($n = 22$). The interassay coefficient of variance for a low control was 19.42% ($n = 16$), and for a high control was 13.00% ($n = 16$). Mean recovery of cortisol in feces was 88.3% ($n = 206$). All samples were run in duplicate. Fecal corticoid levels are reported as nanograms corticoids/gram of dry feces. There is evidence that, as fecal sample size increases, the relative concentration of corticoids may become diluted relative to the fecal mass (Cavigelli, 1999). Among the females studied we found no clear correlation between these two variables, and so fecal sample concentrations were not adjusted according to their mass.

Aggression and affiliation

"Relative group aggression" was assessed for each group by calculating the proportion of all within-group agonistic interactions initiated (both aggressive and nonaggressive) that involved aggression. In other words, if 100 female–female agonistic interactions were recorded within a group and, of these interactions, 55 involved a female displaying an aggressive behavior (e.g., chasing, lunging, etc.), then the relative aggression score for that group would be 0.55. This proportion also was calculated for each female within a group and termed "relative aggression initiated" by a female. In addition, "relative aggression received" was determined for each female—i.e., the proportion of total agonistic interactions in which a female was involved that included her being the subject of an aggressive act from a female group mate.

Spacing relationships were assessed for each female from measures of nearest-neighbor distances (in meters) collected at half-hour intervals throughout daily observation periods. These scores for each female were used to determine how a female's relative proximity to neighbors related to her corticoid levels. A female that is often in close proximity to her neighbors may experience more competition for resources (e.g., food) but at the same time she may experience decreased risk during predatory events. These potential costs/benefits may affect the degree of HPA activation and corticoid titers.

Statistical analyses

The distribution of female corticoid values was skewed to the right: females had several relatively low samples and few high samples. To satisfy the assumption of normal distribution for the statistical analyses, corticoid values were log-transformed and for each female a mean of log-transformed corticoid values was calculated from all her samples. This mean value was used in all analyses. Back-transformed values (geometric means) are presented in the figures and in the text (Sokal and Rohlf, 1995). The following statistical analyses were used. Kruskal–Wallis nonparametric ANOVAs (with multiple comparisons between groups) were used to compare mean fecal corticoid values among sites, among groups, and among ranks. To verify that fecal corticoid rank differences were not driven by results from one or two of the three sites, a two-way ANOVA was conducted using study site and female rank as factors. In addition, five Kruskal–Wallis tests were conducted to determine if fecal corticoid levels within each rank were different across the three study sites. Scatterplots and correlation coefficients were examined to determine if other female characteristics (i.e., age, lactational state, number of offspring, mean number of fecal samples, mean weight of fecal samples, relative aggression initiated, relative aggression received, or mean nearest-neighbor distance) were associated with either dominance rank and/or mean fecal corticoid values. Relative aggression received and relative aggression initiated values were proportion scores; these values were arcsine transformed to arrive at a normal distribution (Sokal and Rohlf, 1995). To determine if any of these individual female characteristics were associated with rank and therefore might explain corticoid differences among ranks, ANOVAs with planned comparisons were used to compare these characteristics among ranks. Finally, a multiple linear regression analysis was used to determine if any of the behavioral variables were predictive of individual corticoid levels. Scatterplots in which each variable was plotted against fecal corticoid values were inspected for linearity and to identify potential outliers; residuals were plotted to verify normality and to identify potential outliers.

Results

Fecal corticoid values among study sites and groups

Overall, mean fecal corticoid levels did not differ across the three study sites ($H_2 = 3.28$, ns). The mean ($\pm$ SD) value for the Berenty groups was 18.3 ± 6.4 ng/g ($n = 19$), for the Beza groups 17.7 ± 11.9 ng/g ($n = 10$), and for the DUPC groups 20.2 ± 3.8 ng/g ($n = 10$). When considered within each dominance rank position, corticoid levels were not significantly different across the three sites (repeated Kruskal–Wallis tests produced P values > 0.10). In addition, there was no interaction effect between rank and study site (interaction of site and rank: $F_{8,24} = 1.12$, ns). However, given the limited numbers of females to compare across sites, the power of these tests was limited.

Mean fecal corticoid values did not differ across the eight study groups ($H_7 = 11.14$, ns, Table 1). The two Beza groups represented the highest and the lowest group means (Green: mean $\pm$ SD = 11.3 ± 5.5 ng/g; Yellow Prime: mean $\pm$ SD = 24.1 ± 13.5 ng/g). At Beza, the Green group had low relative aggression (0.300), and they lived in riverine forest where food was more abundant than for the Yellow Prime group. On the other hand, Yellow Prime had the highest mean fecal corticoid value, high relative aggression (0.667), lived in a more arid portion of the preserve, and fissioned less than 5 weeks after fecal samples for this study were collected.

Given the small number of groups from each site, we had limited power to identify significant site differences; however, visual inspection of the data confirm that fecal corticoid levels were not extremely different among the sites (Tables 1 and 2). Because there were no differences in corticoids among sites, nor an interaction between rank and study site, we pooled data across the study sites to test for rank (and other) effects on corticoid levels. In addition, we repeated all analyses, using data from each study site separately. The directions of results from these within-site analyses were never different from the results of analyses conducted on the complete data set.

Table 2
Characteristics of all females in study

Site (month/year)	Social group	Female ID	Domin. rank	Age (years)	Reprod. state[a]	No. of fecal samples	Relative aggression initiated	Relative aggression received	Mean nearest-neighbor distance (m)[b]	Fecal corticoid geometric mean (ng/g)
Berenty (Sep/ Oct'97)	A1	Fan	1	8	N	5	0.37	0.00	1.2	22.3 (2.1)
		Finch	2	6	N	6	0.36	0.71	1.0	15.8 (2.8)
		Bush	3	10	N	3	0.05	0.49	1.1	14.5 (1.5)
		Scout	4	7	EL	4	0.07	0.37	0.8	15.4 (2.0)
		Kid	5	8	EL	5	0.00	0.61	0.8	13.6 (1.5)
	A2	Possum	1	8	EL	6	0.18	0.00	1.2	24.5 (1.9)
		Shadow	2	10	EL	5	0.44	0.67	1.1	15.4 (2.8)
		Blotch	3	11	EL	6	0.18	0.58	0.8	14.4 (1.4)
		Beatrice	4	3	N	2	0.00	0.46	0.9	17.8 (1.4)
		Susie	5	3	N	3	0.00	0.57	1.1	9.9 (1.1)
	A3	Jessica	1	9	EL	4	0.53	0.00	0.5	22.9 (1.5)
		Honey	2	6	N	4	0.57	0.50	0.7	28.5 (1.3)
		Dove	3	4	EL	7	0.00	0.36	0.7	15.5 (1.3)
	Naturaliste	Tracy	1	8	EL	4	0.74	0.00	—	29.0 (2.1)
		Aroura	2	4	N	3	0.80	0.20	—	32.2 (1.5)
		Tess	3	3	N	5	0.82	0.56	—	16.4 (1.3)
		Bella	3	9	N	3	0.85	0.65	—	15.1 (1.5)
		Rebecca	4	7	EL	3	0.33	0.97	—	11.6 (1.7)
		Emily	5	3	EL	4	0.00	0.84	—	12.2 (2.4)
Beza Mahafaly (Sep/Oct '95)	Green	93	1	11	EL	13	0.26	0.00	1.9	9.2 (1.5)
		143	2	10	EL	9	0.33	0.20	2.4	20.5 (1.6)
		459	3	7	EL	12	0.33	0.51	2.7	11.9 (2.2)
		139	4	7	EL	9	0.24	0.32	3.8	6.9 (1.6)
		419	5	5	EL	10	0.00	0.23	4.2	7.8 (2.0)
	Yellow Prime	465	1	8	EL	6	0.54	0.00	3.0	34.2 (1.4)
		445	2	6	EL	7	0.58	1.00	2.7	42.1 (1.6)
		409	3	3	EL	9	0.85	0.88	2.4	17.2 (1.5)
		101	4	9	EL	10	0.00	0.56	2.6	9.5 (1.5)
		103	5	9	EL	11	0.00	0.69	2.5	17.3 (1.9)
DUPC (July/ Aug'97)	Lc1	Ninna	1	8.5	LL	3	0.44	0.00	1.3	25.1 (1.4)
		Atthis	2	4.5	N	4	0.63	0.00	1.2	27.4 (1.3)
		Corinna	3	13.5	LL	4	0.75	0.73	1.7	18.2 (1.3)
		Alexandra	4	2.5	N	4	0.71	0.71	1.4	21.3 (1.2)
		Katina	5	10.5	LL	1	0.00	0.69	1.7	16.3 (n/a)
	Lc2	Dory	1	8.5	N	7	0.53	0.00	1.7	20.9 (1.3)
		Alice	2	8.5	N	5	0.47	0.67	2.0	19.0 (1.3)
		Cleis	3	12.5	LL	11	0.47	0.60	2.1	20.5 (1.4)
		Charissa	4	3.5	N	10	1.00	0.51	1.8	17.1 (1.2)
		Cleomenis	5	10.5	LL	7	0.00	0.63	2.1	15.7 (1.4)

[a] N, nonlactating and beyond birthing season; EL, early lactation (within 1 month of birth); LL, late lactation (approx. 3.5 months from birth).
[b] No data available from Naturaliste troop.

Female fecal corticoid values along the dominance hierarchy

Across the sites, mean fecal corticoid levels differed significantly among the five dominance positions. Either the first- or second-ranking female in each group exhibited the highest corticoid levels within the group ($H_4 = 16.4$, $P = 0.0025$; Fig. 1). The relationship between rank and corticoids was not linear but rather dichotomous, such that the two top-ranking females had corticoid levels distinctly higher than the lower-ranking females. Corticoid levels did not differ between the first- and second-rank females, nor did they differ among the third-, fourth-, and fifth-rank females. Corticoid levels for the first- and second-rankers were sometimes twice that of the three bottom-rankers (average for top vs bottom-ranking females: 24.3 ± 8.0 vs 14.6 ± 3.8 ng/g). This effect was clear for every group except the Lc2 group at the DUPC (Table 2).
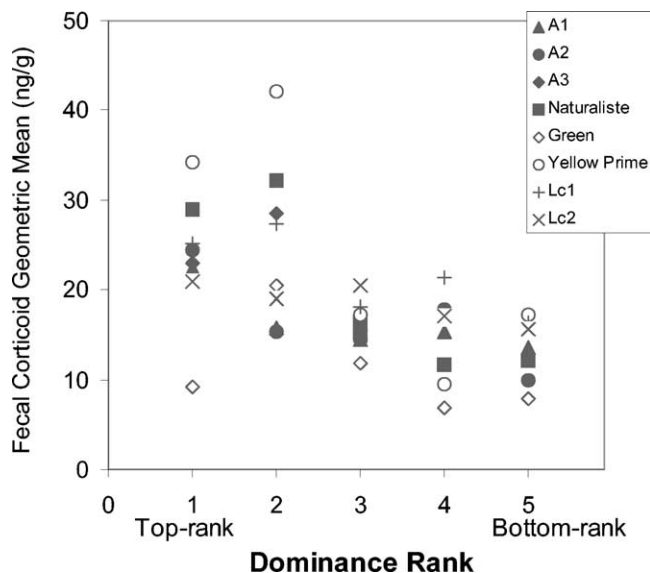
Fig. 1. Mean fecal corticoid level for each female across the eight study groups according to dominance rank.

Female fecal corticoid values and reproductive status

There was no relationship between a female's dominance rank or her corticoid levels and whether she was lactating for an infant during the study (Table 2). Distribution of dominance rank among each of the three lactational states was not biased. That is, there were not more top-ranking females among the nonlactation, early lactation, or late lactation groups. Also, corticoid values did not differ according to lactational state ($H_2 = 3.04$, $P = 0.22$). The mean ($\pm$ SD) fecal corticoid level for nonlactating females was 19.9 ± 6.1 ng/g, for early lactating females 17.6 ± 9.1 ng/g, and for late lactating females 19.2 ± 3.8 ng/g. These values and analyses were similar when repeated within each study site. In addition, the number of offspring a female had did not correlate with her mean fecal corticoid value (Table 3).

Of the females that were lactating (i.e., nursing an off-spring), all of the DUPC females were in late lactation,

whereas all the Madagascar females were in early lactation. To determine the effect of early vs late lactation on corticoid values, a paired t test was performed with the Beza females from whom early and late lactation samples were collected. For these females, the average ($\pm$ SD) fecal corticoid value was 19.6 ± 13.4 ng/g during early lactation and 22.0 ± 11.6 ng/g during late lactation ($t_8 = 0.79$, ns). Also, rank effects were evident during both early and late lactation for these females (top two vs bottom three females during early lactation: 28.6 vs 12.4 ng/g, and during late lactation: 30.8 vs 14.9 ng/g). Because early and late lactation were not associated with differential mean corticoid levels for the Beza females, comparison of corticoid levels among the DUPC females (in late lactation) and the Beza and Berenty females (in early lactation) should not be affected by their different lactational phases.

Given that females may lactate for other females' off-spring, the lack of correlation between lactational state and corticoids may not be surprising. Some females character-ized as nonlactating may have actually been lactating and suckling other's offspring during the evenings and during large group huddles when this behavior was difficult to observe. We know this was the case for one of the "non-lactating" females in the Lc1 group (Atthis) who was ob-served nursing the infant of her mother (Ninna). Thus, a lack of relationship between lactational status and corticoid levels may reflect the fact that some females without infants and characterized as "nonlactating" may have actually been lactating.

Relative aggression, dominance status, and fecal corticoids

Groups that had high proportions of aggressive interac-tions had elevated corticoid levels. For comparison, groups were divided according to their relative group aggression scores. Groups that had scores of greater than 0.50 were labeled "high aggression" (i.e., greater than 50% of their agonistic interactions involved aggressive acts). Those with scores below 0.50 were labeled "low aggression." Interest-ingly, these two kinds of groups were evenly distributed

Table 3
Correlation coefficients between individual traits and fecal corticoid values

Variable	All females ($n = 39$)	Rank 1 and 2 females ($n = 16$)	Rank 3, 4, and 5 females ($n = 23$)
Dominance rank	0.588***	−0.093	0.312
Age (years)	−0.016	−0.628**	0.116
No. of nursing offspring	−0.124	0.014	−0.172
Weight of fecal samples	0.062	−0.028	−0.163
Relative aggression initiated	0.514***	0.617**	0.410
Relative aggression received	−0.226	0.053	0.372
Nearest-neighbor distance[a]	−0.294	0.248	−0.576**

[a] No data available from Naturaliste group ($n = 33, 14, 19$).
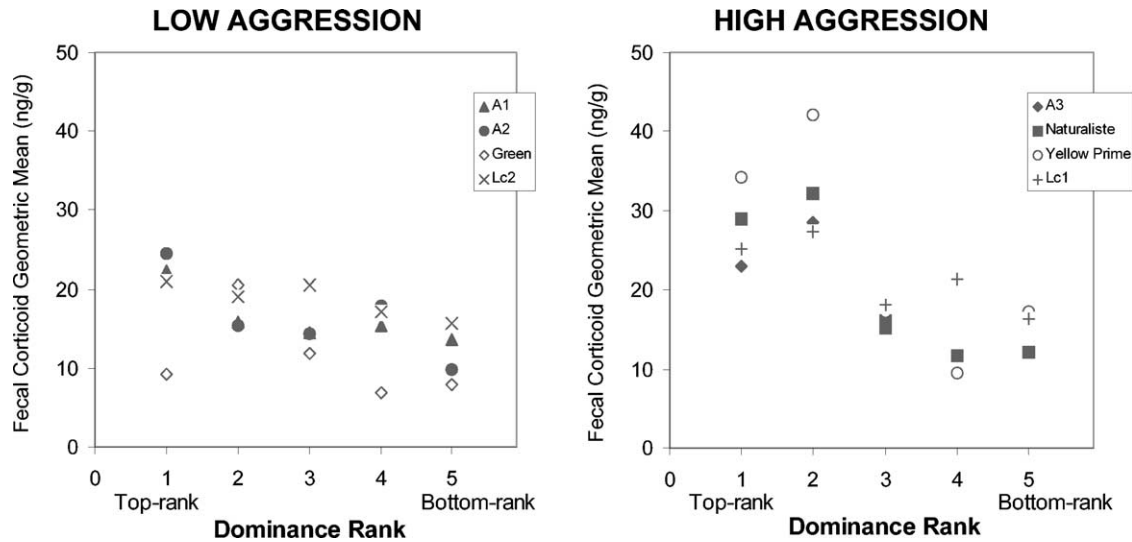
** $P < 0.01$.

*** $P < 0.001$.

Fig. 2. Mean fecal corticoid values according to female dominance ranks for low aggression (left) and high aggression (right) groups.

across the three study sites—i.e., at each site there were equal numbers of high aggression and low aggression groups. The highest relative aggression levels within each of the Madagascar sites were in the groups that probably experienced the highest feeding competition: A3 was a newly formed group actively defending its home range, Naturaliste was in a region of the Berenty reserve that had never experienced supplemental feeding, and Yellow Prime lived in the western dry forest region of the Beza Reserve. Corticoid values were significantly higher in high aggression groups (Fig. 2; $H_4 = 16.42$, $P = 0.0025$) and there was no rank × aggression interaction when a parametric ANOVA was used (i.e., higher corticoid values in the high aggression groups were not attributable to a particular subset of certain ranked females showing elevated corticoid values in those groups). In addition to group aggression measures, individual female aggression (relative aggression initiated) was correlated with individual mean corticoid levels (Fig. 3; $r_{30} = 0.514$, $P < 0.01$). This correlation was strongest in the Berenty and Beza groups ($r_{10} = 0.560$, $P < 0.05$; $r_{19} = 0.594$, $P = 0.07$) and weakest in the DUPC groups ($r_{10} = 0.325$, ns). This correlation was particularly strong for high-ranking females (see below).

Traits associated with dominance rank and fecal corticoid values

To determine if the nonlinear relationship between rank and corticoids may be explained by some trait other than rank, we compared other individual measures to rank and corticoid values. Females along the dominance hierarchy did not differ significantly in age, mean number of nursing offspring, the number or mean weight of fecal samples, or in distance to their nearest neighbor. The two traits that were significantly different among ranks were the relative aggres-

sion initiated and the relative aggression received by a female. Of these two traits, only aggression initiated correlated with mean fecal corticoid levels (Table 3). When analyzed across all study sites, results for high- and low-ranking females differed. For the high-ranking females (ranks 1 and 2), aggression initiated and a female's age were both significantly correlated with a female's corticoid level: females that had higher aggression initiated scores and were younger had higher corticoid levels. In fact, age and aggression initiated were also correlated—it is the younger of the two high-rank females that is also the most aggressive. So, it is either age or aggression that may explain a high-ranking female's corticoid levels. For the lower-ranking females (ranks 3, 4, and 5), the only characteristic significantly correlated with mean corticoid levels was the distance to the nearest neighbor, with increasing distance being associated with decreased corticoid levels. For these females, aggression initiated and aggression received were positively correlated with fecal corticoids but not statistically significant. When the three behavioral traits (aggression initiated, aggression received, and nearest-neighbor distance) were entered as predictors of mean log-transformed fecal corticoids in a multiple linear regression analysis, only aggression initiated was a significant predictor of corticoid levels. These results differed when repeated separately with only the high- or low-ranking females. Taking the first-and second-ranking females across all groups, aggression initiated was the only significant predictor of mean log fecal corticoid levels (Fig. 3), with increasing aggression predicting increased corticoid levels. For the lower-ranking females (third, fourth, and fifth) mean nearest-neighbor distance and aggression received were both significant predictors, with fecal corticoid values increasing as distance to nearest neighbor decreased and as proportion of received aggression increased.
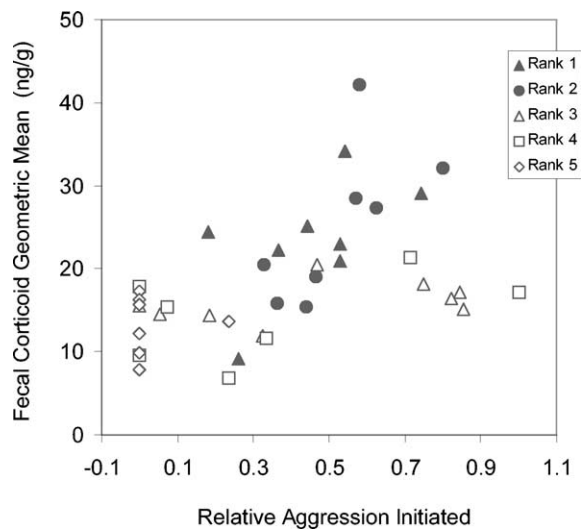
Fig. 3. Mean fecal corticoid values compared to relative aggression initiated by each female.

Discussion

During the lactation season, in all eight social groups of ring-tailed lemurs, either the first- or the second-ranking female had the highest mean fecal corticoid levels within her group. There was a dichotomous relationship between corticoids and rank: the most common pattern to emerge was that the two top-ranking females had significantly higher corticoid levels than the three remaining low-ranking females in their group. These rank differences could not be accounted for by variables such as lactation state, number of nursing offspring, number of fecal samples produced, or mean weight of these samples. However, individual corticoid levels were correlated with relative aggression initiated. Groups and individuals that initiated more aggressive interactions had higher corticoid levels than less aggressive groups and individuals, and this effect was particularly true for the two highest-ranking females in a group. For the lower-ranking females, being the recipient of female aggression and being closer to one's nearest neighbor were associated with elevated corticoid levels. These results suggest two different sets of challenges for these two classes of females. For high-ranking females, the challenge is initiating aggressive agonistic interactions, whereas for low-ranking females the challenge is being the recipient of these kinds of agonistic interactions and being in close proximity to neighbors, perhaps resulting in increased feeding competition (see discussion below).

Elevated corticoid levels in top-ranking ring-tailed lemur females is similar to recent results reported for free-ranging African wild dogs, dwarf mongooses (Creel et al., 1996, 1997), and captive female common marmosets (Saltzman et al., 1994). However, the results of the present study, with low reproductive skew females, refute the hypothesis that reproductive activity is the sole factor driving elevated corticoid levels in top-ranking cooperative breeding females.

Similarly, Saltzman and colleagues (1998) have explored these mechanisms in female marmosets, thus far concluding that differences in reproductive activity cannot account for all the differences in glucocorticoid levels among high- and low-ranking females. There must be some other reason to explain why high-ranking cooperative breeding females exhibit elevated glucocorticoid levels. There are at least three overlapping factors that may account for these results: (1) relatively high aggression rates in high-ranking cooperative breeding females (Creel et al., 1996), (2) increased HPA responsiveness in these females (Saltzman et al., 2000), and/or (3) differential energy stores available to these females, allowing differential HPA axis activity (Cavigelli, 1998). These are discussed below.

Female dominance status, aggression, and glucocorticoids

One possible explanation for elevated corticoid levels in high-ranking females is that they are the most aggressive females in their groups and that this aggression stimulates increased corticoid production. Such increases in circulating glucocorticoids following aggressive encounters have been observed in several other species (castrated male pigs: Fernandez et al., 1994; male Siberian dwarf hamsters: Castro and Matt, 1997; nonbreeding male and female mountain spiny lizards: Woodley et al., 2000). Alternatively, group dynamics preceding aggressive interactions and/or the psychological stress associated with anticipating fights may be enough to elevate corticoid levels well in advance of an aggressive interaction (black tufted-ear marmosets: Smith and French, 1997). The causal direction of this relationship is unknown, such that high-ranking females could experience other forms of stress in their groups, thus activating the HPA axis and in turn stimulating aggressive behavior. Either way, these results are distinctly different from results with male olive baboons in which males that are more likely to initiate fights have the lowest basal circulating cortisol levels (Sapolsky and Ray, 1989). The explanation that elevated aggression in high-ranking females leads to elevated corticoid secretion may hold for female ring-tailed lemurs and African wild dogs (Creel et al., 1996) where high-ranking females tend to be aggressive females, but probably does not hold for female common marmosets where the top-ranking females are not necessarily the most aggressive females of a group (Saltzman et al., 1994). However, with the ring-tailed lemurs in this study, several of the third- and fourth-ranking females were relatively aggressive (more so than their first- and second-ranking group mates), yet their fecal corticoid levels were no higher than other less aggressive females. Thus, in female ring-tailed lemurs, it appears that initiating aggressive agonistic interactions may explain dominant females' corticoid levels but not all females' corticoid levels. Rather some other traits associated with dominance rank, for example being exposed to aggressive agonistic attacks, or being close to one's neighbors within a troop where feeding competition may be enhanced, are also

important. In females, in which competition for food resources is important, such a trait is probably related to a female's ability to gain access to food resources (see below). It is important to note that being exposed to aggressive agonistic attacks does not seem as strong a predictor of corticoids as the trait of initiating aggressive agonistic interactions. This may reflect the situation for free-ranging females in which being the victim of aggressive attacks is not as primary a stressor as it may be for animals living in a social group in a confined (i.e., caged) condition in which escape from attacks is limited.

HPA reactivity

A second explanation for differential corticoid levels may be that dominant females' HPA axis is either more responsive to environmental stimuli or that they maintain overall higher levels of corticoids at all times. In female common marmosets, high-ranking/high cortisol females show an elevated adrenal gland response to injections of adrenocorticotropic hormone (e.g., Saltzman et al., 2000). A similar mechanism may exist in the female ring-tailed lemurs, African wild dogs, and dwarf mongooses, but has not yet been tested. The possibility of elevated HPA (specifically adrenal) responsiveness in top-ranking females would support Rowell's 1974 prediction that, in free-ranging social groups, stress-responsive individuals should obtain relatively high status within their groups. Such adrenal responsiveness would convey benefits to the dominant females, for example: increased energy availability, stimulated cell-mediated immune function (Dhabhar and McEwen, 1997) or enhanced cognitive function (review in Roozendaal, 2000). This trait of responsiveness need not necessarily be a life long trait, but rather it may occur during a certain period of adult life coinciding with elevated dominance status and the demands or benefits associated with this status.

Alternatively, high-ranking females' adrenal glands may be constantly producing more glucocorticoids than their low-ranking group mates in a manner that is not limited to specific brief periods of challenge. Such a state reflects a situation of chronically elevated glucocorticoid secretion, a condition in caged animals that has been shown to have detrimental physiological effects such as impaired immune function and hippocampal cell damage (e.g., Dhabhar and McEwen, 1997; Sapolsky et al., 1990) and altered physiological functioning such as immune cell glucocorticoid resistance (Avitsur et al., 2001). If high-ranking females exhibit chronically elevated corticoid levels, this would suggest a potentially severe cost associated with high rank. However, chronically elevated corticoid levels may only be evident in cage conditions where social instability is experimentally produced or cannot be easily resolved and escape from aggressive interactions is limited. Further research with free-ranging species can help determine if animals experience chronically elevated corticoid levels in the natural habitat, and if so, whether they experience detrimental

physiological effects as a result of these elevations. If so, we should examine if there are any indirect long-term benefits of such chronic elevations.

Energetic stores and glucocorticoids—a unifying hypothesis

A final explanation for elevated corticoid levels in high-ranking female mammals may be that these females, as a result of their elevated dominance status, maintain differential access to resources (either better or worse food supplies or just different kinds of food supplies) and therefore maintain either higher or lower amounts of stored energy (i.e., fat) than their low-ranking group mates. For example, for female ring-tailed lemurs, Sauther (1992) has shown that dominant females (ranks 1 and 2) maintain greater access to quality resources (fruits and water holes). Recent studies are revealing evidence that adrenal activity can be modulated by leptin, a hormone produced by adipose tissue. Circulating leptin levels are closely associated with the degree of adiposity and levels decrease when food is restricted and weight loss occurs (review in Schwartz and Seeley, 1997). Leptin treatment can affect the amount of glucocorticoids an animal secretes, although the specific dynamics of these interacting systems are not clear yet (Morimoto et al., 2000; Nowak et al., 2002). No matter the dynamics, it is becoming evident that adrenal activity can be modulated by leptin, which reflects the amount of adipose tissue an animal has at any given time. High- and low-ranking females may maintain quite different levels of fat stores, given that they have access to different food resources (Sauther, 1992). This energetic demand hypothesis predicts that females with ample fat deposits will have different glucocorticoid secretion patterns than females with limited fat stores. If it is found that high- and low-ranking females have different amounts of fat deposits, this hypothesis may be useful. If there is a rank difference, it could be either the high- or low-ranking females that maintain greater fat stores. For low-ranking females, putting on fat and decreasing corticoid secretion may be a metabolic strategy to prepare for the predictable dry season when they may be restricted from prime food resources by dominant females. Differential fat stores may account for the diminished dominance effect on corticoids found in the DUPC females (Table 2) where daily provisioned foods were distributed in such a way that all females could gain access to the resource.

Another possible example may be that top-ranking females produce more or richer milk for their offspring than lower-ranking group mates (e.g., dairy cows: Phillips and Rind, 2002). Given that female ring-tailed lemurs produce relatively high-energy milk as compared to other infant-carrying lemur species (Tilden and Oftedal, 1997), such increased investment could present a significant cost. If high-ranking females engage in such increased energy-demanding behavior, their glucocorticoid titers will need to increase to help in the energy metabolism needed to support

such a behavior. These scenarios may be particularly true in a species like ring-tailed lemurs that begin lactating for infants at the end of the annual dry season when energy available from the environment may be low but energy stores in the body may be available for mobilization during the predictable and circumscribed dry season (Pereira et al., 1999).

This hypothesis of differential energy intake, storage, and output in high- and low-ranking females could be tested by measuring fat stores, leptin levels, or milk quality in species that have elevated feeding competition and differential corticoid production across the dominance hierarchy. Support of such a hypothesis would illuminate a possible benefit associated with elevated corticoid levels in dominant females, as well as the possible benefit of reduced corticoid secretion in low-ranking females that have restricted access to prime resources. Further data from all seasons and from drought vs normal years would shed light onto the plausibility of this hypothesis.

Species-specific social systems, dominance status, and glucocorticoids

The results of this study probably reflect a unique combination of the above three explanations in mutual interaction and specific to female ring-tailed lemurs. Female ring-tailed lemurs are highly agonistic (Kappeler, 1993) and their agonistic behavior is primarily centered around access to food (Sauther, 1993). In particular, female feeding aggression is high during the lactation season, a period when nutritional demands are probably highest (Rasamimanana and Rafidinarivo, 1993; Sauther, 1992, 1993). During the period following births females also display a behavior identified as "targeting aggression" in which female–female aggression becomes severe and directed toward one or two individuals in a group, often resulting in eviction of young adult females (Nunn and Pereira, 2000; Vick and Pereira, 1989). In the face of this highly agonistic social system, females form small cliques or dyads within their larger social groups (Jolly, 1998; Nakamichi and Koyama, 1997; Pereira, 1995; Taylor and Sussman, 1985). In the majority of groups we studied, the first- and second-ranking females spent the majority of their time in proximity and the third-, fourth-, and fifth-ranking females spent the majority of their time in proximity to one another, in essence forming two cliques within each group. These female kin cliques appear to be crucial when groups fission—females will not leave a troop without a female partner (Jolly and Pride, 1999; Nunn and Pereira, 2000). Risks associated with new group formation may explain the ultimate reason that cooperative breeding has evolved in this species—subordinate females are often better off enduring within-group feeding competition with dominants than trying to form a novel social group. Thus, significant within-group competition for food resources may explain the relatively high degrees of female–

female agonistic interactions and within-group cliques in this species.

For female ring-tailed lemurs, their agonistic lifestyle combined with their affiliative relations limited to close-kin and high within-group feeding competition may explain our results from these lactating females. Our study took place during the costly lactation season for these seasonally breeding females. Feeding competition during this period is probably at its peak given the limited food supplies at the end of the dry season/beginning of the wet season and increased energetic demands of lactation. In addition, because infant survival can be low, females' major concern during this time may be to attain high-energy food supplies to better ensure their offspring's survival. The two most dominant females (ranks 1 and 2), particularly in relatively aggressive groups, may engage in increased feeding contest competition during these times (Sauther, 1993), given their higher rates of aggression and their ability to monopolize fruit and water resources (Sauther, 1992). This defense of high-energy feeding sites may present a constant source of stress for these females, thus explaining their elevated corticoid levels. Alternatively, these females may be able to afford activation of the HPA axis during this period, helping them in defending these resources, whereas low-ranking females may have chosen an alternative route of decreasing their energetic output during these lean times (and therefore decreasing HPA axis activation). This dominance effect may exist only during periods of highest nutritional stress (e.g., birth and lactation) for females living in highly seasonal habitats. Given that lower-ranking females tend to be the females that fission from a natal group and are the most frequent victims of female infanticide (Jolly et al., 2000), it is surprising that low-ranking females do not display elevated corticoid levels in this species. These results may be explained by the fact that these females do not spend energy to actively defend monopolizable resources and that the stressors associated with infanticide and expulsion can be moderated by retaining one's distance from potential perpetrators. However, for these females this strategy seems to lead to more feeding competition with males during this time (Sauther, 1993). These species-specific affiliation and aggression parameters may explain the dichotomy we found in corticoid levels between the two highest-ranking and the three lowest-ranking ring-tailed lemur females.

The specific social structure in which a dominance hierarchy is formed undoubtedly affects the physiological stress associated with different positions in that hierarchy. For example, highly aggressive groups or groups in which food supplies are limited may predict higher corticoid levels in those animals actively defending limited resources. What, then, is it about cooperative breeding species that biases their dominant individuals toward having high corticosteroid levels (Creel, 2001)? Based on results of our research and the results with black tufted-ear marmosets (Smith and French, 1997), it appears that the stress of reproducing in high-ranking females is not the only stressor associated with

high rank in cooperatively breeding females. More specifically, it may reflect the reason that these species have evolved the behavioral trait of cooperative breeding. Cooperative breeding may have evolved in species that live in relatively impoverished environments relative to the energetic demands associated with raising offspring, where helping behavior is necessary for infant survival (Emlen, 1991). Given these constraints, it is in dominant individuals' interests to maintain a few subordinate females in a social group to assist with raising/protecting offspring, although probably not too many so as to moderate within-group competition. In such a social system, the dominant position may bring with it many stressful social conditions associated with maintaining dominance and access to key resources (e.g., fruit and water for ring-tailed lemurs) without pushing out subordinates prematurely. This careful balance of agonistic and affiliative interactions may be associated with a high degree of psychological or energetic stressors that may explain elevated corticoid production in dominant individuals in cooperative breeding species.

Further analyses of specific behavioral traits and costs and benefits associated with differential female dominance status and corticoid levels will help to clarify the relationship that is beginning to emerge with cooperative breeding species (Creel, 2001) and to understand the consequences of such differences among ranks. The results with the female ring-tailed lemurs emphasize that the relationship between rank and glucocorticoids is not necessarily linear and that this relationship is dependent on the species-specific and gender-specific social structure of the animals studied, as well as the environmental and reproductive conditions present during the study. Many relationships have been found between dominance and adrenal activity and these diverse relationships may be best explained by the specific behavioral mechanisms underlying the dominance relationships at the time. More information from free-ranging animals will help us to determine the specific situations in which HPA activity differs among high- and low-ranking individuals, and to determine potential costs and benefits associated with these differences.

Female dominance hierarchies and glucocorticoids

Female dominance hierarchies will probably have a different relationship to HPA activity than male hierarchies. To fully understand the relationship between aggression and glucocorticoid levels specific to female mammals, future studies will need to incorporate the issue of female feeding competition. Classically, the most common context for conflict among female primates is for access to food resources (Silk, 1993), and specifically for ring-tailed lemurs, agonistic interactions in a feeding context are more frequent between female pairs than between male pairs (Sauther, 1993). Specifically, overt female–female aggression is observed in situations in which contest competition (as compared to scramble competition) is predominant—i.e., in situations

where a primary food source is distributed in such a way as to make it monopolizable (e.g., clumped) (Pruetz and Isbell, 2000; van Schaik, 1989; Wrangham, 1980). For ring-tailed lemurs, it has been shown that female agonistic interactions increase during times of resource competition and during the energetically expensive lactation season (Sauther, 1993) and only resources that can be monopolized are associated with any rank-related feeding advantages (Sauther, 1992). Thus, the correlation between female aggression and glucocorticoid production in high-ranking females in this study might only be seen in groups of females that engage in contest competition. Specifically, in this study the highest dominant female corticoid values were in the groups that were aggressive and that lived in the least productive environments (i.e., the Yellow Prime and Naturaliste groups). These high levels could reflect nutritional stress in these environments or more likely increased contest competition and increased aggressive behavior, particularly by the dominant females as they work to monopolize important resources to maximize the chances of their infant surviving the first year of life. Rank effects in the seasonally breeding ring-tailed lemur females may only be apparent during the period of high feeding competition or during lactation, when our study was conducted. In any case, results from group-living female mammals strongly support the need for further research with females at different stages of reproduction and living under different levels of feeding competition.

Glucocorticoids in the natural habitat

Studies of free-ranging animals have revealed new information on the interaction among reproduction, dominance, and glucorticoids (Cavigelli, 1999; Creel et al., 1996, 1997; Goymann et al., 2001). Further studies will provide a better understanding of the many possible contexts in which elevated corticoids provide an advantage or a cost to the individual. Fecal steroid measures provide one methodological advance that can make field studies more feasible and informative. Fecal measures eliminate the need to disturb either behavioral or physiological processes by capturing animals for blood sampling (Whitten et al., 1998) and this method allows for frequent repeated sampling to determine changes over time within individuals and groups (e.g., seasonal or developmental changes). With the help of novel physiological measures, studies of physiological processes in the natural habitat will provide greater insights into the array of strategies individuals invoke to balance the functions of interacting physiological systems as to promote survival in complex social and physical environments.

Acknowledgments

References

Allolio, B., Hoffman, J., Linton, E.A., Winkelman, W., Kusche, M., Schulte, H.M., 1990. Diurnal salivary cortisol patterns during pregnancy and after delivery: relationship to plasma corticotropin-releasing hormone. Clin. Endocrinol 33, 279–290.

Altemus, M., Deuster, P., Gallivan, E., Carter, C., Gold, P., 1995. Suppression of hypothalamic–pituitary–adrenal responses to exercise stress in lactating women. Clin. Endocrinol. Metab. 80, 2954–2959.

Avitsur, R., Stark, J.L., Sheridan, J.F., 2001. Social stress induces glucocorticoid resistance in subordinate animals. Horm. Behav. 39, 247–257.

Bronson, F.H., Eleftheriou, B.E., 1964. Chronic physiological effects of fighting in mice. Gen. Comp. Endocrinol. 4, 9–18.

Castro, W.L.R., Matt, K.S., 1997. The importance of social condition in the hormonal and behavioral responses to an acute social stressor in male Siberian dwarf hamster (*Phodopus sungorus*). Horm. Behav. 32, 209–216.

Cavigelli, S.A., 1998. Fecal cortisol levels relative to behavior in a free-ranging primate: adaptive aspects of a glucocorticoid hormone. Ph.D., Duke University.

Cavigelli, S.A., 1999. Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs, *Lemur catta*. Anim. Behav. 57, 935–944.

Christian, J.J., Davis, D.E., 1964. Endocrines, behavior and population. Science 146, 1550–1560.

Coe, C.L., Mendoza, S.P., Levine, S., 1979. Social status constrains the stress response in the squirrel monkey. Physiol. Behav. 23, 633–638.

Creel, S., 2001. Social dominance and stress hormones. Trends Ecol. Evol. 16, 491.

Creel, S., Creel, N.M., Mills, M.G.L., Monfort, S.L., 1997. Rank and reproduction in cooperatively breeding African wild dogs: behavioral and endocrine correlates. Behav. Ecol. 8, 298–306.

Creel, S., Creel, N.M., Monfort, S.L., 1996. Social stress and dominance. Nature 379, 212.

Dhabhar, F.S., McEwen, B.S., 1997. Acute stress enhances while chronic stress suppresses cell-mediated immunity in vivo: a potential role for leukocyte trafficking. Brain Behav. Immun. 11, 286–306.

Emlen, S.T., 1991. Evolution of cooperative breeding in birds and mammals, in: Krebs, J.R., Davies, N.B (Eds.), Behavioural Ecology: An Evolutionary Approach, Blackwell Scientific Publications, Boston, pp. 301–337.

Fernandez, X., Meunier-Salaun, M-C., Mormede, P., 1994. Agonistic behavior, plasma stress hormones, and metabolites in response to dyadic encounters in domestic pigs: interrelationships and effect of dominance status. Phys. Behav. 56, 841–847.

Gould, L., 1992. Alloparental care in free-ranging Lemur catta at Berenty Reserve, Madagascar. Folia Primatol. 58, 72–83.

Gould, L., Sussman, R.W., Sauther, M.L., 1999. Natural disasters and primate populations: the effects of a 2-year drought on a naturally occurring population of ring-tailed lemurs (*Lemur catta*) in southwestern Madagascar. Int. J. Primatol. 20, 69–84.

Goymann, W., East, M.L., Wachter, B., Höner, O.P., Möstl, E., Van't Hof, T.J., Hofer, H., 2001. Social, state-dependent and environmental modulation of faecal corticosteroid levels in free-ranging female spotted hyenas. Proc. R. Soc. London B: Biol. Sci. 268, 2453–2459.

Hausfater, G., 1975. Dominance and reproduction in baboons (*Papio cynocephalus*): a quantitative analysis. Contrib. Primatol. 7, 2–150.

Hood, L.C., Jolly, A., 1995. Troop fission in female *Lemur catta* at Berenty Reserve, Madagascar. Int. J. Primatol. 16, 997–1015.

Jolly, A., 1966. Lemur Behavior. University of Chicago Press, Chicago.

Jolly, A., 1998. Pair-bonding, female aggression and the evolution of lemur societies. Folia Primatol. 69, 1–13.

Jolly, A., Pride, R.E., 1999. Troop histories and range inertia of *Lemur catta* at Berenty, Madagascar: a 33-year perspective. Int. J. Primatol. 20, 359–373.

Jolly, A., Caless, S., Cavigelli, S., Gould, L., Pereira, M.E., Pitts, A., Pride, R.E., Rabenandrasana, H.D., Walker, J.D., Zafison, T., 2000. Infant killing, wounding and predation in *Eulemur* and *Lemur*. Int. J. Primatol. 21, 21–40.

Jolly, A., Dobson, A., Rasamimanana, H.M., Walker, J., O'Connor, S., Solberg, M., Perel, V., 2002. Demography of *Lemur catta* at Berenty Reserve, Madagascar: effects of troop size, habitat and rainfall. Int. J. Primatol. 23, 327–353.

Jolly, A., Rasamimanana, H.R., Kinnaird, M.F., O'Brien, T.G., Crowley, H.M., Harcourt, C.S., Gardner, S., Davidson, J.M., 1993. Territoriality in Lemur catta groups during the birth season at Berenty, Madagascar, in: Kappeler, P.M., Ganzhorn, J.U. (Eds.), Lemur Social Systems and Their Ecological Basis, Plenum Press, New York, pp. 85–109.

Kappeler, P.M., 1993. Variation in social structure: The effects of sex and kinship on social interactions in three lemur species. Ethology 93, 125–145.

Koyama, N., Nakamichi, M., Oda, R., Miyamoto, N., Takahata, Y., 2001. A ten-year summary of reproductive parameters for ring-tailed lemurs at Berenty, Madagascar. Primates 42, 1–14.

Kriesten, K., Murawski, U., 1988. Concentrations of serum cortisol, progesterone, estradiol-17β, cholesterol and cholesterol ester in the doe during the reproductive stadium, in the fetal serum, in the amniotic fluid and in the milk of rabbits, as well as correlations between these parameters. Comp. Biochem. Physiol. 90A, 413–420.

Lewis, S.E., Pusey, A.E., 1997. Factors influencing the occurrence of communal care in plural breeding mammals, in: Solomon, N.G., and French, J.A. (Eds.), Cooperative Breeding in Mammals, Cambridge University Press, Cambridge, pp. 335–363.

Lockwood, C.J., Radunovic, N., Nastic, D., Petkovic, S., Aigner, S., Berkowitz, G.S., 1996. Corticotropin-releasing hormone and related pituitary-adrenal axis hormones in fetal and maternal blood during the second half of pregnancy. J. Perinat. Med. 24, 243–251.

Mendel, C.M., 1989. The free hormone hypothesis: a physiologically based mathematical model. Endocr. Rev. 10, 232–274.

Morimoto, I., Yamamoto, S., Kai, K., Fujihira, T., Morita, E., Eto, S., 2000. Centrally administered murine-leptin stimulates the hypothalamic–pituitary–adrenal axis through arginine-vasopressin. Neuroendocrinology 71, 366–374.

Nakamichi, M., Koyama, N., 1997. Social relationships among ring-tailed lemurs (*Lemur catta*) in two free-ranging troops at Berenty Reserve, Madagascar. Int. J. Primatol. 18, 73–93.

Nowak, K.W., Pierzchala-Koziec, K., Tortorella, C., Nussdorfer, G.G., Malendowicz, L.K., 2002. Effects of prolonged leptin infusion on rat pituitary–adrenocortical function. Int. J. Mol. Med. 9, 61–64.

Nunn, C.L., Pereira, M.E., 2000. Group histories and offspring sex ratios in ringtailed lemurs (*Lemur catta*). Behav. Ecol. Sociobiol. 48, 18–28.

Pereira, M.E., 1993. Agonistic interaction, dominance relation, and ontogenetic trajectories in ring-tailed lemurs, in: Pereira, M.E., Fairbanks, L. (Eds.), Juvenile Primates, Oxford University Press, New York, pp. 285–309.

Pereira, M.E., 1995. Development and social dominance among group-living primates. Am. J. Primatol. 37, 143–176.

Pereira, M.E., Izard, M.K., 1989. Lactation and care for unrelated infants in forest-living ring-tailed lemurs. Am. J. Primatol. 18, 101–108.

Pereira, M.E., Kappeler, P.M., 1997. Divergent systems of agonistic relationships in lemurid primates. Behaviour 134, 225–274.

Pereira, M.E., Strohecker, R., Cavigelli, S., Hughes, C., Pearson, D., 1999. Metabolic strategy and social behavior in Lemuridae, in: Rasamimanana, H., Rakotosamimanana, B., Ganzhorn, J., Goodman, S. (Eds.), New Directions in Lemur Studies, Plenum Press, New York, pp. 93–118.

Phillips, C.J.C., Rind, M.I., 2002. The effects of social dominance on the production and behavior of grazing dairy cows offered forage supplements. J. Dairy Sci. 85, 51–59.

Pruetz, J.D., Isbell, L.A., 2000. Correlations of food distribution and patch size with agonistic interactions in female vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. Behav. Ecol. Sociobiol. 49, 38–47.

Rasamimanana, H.R., Rafidinarivo, E., 1993. Feeding behavior of *Lemur catta* females in relation to their physiological state, in: Kappeler, P.M., Ganzhorn, J.U. (Eds.), Lemur Social Systems and Their Ecological Basis, Plenum Press, New York, pp. 123–133.

Ray, J.C., Sapolsky, R.M., 1992. Styles of male social behavior and their endocrine correlates among high-ranking wild baboons. Am. J. Primatol. 28, 231–250.

Roozendaal, B., 2000. Glucocorticoids and the regulation of memory consolidation. Psychoneuroendocrinology 25, 213–238.

Rowell, T.E., 1974. The concept of social dominance. Behav. Biol. 11, 131–154.

Saltzman, W., Prudom, S.L., Schultz-Darken, N.J., Abbott, D.H., 2000. Reduced adrenocortical responsiveness to adrenocorticotropic hormone (ACTH) in socially subordinate female marmoset monkeys. Psychoneuroendocrinology 25, 463–477.

Saltzman, W., Schultz-Darken, N.J., Scheffler, G., Wegner, F.H., Abbott, D.H., 1994. Social and reproductive influences on plasma cortisol in female marmoset monkeys. Physiol. Behav. 56, 801–810.

Saltzman, W., Schultz-Darken, N.J., Wegner, F.H., Wittwer, D.J., Abbott, D.H., 1998. Suppression of cortisol levels in subordinate female marmosets: reproductive and social contributions. Horm. Behav. 33, 58–74.

Sapolsky, R.M., 1982. The endocrine stress-response and social status in the wild baboon. Horm. Behav. 16, 279–292.

Sapolsky, R.M., 1993. The physiology of dominance in stable versus unstable social hierarchies, in: Mason, W.A., Mendoza, S.P. (Eds.), Primate Social Conflict, State University of New York Press, Albany, pp. 171–204.

Sapolsky, R.M., Ray, J.C., 1989. Styles of dominance and their endocrine correlates among wild olive baboons (*Papio anubis*). Am. J. Primatol. 18, 1–13.

Sapolsky, R.M., Uno, H., Rebert, C.S., Finch, C.E., 1990. Hippocampal damage associated with prolonged glucocorticoid exposure in primates. J. Neurosci. 10, 2897–2902.

Sauther, M.L., 1992. The effect of reproductive state, social rank and group size on resource use among free-ranging ringtailed lemurs (*Lemur catta*) of Madagascar. Ph.D. Washington University.

Sauther, M.L., 1993. Resource competition in wild populations of ring-tailed lemurs (*Lemur catta*): implications for female dominance, in: Kappeler, P.M., Ganzhorn, J.U. (Eds.), Lemur Social Systems and Their Ecological Basis, Plenum Press, New York, pp. 135–152.

Sauther, M.L., 1998. Interplay of phenology and reproduction in ring-tailed lemurs: implications for ring-tailed lemur conservation. Folia Primatol. 69, 309–320.

Sauther, M.L., Sussman, R.W., 1993. A new interpretation of the social organization and mating system of the ring-tailed lemur (*Lemur catta*), in: Kappeler, P.M., Ganzhorn, J.U. (Eds.), Lemur Social Systems and Their Ecological Basis, Plenum Press, New York, pp. 111–121.

Sauther, M.L., Sussman, R.W., Gould, L., 1999. The socioecology of the ringtailed lemur: thirty-five years of research. Evol. Anthropol. 8, 120–132.

Schwartz, M.W., Seeley, R.J., 1997. Neuroendocrine responses to starvation and weight loss. N. Engl. J. Med. 336, 1802–1811.

Shively, C.A., Laber-Laird, K., Anton, R.F., 1997. Behavior and physiology of social stress and depression in female cynomolgus monkeys. Biol. Psychiatry 41, 871–882.

Silk, J.B., 1993. The evolution of social conflict among female primates, in: Mason, W.A., Mendoza, S.P. (Eds.), Primate Social Conflict, State University of New York Press, Albany, pp. 49–83.

Smith, T.E., French, J.A., 1997. Social and reproductive conditions modulate urinary cortisol excretion in black tufted-ear marmosets (*Callithrix kuhli*). Am. J. Primatol. 42, 253–267.

Sokal, R.R., Rohlf, F.J., 1995. Biometry. W. H. Freeman, New York.

Stavisky, R.C., Adams, M.R., Watson, S.L., Kaplan, J.R., 2001. Dominance, cortisol, and behavior in small groups of female cynomolgus monkeys (*Macaca fascicularis*). Horm. Behav. 39, 232–238.

Sussman, R.W., 1991. Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve Madagascar. Am. J. Phys. Anthrop. 84, 43–58.

Taylor, L., Sussman, R.W., 1985. A preliminary study of kinship and social organization in a semi-free-ranging group of *Lemur catta*. Int. J. Primatol. 6, 601–614.

Tilden, C.D., Oftedal, O.T., 1997. Milk composition reflects pattern of maternal care in prosimian primates. Am. J. Primatol. 41, 195–211.

van Schaik, C.P., 1989. The ecology of social relationships amongst female primates, in: Standen, V., Foley, R.A. (Eds.), Comparative Socioecology: The Behavioral Ecology of Human and Other Mammals, Blackwell Scientific Publications, Boston, pp. 195–218.

Vick, L.G., Pereira, M.E., 1989. Episodic targeting aggression and the histories of *Lemur* social groups. Behav. Ecol. Sociobiol. 25, 3–12.

Virgin, C.E., Sapolsky, R.M., 1997. Styles of social behavior and their endocrine correlates among low-ranking baboons. Am. J. Primatol. 42, 25–39.

Wasser, S.K., Monfort, S.L., Southers, J., Wildt, D.E., 1994. Excretion rates and metabolites of oestradiol and progesterone in baboon (*Papio cynocephalus cynocephalus*) faeces. J. Reprod. Fertil. 101, 213–220.

Whitten, P.L., Brockman, D.K., Stavisky, R.C., 1998. Recent advances in noninvasive techniques to monitor hormone–behavior interactions. Ybk. Phys. Anthropol. 41, 1–23.

Woodley, S.K., Matt, K.S., Moore, M.C., 2000. Neuroendocrine responses in free-living female and male lizards after aggressive interactions. Phys. Behav. 71, 373–381.

Wrangham, R.W., 1980. An ecological model of female-bonded primate groups. Behaviour 75, 262–300.