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Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*)

R. Ethan Pride
Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08525, USA

Adaptive explanations for social grouping assume that there are fitness consequences associated with group size, and individuals maintain membership in groups of favorable size to maximize fitness. Here I examine fecal cortisol concentrations as a hormonal measure of stress to assess the relative well-being of *Lemur catta* in groups of different size and in seasons of normal and low tamarind fruit availability. I test the hypotheses that there is an optimal group size at which cortisol is lowest and that optimal group size changes in food-scarce conditions. I collected 799 fecal samples from 87 individuals in seven free-ranging *L. catta* groups at Berenty Reserve, Madagascar, over a 1-year period (August 1999–July 2000) and determined fecal cortisol concentrations using a radioimmunoassay. Expressing these as residuals from monthly population means to control for temporal fluctuations in cortisol concentration, I calculated mean fecal cortisol levels for each animal in seasons of normal and low tamarind fruit abundance and over the entire year. Overall, females exhibited lowest mean cortisol levels in groups of intermediate size, suggesting that there are benefits to maintaining membership in these groups. Females in groups that were atypically large or small for their habitat type had higher mean cortisol levels than typical groups. Cortisol levels increased in food-scarce conditions for larger groups, suggesting that intergroup competitive advantages do not outweigh intragroup feeding competition at this time. Group size may be optimized for long-term average conditions, and short-term stresses may intermittently alter the costs associated with group size. *Key words:* cortisol, group size, *Lemur catta*, stress. *[Behav Ecol 16:550–560 (2005)]*

The general theoretical framework for explaining variation in group size assumes that there are fitness consequences associated with group size and that individuals maintain membership in groups of favorable size to maximize fitness (Wrangham, 1980). Many studies of nonhuman primates have examined various costs and benefits associated with social grouping (Sterck et al., 1997), typically by comparing differences in behavior (Chapman and Chapman, 2000) and fitness parameters (Takahata et al., 1998; van Noordwijk and van Schaik, 1999) among groups of different size. In this paper, I complement these studies by examining cortisol, a steroid hormone secreted in response to environmental stressors, to investigate how stress levels vary with group size in *Lemur catta*, a social primate, and how the stress pattern responds to short-term changes in food availability.

Advantages of cortisol as an indicator

Behavioral studies are capable of showing with great sensitivity how organisms respond to short-term or subtle environmental stressors, and many studies have shown behavior varying with group size in primates (reviewed in Chapman and Chapman, 2000). However, it may be difficult to assess the relative importance of different stressors based solely on behavior. Some behavioral costs may increase with group size (e.g., foraging effort, day range, agonism), while others simultaneously decrease with group size (e.g., predator detection, territory or food patch defense). Without the ability to determine their relative scaling, we are unable to weigh the importance of these opposing costs that animals trade off and cannot therefore determine what the optimal group size would be or even if an optimum exists at all.

Address correspondence to R.E. Pride, who is now at Department of Biology, The College of New Jersey, Ewing, NJ 08628, USA. E-mail: pride@tcnj.edu.

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However, we can use cortisol analysis to estimate animals' overall physiological well-being in these various social conditions. Cortisol is a steroid hormone secreted in the general vertebrate stress response to noxious environmental stimuli and is commonly used as an indicator of stress in wild animals (Wingfield and Romero, 2001). High cortisol levels are characteristic of animals facing immediate environmental challenges such as cold weather (Rogers et al., 1993), predation (Bateson and Bradshaw, 1997; Scheuerlein et al., 2001), conspecific agonism (Alberts et al., 1992; Sapolsky, 1983), and food scarcity (Foley et al., 2001; Romero and Wikelski, 2001). One of cortisol's primary metabolic functions is to divert energy from long-term storage for immediate use (Sapolsky et al., 2000). Although this current expenditure does not necessarily mean lower lifetime reproductive success, it does indicate metabolic costs imposed by current environmental stressors, which will lower lifetime reproductive success if sustained. As high cortisol levels are associated with well-studied detrimental health risks (Sapolsky, 1998), and can predict mortality risk in *L. catta* and other wild animal populations (Pride, in press; Romero and Wikelski, 2001), the "stress landscape" shown by cortisol patterns may approximate the fitness landscape to which animals adapt. Cortisol analysis therefore offers an independent assessment of costs based on the subject's internal state, complementing those deduced from external behavior or ecological conditions.

Because cortisol levels can be estimated from fecal samples (Wasser et al., 2001; Whitten et al., 1998), it is possible to obtain noninvasive measurements of physiological well-being from each individual. More importantly, because animals defecate far more often than they reproduce or die, we can obtain measurements with much greater frequency than studies of reproductive success alone. This allows us to identify even brief or low-level environmental stressors that would not be revealed in short-term fitness measures. Cortisol provides a measure of current physiological status and therefore can more directly indicate instantaneous costs that are integrated through time to produce an effect on fitness. In addition, cortisol analysis yields a graded response, whereas short-term reproductive success in

species such as *L. catta* is annually discrete, involving only one reproductive attempt per year. While Darwinian fitness remains the ultimate dependent variable of interest, cortisol offers greater sensitivity to environmental stressors and thus may be better at allowing us to characterize potential selection pressures in advance of the long-term demographic study that is necessary to demonstrate numerical responses to these pressures. Insofar as cortisol or other glucocorticoid measures can be taken to approximate fitness costs (Pride, in press; Romero and Wikelski, 2001), they may help us determine if there is an optimal group size and the extent to which the optimal group size is modulated by the environmental context.

Here, I define "optimal group size" to be the size at which animals have maximum expected fitness in a given environment. I make the assumptions that animals are most likely to achieve maximum fitness when they are exposed to fewest environmental challenges and that in this condition they exhibit lowest cortisol levels.

Costs associated with primate group size

Theoretical treatments of primate group size state that there are net fitness costs associated with being in groups that are too large or too small (Chapman and Chapman, 2000) and that these opposing costs are minimized at an intermediate optimum size (Figure 1a). The primary cost of being in a large group is generally considered to be greater intragroup food competition: as group size increases, a given food supply will be divided among more rivals (exploitation competition), and interaction among rivals may prevent individuals from harvesting the food efficiently (interference competition) (Sterck et al., 1997). There are several possible benefits of being in a large group. According to the "resource defense model" (Wrangham, 1980), animals in small groups have fewer partners to defend territory or food patches against larger rival groups and a greater risk of exclusion from food patches. If food patch quality is variable and patches are defensible, intergroup food competition may favor larger groups that can monopolize the most valuable resources. When defense of food patches (or other resources) does not provide net benefits, then large group size may still be favored as defense against predation or infanticide because animals in large groups have more partners to detect and deter attacks and a lower chance of being the victim given an attack (van Schaik, 1983; van Schaik and Kappeler, 1997).

Cortisol and optimal group size: predictions

If group size is adjusted to minimize the opposing costs associated with larger and smaller groups (Figure 1a), as is generally believed, we may expect that atypically small and atypically large groups have higher cortisol levels than groups of intermediate size, as animals in deviant groups suffer greater costs. Because optimal group size depends on the intensity of competition for food, we would expect that cortisol levels increase when food is scarce. Furthermore, we would expect that the optimal group size could either increase or decrease when food is scarce, depending on changes in the relative strength of intergroup versus intragroup feeding competition.

Food scarcity will *decrease* optimal group size when large groups face more intense intragroup food competition that is not compensated by their intergroup competitive advantages (Figure 1b). This can occur when scarcity results in less variation in food patch quality such that the even the best patches are not worth defending or when food sources are less defensible (Wrangham, 1980). Cortisol should rise most in large groups in these conditions due to greater intragroup competition.

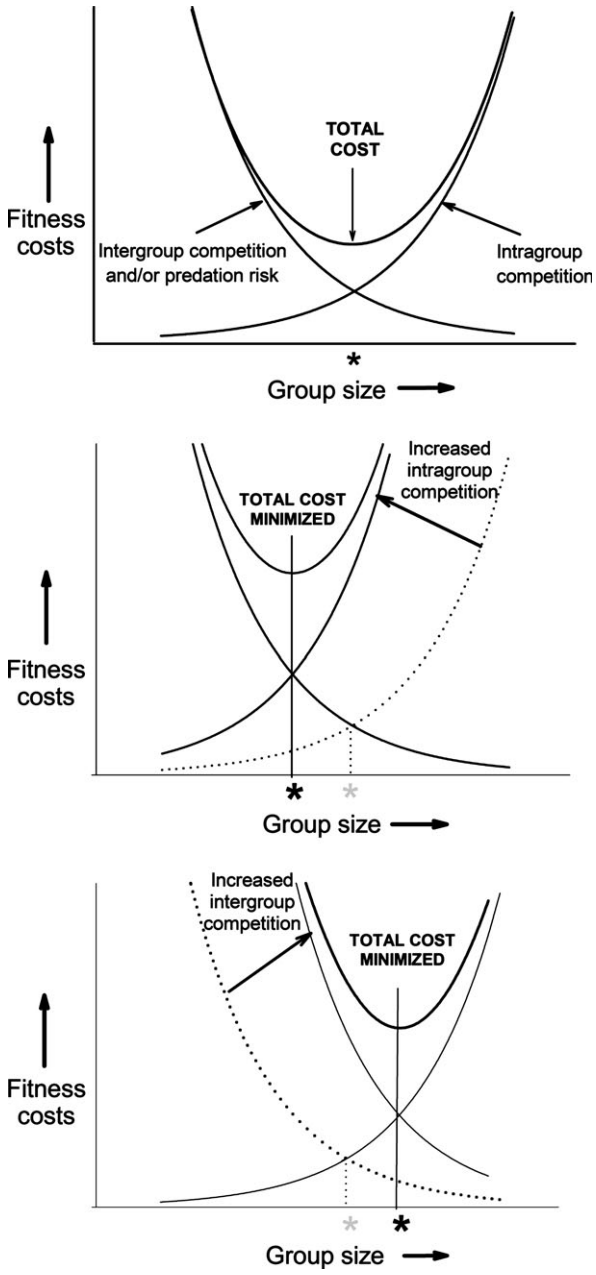

Figure 1
(a) Basic group size model. The central U-shaped curve represents the sum of fitness costs associated with group size, and the asterisk indicates the optimal size at which individuals experience lowest costs. (b) If food scarcity primarily increases intragroup feeding competition (e.g., if food patches are less productive), large groups suffer disproportionately, decreasing the optimal group size. (c) If food scarcity primarily increases intergroup competition for food patches (e.g., if food patches are fewer), small groups suffer disproportionately as they are excluded from food patches by larger groups. Optimal group size increases.

Food scarcity will *increase* optimal group size when resource defense benefits outweigh high intragroup feeding competition in large groups (Figure 1c). This can occur if food scarcity increases the supply or defensibility of high-quality food patches, thus increasing intergroup competition. Cortisol should rise most in small groups as they are excluded from these food patches by larger groups.

Hypotheses

In this paper, I evaluate the relationship between cortisol and group size in *L. catta*. I test the hypotheses that:

1) Cortisol will be higher in atypically large and small groups than in groups of intermediate size. If cortisol is lowest in groups of intermediate size, this will support the assumption of group size models that costs vary with group size and that animals tend to maintain membership in group sizes that minimize these costs. While the group size most commonly observed is not necessarily the optimum, as immigration and successful reproduction tend to push groups above the optimal size (Giraldeau, 2003; Sibley, 1983), groups that deviate substantially from an optimal size will suffer costs and therefore are likely to be found less frequently.
2) Optimal group size, as indicated by lowest cortisol, will change in months of low food availability due to greater feeding competition. If group size associated with lowest cortisol varies with food availability, this will further support the assumption that group size is regulated by ecological pressures and demonstrate that the effects of group size depend on ecological context. Furthermore, the direction of the change will indicate the relative importance of intragroup versus intergroup food competition in food-scarce conditions.

If these hypotheses are not supported, then group size may be determined by forces other than those proposed by current optimality models and further influences must be considered.

STUDY SUBJECTS

L. catta are diurnal prosimian primates that inhabit southern and southwestern Madagascar. They are eclectic omnivores (Budnitz and Dainis, 1975; Rasamimanana and Rafidinarivo, 1993; Sauther et al., 1999; Sussman, 1974). They are characterized by strict female dominance and feeding priority over males as well as by intrasex dominance relationships (Jolly, 1966, 1984; Sauther, 1993). They live in female-bonded social groups of variable size that defend food patches or territory from rival groups (Sauther et al., 1999). Males emigrate between groups at maturity and every 3–5 years thereafter, while females typically spend their entire lives with their natal groups or a fissioned splinter group (Jones, 1983; Koyama et al., 2002; Sussman, 1992). Groups therefore consist of related females, their offspring, and immigrant males; adult sex ratio within groups is approximately 1:1 (Koyama et al., 2001) or slightly female biased (Gould et al., 2003).

Group sizes vary across field sites in Madagascar. Long-term demographic studies at Beza Mahafaly Reserve report an average group size of 11.5 animals (4 adult females), with groups tending to fission at sizes of 14–21 animals (Gould et al., 2003; Sussman, 1991). Parallel studies at Berenty Reserve show an average group size of 12–16 noninfant animals (4–6 adult females), with groups tending to fission when they exceed 20–25 animals (Jolly et al., 2002; Koyama et al., 2002). This variation is likely to be due at least in part to differences in habitat quality, as average group size varies in different habitat regions of Berenty Reserve, with larger groups found in the most productive areas (Jolly et al., 2002), where population density is higher than at other field sites.

L. catta are highly adapted to a seasonally variable environment, with large fluctuations in rain and food availability across months. At Berenty Reserve, where this study was conducted, long-term meteorological data show 70% of annual rainfall (400/580 mm) falling in the months between November and February, with very little rainfall between May and September (Jolly et al., 2002). Phenological studies at Beza-Mahafaly Reserve show that availability of key food sources peaks in the months between October and March (Sauther, 1998), although these appear to be 1 month earlier at Berenty (Jolly A, personal communication; personal observation). *L. catta* reproduction is strictly seasonal, with infants weaned when food availability is usually highest (February), as would be predicted by life-history theory (Jolly, 1966; Lack, 1968; Petter-Rousseaux, 1968). Other apparent adaptations to the predictable seasonal harshness include endogenous seasonal changes in food intake/satiation levels, metabolic hormones, fatness, and fur growth (Pereira, 1993b; Pereira et al., 1999). Two distinctive *L. catta* social traits, female dominance and targeted aggression, are also possible adaptations to the seasonally harsh environment (Jolly, 1984; Pereira, 1995), as are seasonal changes in aggression (Sauther, 1993). In general, *L. catta* have been selected to respond to predictable seasons of harshness and abundance.

STUDY SITE

Berenty Reserve is a 240-ha private reserve in southern Madagascar. Its resident *L. catta* population, currently 350 animals distributed in 30 groups, has been the subject of demographic and behavioral study for four decades (Jolly and Pride, 1999; Koyama et al., 2001, 2002; Petter-Rousseaux, 1968). The reserve is well protected from hunting and receives approximately 7000 tourists each year (Rakotomalala C, personal communication), so animals are habituated to humans.

Berenty contains three habitat zones (Gallery, Scrub, Tourist), each of which differs in vegetation: closed-canopy gallery forest (dominated by *Tamarindus*, *Rinorea*, *Acacia*, *Celtis* trees), emergent canopy spiny forest (dense underbrush with *Tamarindus*, *Acacia*, *Euphorbia*, *Alluaudia* trees), and an open hotel garden with exotic ornamental vegetation (*Azadirachta*, *Eucalyptus*, *Cassia*) as well as many native species. Mean group sizes for each habitat zone are 16 animals in the Tourist zone, 13 animals in the Gallery forest, and 9 animals in the Scrub, determined by 290 group counts in 19 years between 1963 and 2000 (Jolly et al., 2002) and 52 group counts in 10 years between 1989 and 1999 (Koyama et al., 2002). Variation in group sizes within each habitat is centrally distributed around the mean group size, such that the mean group size is representative for each habitat.

While most years the weather at Berenty Reserve shows the predictable seasonality to which *L. catta* have adapted, annual rainfall and fruit abundance can deviate dramatically in some years. Recent recorded annual precipitation levels (1983–2000) have ranged between 226 and 911 mm (Jolly et al., 2002), while *Tamarindus indica* fruit counts show similarly large fluctuations (Koyama et al., 2002). This variability intermittently intensifies environmental stresses; in some years (as during this study) the rain and fruit abundance of the typical rainy season fails to appear. The deviation from the expected seasonal pattern provides an excellent opportunity to examine the effect of ecological stressors that may have shaped the adaptations listed above and the role they may play in determining group size.

METHODS

Study design

I observed five groups of ring-tailed lemurs at Berenty Reserve, Madagascar, over a 1-year period (August 1999–July 2000).

Table 1
Groups studied: size and composition

Group	Total group size	Adults: ♂/♀	Habitat	Relative size for habitat?
A2	26 (26)	9/10	Tourist	Atypical (153%)
A1	19 (19)	6/6	Tourist	Typical (118%)
D1	14.5 (13–16)	4–6/6–8	Gallery	Typical (112%)
CX	9 (8–10)	1–3/4	Gallery	Atypical (69%)
SB	9 (9)	2/4	Scrub	Typical (100%)
SB2	9.5 (9–10)	3/5	Scrub	Typical (106%)
SE2	5.5 (4–8)	1–4/3	Scrub	Atypical (61%)

I observed an additional group from August to November 1999, after which it shifted its range out of the Reserve, and I observed a neighboring group for the remainder of the study. Table 1 lists the groups studied, their size, and whether they were of typical size for their habitat, based on long-term mean group sizes reported by Jolly et al. (2002) and Koyama et al. (2002). The total group size reported in Table 1 is the mean group size for each troop across months it was studied, with the range in brackets.

Fecal samples

I collected 799 fecal samples opportunistically from noninfant animals during this time. Samples were collected immediately after an animal's defecation: date, time, and identity of the donor animal were recorded. Samples were stored in 95% ethanol at room temperature for 2–7 months and then stored frozen (−86°C) for 1–4 months until processing. To extract fecal cortisol, I evaporated off excess ethanol by leaving samples overnight under a fume hood and then freeze-dried the samples. I sifted each freeze-dried sample manually through a fine wire mesh, collected the fecal powder, and extracted steroids from 0.2 g of dried fecal powder into 2 ml of methanol by vortexing on a multipulse vortexer (Glas-Col, Terre Haute, Indiana, USA; pulse rate 1/s, speed 70, 30 min), centrifuging 20 min at 1 *g*, and collecting the supernatant (Wasser et al., 2001). Both powder and extract were stored at −20°C. Percent recovery was 89 ± 5% (mean ± SE, $n = 8$), comparable to that of previous methods (Cavigelli, 1999).

Glucocorticoid concentration

To quantify the concentration of glucocorticoids in each fecal sample, I used an I^{125} serum cortisol double-antibody radioimmunoassay kit (Pantex, Santa Monica, California, USA), as in prior *L. catta* studies (Cavigelli, 1999), with the following modifications. I further diluted the standard curve (1:20 instead of 1:10) because I extracted into twice the volume of methanol as Cavigelli (1999). I also evaporated off the methanol from each sample using forced nitrogen gas through an Evap-o-rac instead of using a centrifuge evaporation system. To achieve parallelism between the assay standard curve and the serially diluted fecal extract (1:1–1:16), I added 5 µl of charcoal-stripped fecal extract to the standard curve. The assay standard curve was parallel to the serially diluted fecal extract (ANCOVA: $F_{3,28} = 57.014$, $r^2 = .86$, $p = .0001$; Dilution $F_1 = 162.751$, $p = .0001$; Treatment $F_1 = 0.632$, $p = .433$; Dilution × Treatment $F_1 = 1.157$, $p = .291$). Because no chromatographic purification or high-performance liquid chromatography analysis of fecal extract was performed, glucocorticoid concentrations reported as "cortisol" comprise cortisol as well as other fecal steroid metabolites detected by the Pantex cortisol antibody. These fecal glucocorticoid concentrations have been shown to correlate with plasma glucocorticoid concentrations in *L. catta* (Cavigelli, 1999). Reported cross-reactivity for this antibody is 35% with corticosterone, 30% with 21-desoxycortisol, 17.5% with 11-desoxycortisol, 2.9% with progesterone, and <0.01% with androstenedione, androsterone, cholesterol, cortisone, dehydroepiandrosterone, dihydrotestosterone α- and β-estradiol, estriol, estrone, and testosterone. Assay sensitivity was 1 ng/ml.

Table 2
Mean cortisol concentrations by month

Month	Cortisol (mean ± SEM; log ng/g dry feces)	Samples collected
August	1.52 ± 0.05	104
September	1.50 ± 0.03	181
October	1.39 ± 0.04	102
November	1.52 ± 0.04	73
December	No data collected	
January	No data collected	
February	1.63 ± 0.06	48
March	1.67 ± 0.06	49
April	1.52 ± 0.08	44
May	1.39 ± 0.05	60
June	1.23 ± 0.04	77
July	1.37 ± 0.05	61

Samples were assayed in duplicate over 20 assays; intraassay variation was 6%; interassay variation from high, medium, and low serum controls (Bio-Rad Clinical, Anaheim, California, USA) was 6%, 7%, and 18%. Assay accuracy (100 × observed/expected) based on three controls/assay was 116 ± 5% ($n =$ 20 assays). Samples were rerun if duplicates had coefficients of variation greater than 5%. Fecal glucocorticoid concentrations are expressed in units of log ng/g dry feces as in prior studies (Cavigelli, 1999).

Because fecal samples were collected opportunistically, animals are not equally sampled in each month. To avoid confounding effects due to unequal sampling of individuals through seasonal variations, as well as to control for potential sample degradation (Khan et al., 2002), cortisol levels analyzed here are residuals from population mean levels in each month (Table 2). For each individual sampled, I calculated the mean fecal cortisol residuals over the entire year and analyzed these cortisol levels by group size for males and for females.

Using the individual animal as the sampling unit allows me to assess variation within a group as well as across groups. This is justified by evolutionary theory, as selection is generally strongest at the level of the individual, and biologically sensible, because individuals may respond differently to the same environmental stimuli. While the groups sampled in this study cover the full range of sizes observed in wild *L. catta*, coefficients of determination reported here reflect individuals in only seven groups. Due to the lack of replication at most group sizes, the predictive power of group size in general is expected to be lower than suggested by coefficients of determination reported here.

Because effects of group size may be stepwise rather than continuous, and I sample only seven points on the continuum of possible group sizes, here I analyze group size as a discrete independent variable using analysis of variance (ANOVA).

Habitat-specific comparisons

To account for possible differences in optimal group size by habitat (Tourist, Gallery, Scrub) that could confound overall group size comparisons, I compared cortisol of animals in groups that were close to the mean group size of their habitat

("typical": SB, SB2, D1, A1) with those that were substantially larger or smaller than the mean group size for their habitat ("atypical": SE2, CX, A2). Mean group sizes for each habitat were taken from long-term studies described above (Jolly et al., 2002; Koyama et al., 2002); I categorized a group as atypical if it was >30% larger or smaller than the mean group size in its habitat.

Seasonal changes

To determine if the lowest cortisol group size decreases under harsher ecological conditions, I divided the year into three seasons (based on the *L. catta* annual reproductive cycle) and characterized them based on rainfall and *T. indica* fruit abundance (described below). Seasons were birth/lactation (August–November), weaning/courtship (February–April), and postmating/gestation (May–July). Data are not available for December and January.

Characterization of *T. indica* fruit abundance

I performed monthly counts of mature *T. indica* fruit on two trees within each troop's home range. Because *L. catta* diets comprise a diverse assortment of fruit, flowers, and leaves, *T. indica* fruit counts represent only one food source. However, it was the dominant food source (personal observation: 20% of all foraging and 50% of all foraging on fruit based on point samples collected on all individuals in all months) and unlike most other food sources was used by all troops and across seasons.

Tamarind fruit was initially abundant but declined during the birth/lactation season, possibly due to depletion by lemurs (mean ± SD: 402 ± 600 fruit/tree). During a cyclone in October, most remaining fruit were blown off the trees, and trees themselves suffered serious damage. There was subsequently an abundance of fruit on the forest floor, which the lemurs exploited through November (personal observation), but by the end of January, the normally abundant tamarind fruit were completely absent. Immature fruit were starting to grow on the surviving trees at this time, but mature fruit abundance remained low (96 ± 160 fruit/tree) during the weaning/courtship season (February–April). In the postmating/gestation season (May–July), abundance returned to original high levels (427 ± 575 fruit/tree).

Scarcity shown by tamarind fruit in the weaning/courtship season was reinforced by the pattern of tourism; there are almost no tourists in the weaning/courtship season, so at the time that tamarind fruit were unavailable, the lemurs had no dietary supplementation by food scraps, garbage, or occasional proffered bananas that they may have received in the other "normal" seasons. Although the importance of such provisioning is uncertain (<1% of all recorded foraging in the Tourist region), it may have contributed to food scarcity in the weaning/courtship season. The only trees producing abundant fruit at this time were *Azadirachta indica*, planted at the edge of the reserve (personal observation), to which most groups did not have access. Based on half-hourly point samples collected 1 day per month on all individuals, total foraging on fruit other than *T. indica* and *A. indica* declined from 44 observations/month in the birth/lactation season to 11 observations/month in the weaning/courtship season, suggesting that availability of other fruit was also lower at this time.

Characterization of rainfall

Figure 2 displays rainfall observed during this study and expected rainfall based on long-term data for this study site

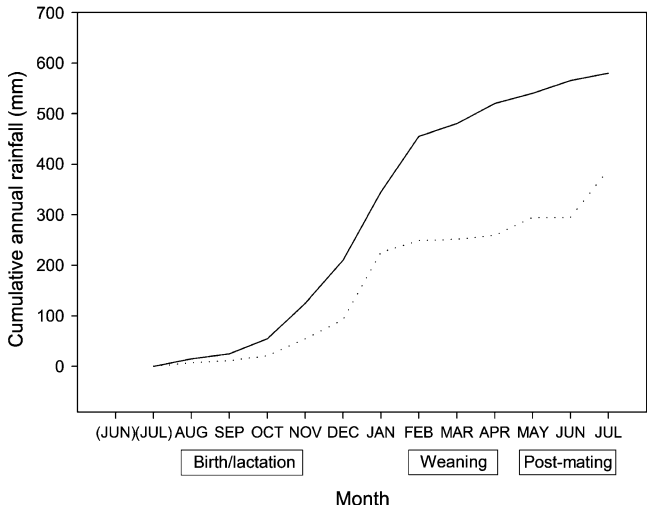

Figure 2
Annual cumulative rainfall during this study (1999–2000; dotted line) was lower than long-term averages (1985–2000; solid line). Rainfall in the birth/lactation season was not substantially different from normal levels (median deficit 10 mm/month), but rainfall in the weaning/courtship season was ~80% lower than normal (median deficit 35 mm/month). Rainfall in the postmating season was greater than normal, although this did not compensate for prior deficits.

(Jolly et al., 2002). Deviation from expected values may be more informative than raw values because *L. catta*'s many adaptations to their seasonally harsh habitat lessen the impact of predictable seasonal fluctuations, whereas unpredictable interannual variation (e.g., a drought) may considerably disrupt homeostasis. In the birth/lactation season (August–November), rainfall was slightly below long-term average levels, with a median monthly deficit of 10 mm. Rainfall was much below long-term average levels in the weaning/premating season (February–April), with a median monthly deficit of 35 mm. Rainfall in the postmating season (May–July) was not high enough to offset deficits accrued in the previous months but was greater than that observed in these months in typical years.

Summary of seasonal comparisons

Based on these characterizations, I classified the weaning/courtship season as *atypically harsh* and the other seasons as *normal*.

I calculated mean cortisol levels for each individual in each season and compared cortisol of individuals in groups of different sizes in each season. Because males and females are expected to be differently affected by environmental stressors, optimal group size may not be the same for males and females, and I considered the sexes separately in my analysis.

Comparison across years

Finally, to test whether the cortisol/group size relationship is consistent across years, I analyzed cortisol by group size for data collected in the birth/lactation season of the previous year (293 fecal samples, August–November 1998). The same groups were studied with the exception of one group (SE instead of SE2), and group sizes were different because of deaths, subsequent births, and emigrations: (SE and CX: 9.5 animals; SB and A1: 14.5 animals; D1: 18 animals; A2: 21 animals). Environmental conditions at that time showed that tamarind fruit and rainfall were abundant and therefore both

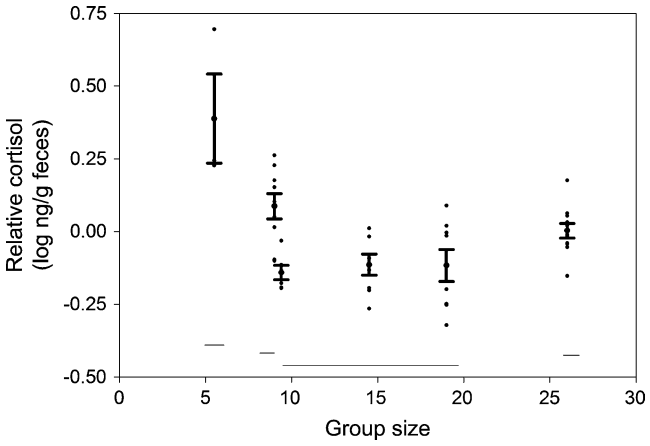

Figure 3
Average female cortisol levels were lowest in groups of intermediate size (9.5–19 animals). Each point represents the mean of all samples collected for a single individual from August 1999 to July 2000. Error bars on this figure and all subsequent figures show means ± SE. The three groups of intermediate size had significantly lower cortisol levels, and the smallest group was significantly higher than all other groups: 5.5 > (9 = 26) > (9.5 = 14.5 = 19).

1998 and 1999 birth season data would be expected to show the same pattern.

RESULTS

Average cortisol and group size

Females

Female mean cortisol levels were lowest at intermediate group size, with higher cortisol levels found in both very large and very small groups (Figure 3). Females in the smallest group (5.5 animals) had significantly higher cortisol than all other groups (mean ± SE: 0.39 ± 0.15 log ng/g feces); females in the largest group (26 animals) and the second smallest group (9 animals) had higher cortisol (0.00 ± 0.03 and 0.09 ± 0.04 log ng/g feces, respectively) than all other groups; and cortisol of females in the intermediate groups (9.5, 14.5, and 19 animals) did not differ significantly (mean range: −0.14 to −0.11; SE: 0.03 to 0.05) (Tukey-Kramer: $F_{5,39} = 10.800$, $r^2 = .58$, $p = .0001$). More of the variation (r^2) is accounted for if each group's mean cortisol is examined with respect to the number of adult females (Spline smoothing fit, $\lambda = 1$: $r^2 = .94$, SSE = 0.012) than the number of adult males (Spline smoothing fit, $\lambda = 1$: $r^2 = .77$, SSE = 0.049).

Mean cortisol levels did not differ between dominant females (two highest ranking females from each group) and subordinate females (Student's t test: $N_{dom} = 14$, $N_{sub} = 31$, $t = 0.876$, $p = .386$), and there was no interaction between dominance status and group size in predicting cortisol (ANOVA: Group size ($F_{5,33} = 8.56$, $p = .0001$); Status ($F_{1,33} = 1.94$, $p = .173$); Group size × Status ($F_{5,33} = 0.89$, $p = .500$)).

Habitat-based comparisons (females)

Female cortisol levels were significantly lower in groups of typical size for their habitat than those in groups that were larger or smaller (Student's t test: $N = 55$, $t = 3.488$, $p = .001$; Figure 4). Mean residual cortisol for females in typical groups was −0.10 ± 0.03 ($N = 33$) versus 0.08 ± 0.04 for atypical groups ($N = 22$). All three groups identified as having lowest female cortisol (SB2, D1, A1) were approximately at the mean size for their habitat types as revealed by long-term demography.

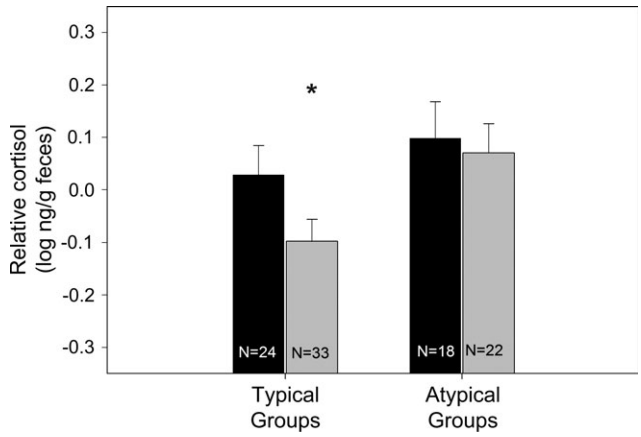

Figure 4
Females (light bars) in habitat-typical groups had significantly lower cortisol levels than those in larger or smaller groups. Males (dark bars) in habitat-typical groups did not have significantly lower cortisol levels.

Males

Male cortisol levels were elevated only in the smallest group (mean size of 5.5 animals: cortisol mean ± SE = 0.39 ± 0.16 log ng/g feces; other groups' means: −0.02 to 0.03, SE: 0.04 to 0.08) (Tukey-Kramer: $F_{5,36} = 3.524$, $r^2 = .33$, $p = .011$; Figure 5). The higher cortisol level in this smallest group was due exclusively to three males who were in the process of emigrating from the group. A fourth emigrating male had cortisol only slightly higher than the population mean level. Considering only nonemigrant males, then, group size did not predict male cortisol (ANOVA: $F_{5,24} = 0.544$, $r^2 = .10$, $p = .740$).

Male cortisol levels (mean ± SE = 0.059 ± 0.03) tended to be higher than female cortisol levels (−0.016 ± 0.03), although the difference is not significant (Student's t test: $N = 87$, $t = 1.757$, $p = .083$).

Habitat-based comparisons (males)

Cortisol was not significantly different between males in groups that were of typical size for their habitat (SB, SB2, D1, A1) versus those in groups that were larger or smaller (SE2, CX, A2) (Student's t test: $N = 42$, $t = 1.157$, $p = .254$;

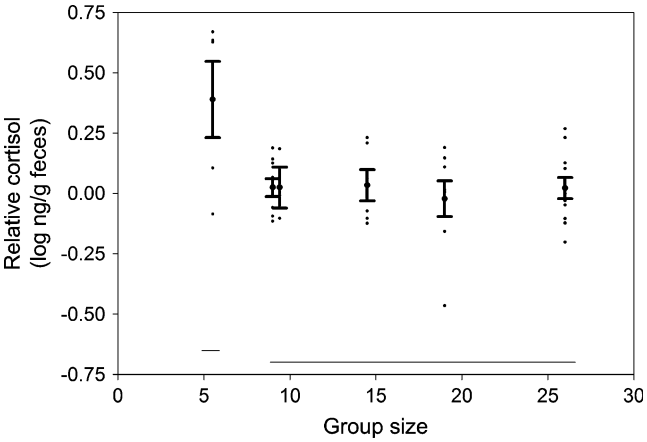

Figure 5
Male cortisol levels were elevated only in the smallest group of 5.5 animals. Each point represents the mean of all samples collected for a single individual from August 1999 to July 2000. Elevated levels in the smallest group are due entirely to emigrating males.

Figure 4). Mean residual male cortisol for typical groups was 0.03 ± 0.04 ($N = 24$) versus 0.10 ± 0.05 for atypical groups ($N = 18$).

Seasonal changes

Mean population cortisol was highest in February and March, the months of lowest rainfall and tamarind fruit availability (Table 2). However, as stated previously, comparisons across months are potentially confounded by sample degradation or endogenous cycling and should be interpreted with caution. All further analysis was done using residuals from these population monthly mean levels to show, at any given time, relative stress associated with group size.

Seasonal changes (females)

In the normal season of birth and early lactation (Figure 6a), females in the largest groups had significantly lower cortisol levels (5.5 animals: 0.39 ± 0.09; 9 animals: 0.14 ± 0.05; 14.5 animals: 0.01 ± 0.06; 19 animals: −0.19 ± 0.06; 26 animals: −0.10 ± .05) (Tukey-Kramer: $F_{4,34} = 10.574$, $r^2 = .55$, $p = .0001$). In contrast, during the unusually harsh weaning/courtship period (Figure 6b), females in the largest group had significantly higher mean cortisol (9 animals: −0.07 ± 0.10; 9.5 animals: −.0.23 ± 0.12; 14.5 animals: −0.37 ± 0.10; 19 animals: −0.01 ± 0.10; 26 animals: 0.41 ± 0.11) (Tukey-Kramer: $F_{4,32} = 7.374$, $r^2 = .48$, $p = .0003$). In the normal postmating/gestation season (Figure 6c), female cortisol did not significantly vary with group size (9 animals: 0.05 ± 0.09; 9.5 animals: −0.07 ± 0.11; 14.5 animals: 0.00 ± 0.11; 19 animals: −0.24 ± 0.10; 26 animals: 0.04 ± 0.08) (ANOVA: $F_{4,33} = 0.503$, $r^2 = .06$, $p = .503$).

Seasonal changes (males)

In the birth/lactation season (Figure 7a), cortisol was significantly higher only in the smallest group (group of 5.5 animals: mean ± SE: 0.51 ± 0.13; groups of 9–26 animals; mean range −0.06 to 0.14, SE range 0.09 to 0.15) (Tukey-Kramer: $F_{5,34} = 3.481$, $r^2 = .24$, $p = .012$). As discussed previously, the elevated cortisol in the smallest group was due to emigrating males, and cortisol did not differ among resident males at this time. In contrast, during the weaning/premating season (Figure 7b), male cortisol level increased linearly with group size (means ± SE: 9 animals: −0.18 ± 0.09; 9.5 animals: −0.22 ± 0.16; 14.5 animals: 0.01 ± 0.11; 19 animals: 0.28 ± 0.09; 26 animals: 0.49 ± 0.10) (Tukey-Kramer: $F_{4,18} = 8.376$, $r^2 = .57$, $p = .001$). A group's mean male cortisol level at this time was predicted better by the number of adult males in the group ($F_{1,4} = 74.009$, $r^2 = .95$, $p = .001$) than by number of adult females ($F_{1,4} = 5.661$, $r^2 = .59$, $p = .076$). In the postmating/gestation season (Figure 7c), male cortisol did not change with group size (ANOVA: $F_{4,26} = 2.592$, $r^2 = .19$, $p = .230$).

Comparison across years

Cortisol patterns from the previous 1998 birth/lactation season (normal rainfall and fruit abundance) were qualitatively similar to cortisol patterns observed in the 1999 birth/lactation season for both females and males (Figure 8). In 1998, mean female cortisol did not differ significantly among groups (ANOVA: $F_{3,40} = 4.264$, $r^2 = .16$, $p = .076$), but the trend suggests lower cortisol at an aboveaverage group size (18 animals), as was observed in 1999. Male cortisol levels in 1998 did not vary over the range of group sizes sampled (ANOVA: $F_{5,32} = 0.673$, $r^2 = .09$, $p = .647$); in 1999, cortisol levels were elevated in males emigrating from an even smaller group, but did not differ among groups over the same size range as sampled in 1998. Data from both males and females showed that the patterns observed in the normal birth/lactation season are consistent across years.

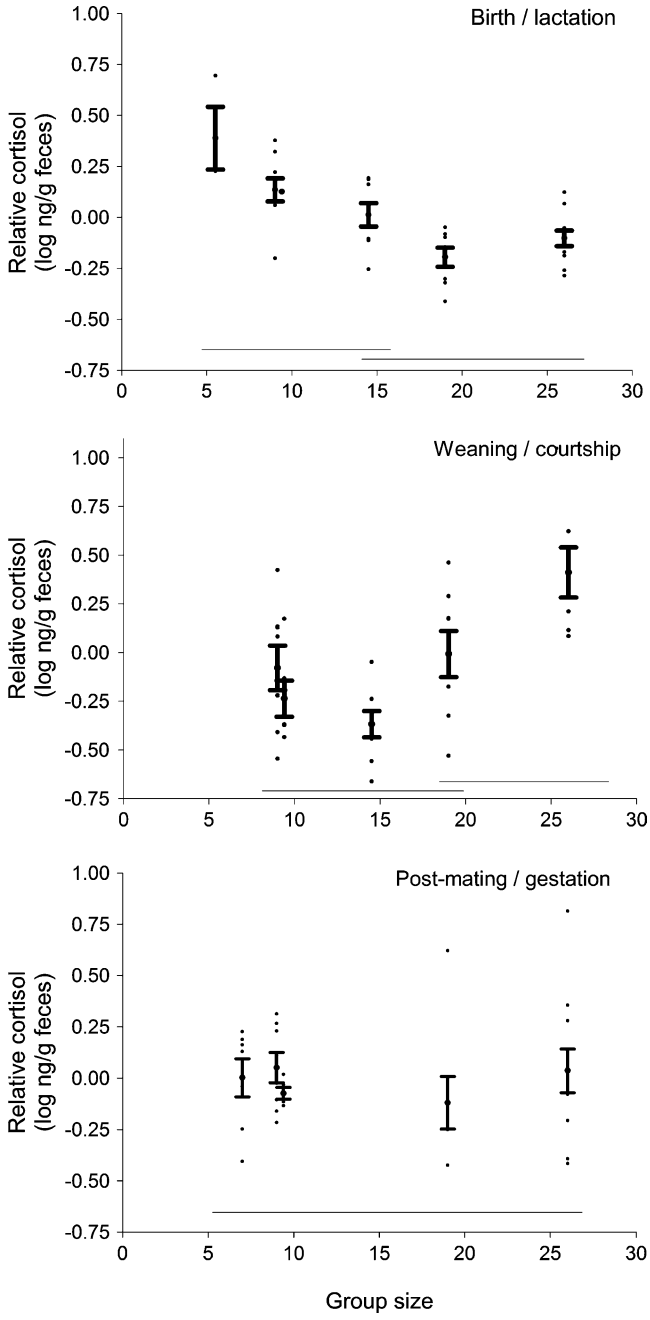

Figure 6
(a) In the birth/lactation season, female cortisol levels decreased with group size. (b) In the weaning/courtship season, female cortisol levels were elevated in the large groups. The group of 14 animals showed lowest cortisol. (c) In the postmating season, female cortisol levels did not vary with group size. Results at this time may have been confounded by a fission in one intermediate-sized group.

DISCUSSION

Female cortisol levels were lowest at intermediate group size

When averaged over the entire year, female cortisol levels were lowest at intermediate group size. As high cortisol

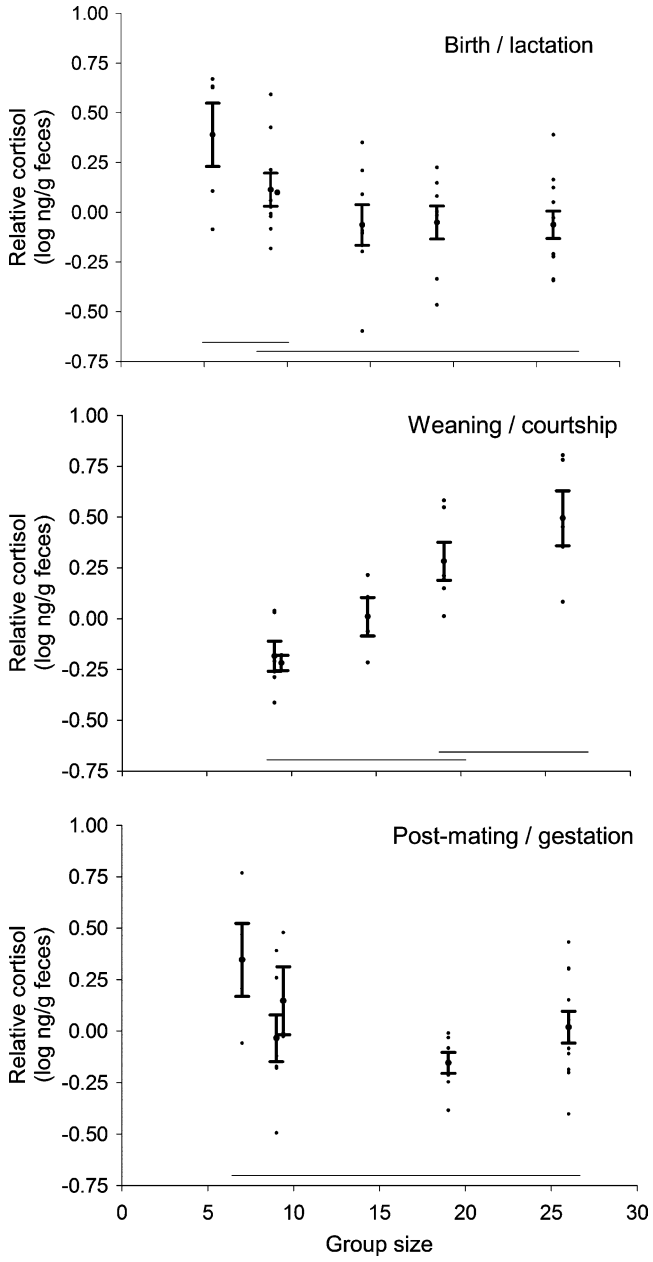

Figure 7
(a) Male cortisol levels were elevated only in emigrant males in the smallest group. (b) Male cortisol levels increased linearly with group size in the weaning/courtship season. (c) In the postmating season, male cortisol levels did not vary with group size.

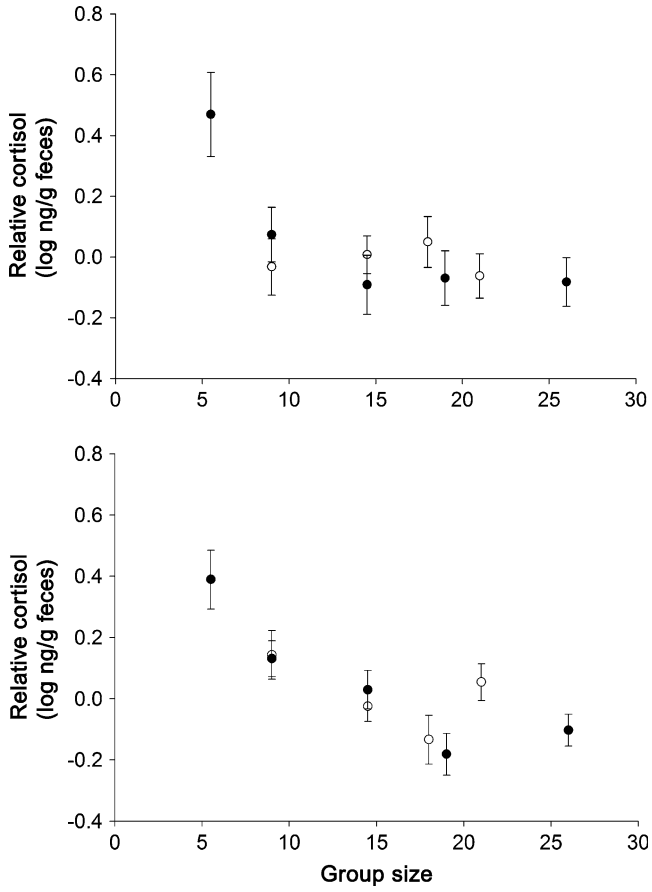

Figure 8
Cortisol patterns were consistent across years (open circles = 1998; closed circles = 1999) for (a) males; and (b) females. Rain and fruit availability were similar in both years.

indicates higher risk of mortality and disease (Pride, in preparation; Romero and Wikelski, 2001; Sapolsky, 1998), females in very large or very small groups may suffer higher survival costs. The range of group sizes at which lowest cortisol was observed (9–19 animals) brackets the mean group sizes observed in long-term studies at Berenty Reserve (Jolly et al., 2002). Groups are most likely to fission when they exceed 20 animals (Koyama et al., 2002), a size that was associated with higher cortisol in the present study. Groups of less than five animals are rarely found at Berenty (Jolly et al., 2002), and female cortisol was found to be very high in a group approximately this size. These data support the assumptions of general models of optimal group size, as there are costs associated with large and small group size. Females may maintain membership in groups of an intermediate size to minimize these costs.

Because optimal group size is habitat specific, differences in habitat among groups may confound the relative costs associated with a given group size. Groups sampled here were taken from all three of Berenty's habitat zones, each of which differs in vegetation and mean size of groups. This may be partly responsible for the broad range of group sizes (9.5–19 animals) across which cortisol was equally low. However, within-habitat comparisons suggest that individuals in group sizes typical for their habitat have lower cortisol than deviant (larger or smaller) groups. Furthermore, when cortisol levels are compared between the two groups of equal size (9 animals: CX and SB), there was a trend suggesting that mean cortisol was higher in the group that was more deviant from the typical size of its habitat. Overall, the data suggest that the relationship between low cortisol and typical group size is borne out both within and across habitat types.

However, it must be noted that typical group size was associated with low cortisol only when cortisol levels were averaged over normal and *atypically* harsh conditions. In normal conditions, larger group size was favored. If the weaning season had been highly productive, as usually occurs, intragroup competition would be lower and larger groups may be favored. If *L. catta* are maintaining membership in groups that minimize stress, they are optimizing over periods of time that include intermittently harsh conditions.

Cortisol levels were affected by group composition as well as group size, as female cortisol levels were better predicted by the number of females in the group than by the number of males. Females are dominant to males, have feeding priority over males, receive no aggression from males, and maintain some spatial segregation from males; so it is not surprising that their stresses may be intrasexually induced.

It is more surprising that cortisol levels of dominant and subordinate females did not systematically differ, as prior work has shown dominant females having higher levels (Cavigelli et al., 2003). This lack of concordance supports the conclusion that hormonal correlates of dominance are context dependent rather than intrinsically associated with dominance status. However, it is also notable that the study reporting the "stressed dominant" pattern had been found during the birth/lactation season on groups that were of typical size. In my study, I found that mean cortisol of dominant females was higher than that of subordinate females in each of the four smaller groups (<15 animals, similar in size to those observed by Cavigelli et al., 2003), whereas in the two largest groups (19 and 26 animals), it was the subordinate females that exhibited higher cortisol levels. It may be that as groups become very large, costs of subordination increase (e.g., due to greater intragroup feeding competition and targeted aggression), provoking a group fission. However, the differences across dominance status here were not significant, so any difference in optimal group size for dominants and subordinate individuals remains speculative.

Male cortisol levels varied with group size only prior to mating

Male cortisol averaged over the entire year did not depend on group size, within or across habitat types. Most males remain peripheral to the group of females they are associated with; if group size effects are due to crowding, males may not experience these effects as intensely as females. Males are also unlikely to face the same stressors as females; for example, the strongest behavioral predictor of high cortisol in *L. catta* females is intergroup agonism rate (Pride, in press), but males participate only minimally in intergroup conflicts.

The most likely reason that males in different groups exhibited similar cortisol levels is that, unlike females, males emigrate between groups, and may consequently be able to adopt an ideal free distribution with respect to the stress landscape, such that males in all groups experience similar conditions.

Seasonally, though, male cortisol is group size–dependent, increasing linearly with group size in the weaning/courtship period. This could be due to food scarcity, as males have lowest feeding priority within the group, and even females in large groups show increased cortisol at that time. However, as male-male competition intensifies in the premating period, with increased scent-marking displays and dominance contests (Gould and Overdorff, 2002; Jolly, 1966), it is also plausible that increased competition from having more male rivals is stressful for males. This would explain why cortisol variation is better predicted by number of males than females in the group at that time. It would also explain the abrupt change in group size of lowest cortisol for males that occurs just after mating. Prior to mating, males in large groups may pay higher costs of aggression, as they have more rivals for dominance than males in smaller groups. Because dominant males experience mating priority with estrous females (Koyama, 1988; Sauther, 1991) and may father most of the offspring, as has been shown in studies of captive groups (Pereira & Weiss, 1991), the payoff of being the dominant male could be greater in larger groups, with more females at stake, intensifying competition. After estrus, these costs immediately disappear, and group size no longer explains variation in male cortisol between groups. At least some of the male stress pattern may therefore be attributable to male mating competition. The additional costs of mate competition may be responsible for the trend of higher cortisol in males.

Males in the process of dispersal may also experience more stress and higher cortisol levels than resident males, as suggested by the high cortisol levels of males dispersing from the smallest study group, although further study is needed to determine the generality of these observations.

Cortisol levels increased when food was scarce

As data are available only for one harsh season, it is impossible to draw strong conclusions about the generality of this relationship. However, there are reasons to believe that the food scarcity had a direct role in elevating cortisol levels during the weaning/courtship season. First, the individual behaviors found to best predict females' cortisol at this time were daily food intake and intergroup agonism rates, which suggest the importance of feeding competition, while other factors (e.g., predator alarm rates) did not correlate (Pride, in press). It is also likely that *L. catta* have especially high energy demand during this time (February–April): physiological adaptations to the seasonal environment encourage fat storage and fur regrowth at this time (Pereira et al., 1999), intragroup feeding agonism increases (Sauther, 1993), females must transport and nurse increasingly large infants, and males engage in increased scent-marking displays and dominance contests (Jolly, 1966). During this study's weaning/courtship season, animals faced the combined effects of high energy demand and low food supply, and the increased competition for scarce food could have induced high cortisol levels. The increase in cortisol levels did not occur uniformly throughout the population and is therefore more likely to be due to environmental stress than to endogenous changes or sample degradation (Khan et al., 2002; Romero, 2002). One prior study of free-ranging elephants has also shown that cortisol levels elevate in the resource-poor dry season and that large groups have higher cortisol at this time (Foley et al., 2001), indicating that the patterns observed here may be generalized across taxa.

Optimal group size decreased when tamarind fruit was scarce

The group sizes associated with lowest cortisol levels changed with food availability, decreasing when abundance of tamarind fruit (and apparently all other fruit except *A. indica*) was lowest. This supports prevailing ecological models of group size, which assume that relative costs and benefits of group size are determined at least in part by competition for food (Chapman and Chapman, 2000). The increase in cortisol levels during the harsh season was most pronounced in large groups, suggesting that greater intragroup feeding competition was not outweighed by the ability to defend patches against rival groups.

There are two possible explanations for why larger groups would not derive food resource defense benefits: either the food patches were not worth defending or they were not defensible (Carpenter and MacMillen, 1976). It is highly doubtful that food resources were not worth defending in the harsh season: although no groups had access to fruiting *T. indica* trees, some groups did have access to (and exploited) *A. indica* trees, which were the only trees in the reserve producing abundant fruit at this time (personal observation), while other groups did not have access to them. However, these food resources may not have been defensible. Territorial incursions were more common in the harsh weaning season (Pride, in press), as many groups foraged in *A. indica* trees

planted in rows along roads at the edge of the reserve. While much of this food source was contained within large groups' ranges, the large linear arrangement may not have permitted the large groups to monopolize these resources. Although the large groups did actively evict rivals from them, their defense efforts clearly did not allow them to maintain exclusive use of these food patches. Indefensibility of food resources against stealthy intruders may have prevented larger groups from gaining resource-defense benefits to offset greater costs of intragroup feeding competition. Larger groups *were* favored in the birth season, when there was greater fruit productivity among tamarind trees, which are discrete and defensible patches. It is notable that Berenty's larger groups are found only where intergroup conflict rates are high (the Tourist region) (Pride, 2003), suggesting that the differences in typical group size across habitat regions results from individuals choosing to remain in larger groups where defense of food resources is most important. In Berenty's less productive (Gallery and Scrub) regions and at Beza Mahafaly Reserve lower intergroup encounter rates may favor a lower optimal size.

Intermittent stressors may limit group size

L. catta at Berenty maintain group sizes that have lowest cortisol when averaged across both normal *and* "atypically harsh" conditions. In the normal birth/lactation season, larger-than-average groups had lower cortisol. The fact that groups of this size are not more common may be due to the high interannual variation in ecological conditions (e.g., rainfall, fruit), which impose stresses on larger groups frequently enough to limit group size. Species with fission-fusion social systems manipulate the size of social groups to respond to these fluctuations in optimal group size on short timescales. *L. catta*, on the other hand, apparently regulate group size on a coarser temporal scale (Gould et al., 2003; Jolly et al., 2002; Koyama et al., 2002; Pereira, 1993a). By doing so, they sometimes bear costs of maintaining a sub-optimal group size, as cortisol data show here, and must rely on behavioral strategies, such as changing ranging behavior or time budgets, to mitigate this stress. However, as large groups showed increased cortisol in the harsh season, there are limits to the effectiveness of such measures. Maintaining a large group through drought conditions may be disadvantageous due to high food competition within the group, offsetting benefits accrued in more favorable times from antipredator or resource-defense advantages. Group size may be regulated not by costs that are uniformly present through time but rather by intermittent stressors in a temporally variable environment.

However, given that *L. catta* experience short-term environmental fluctuations that alter optimal group size, why do they not adjust group size on the same timescale, as in fission-fusion systems? Altering group size may require that individuals and subgroups reassess and reestablish territorial or dominance relationships, which can involve costs of increased agonism. Increased agonism in periods of social instability can substantially raise cortisol levels (Alberts et al., 1992) and is often seen when *L. catta* groups fission (Hood and Jolly, 1995; Koyama, 1991) as well as in the rare cases of troop fusion (Koyama et al., 2002). If these assessment costs are high, relative to the benefit of altering group size, animals may be better off maintaining stable groups that are intermittently suboptimal than attempting to regulate group size to match their changeable environment, particularly if the intermittent stress is unpredictable and short lasting. *L. catta* do optimize group size to match long-term average expectations, but fine tuning on a rapid timescale may simply be less efficient.

CONCLUSIONS

In summary, cortisol data provide a powerful validation of ecologically based group size models, showing physiological evidence that there are costs associated with group size and that these costs change in relation to food availability. I demonstrate that group size and ecological context interact to affect an animal's internal state, which may be a critical proximate factor linking these environmental pressures to individual fitness. In particular, data from cortisol suggest that in *L. catta*: (1) females experience lowest stress in groups of intermediate size and therefore benefit from maintaining membership in these groups; (2) male stress is only group size–dependent during the courtship season and may be due to mate competition; (3) short-term food scarcity is stressful, particularly for larger groups, suggesting that resource defense does not provide net benefits for large groups at this time; and (4) group size may be optimized for long-term average conditions, and short-term stresses may intermittently alter the costs associated with group size. Future work should address the mechanisms producing these patterns.

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