13
Resource Defense in *Lemur catta*: The Importance of Group Size

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13.1. Introduction

Why do *Lemur catta* live in groups? And why does this species form groups of different sizes in different areas? Long-term demographic studies have demonstrated persistent differences in typical *Lemur catta* group size in different locations, both within and across field sites (Sussman, 1991; Jolly et al., 2002; Koyama et al., 2002; Gould et al., 2003). At Berenty Reserve, these differences coincide with differences in habitat and population density (Jolly et al., this volume), ranging from 9 animals per group in the southern open-canopy "scrub" to 14–16 animals per group in the northern "tourist front" and Ankoba sections (Jolly et al., 2002; Koyama et al., 2002). In this chapter, we explore the hypothesis that female *L. catta* adjust group size in response to the intensity of intergroup competition for food resources. We also examine the ecological conditions in which intergroup resource defense may provide foraging advantages and thereby promote increased group size.

A simple ecological model of group size can be derived from the assumptions that (1) larger groups gain foraging advantages by acquiring or defending high-quality food resources from smaller groups; and (2) animals in larger groups suffer foraging disadvantages due to intragroup feeding competition. Animals should seek to maintain membership in larger groups until the costs of intragroup feeding competition balance the benefits of intergroup resource defense. This has been considered as one of the possible ultimate causes of social grouping in primates (Wrangham, 1980).

The model assumes that large groups can supplant smaller groups from food resources due to their greater fighting ability, that there is variation in food resource quality such that animals in large groups can gain energetic benefits by doing so, and that these resources are defendable (Wrangham, 1980). The model predicts that group size will be proportional to intergroup conflict rate, and large groups will always occupy the highest quality habitats or food patches (i.e., those in which their daily energy intake is highest).

Here we examine how well this model describes the behavior *L. catta* of Berenty Reserve. In particular, we ask the following questions:

1. Are observed group sizes proportional to intergroup conflict rates?
2. Does membership in a large group increase the chance of winning intergroup conflicts and/or lower resource defense costs?
3. Does resource defense provide foraging benefits to individuals in large groups (occupying best habitat and gaining greater food intake rates)?

13.2. Methods

We report data collected on six *L. catta* groups, representating the full range of group sizes typically observed at Berenty (Jolly et al., 2002). Data were collected over a 1-year period (August 1999 to July 2000). Groups studied are presented in Table 13.1.

13.2.1. Seasonal Characterization

Because costs and benefits of resource defense may vary with resource availability, we compare behavior of these groups in two distinct ecological conditions ("typical" and "food-scarce"), as well as based on year-long averages. The conditions of food scarcity described here refer not to the annual dry season to which *L. catta* are adapted (Sauther and Sussman, 1993; Pereira et al., 1999), but to an atypical period of food scarcity, occurring at a time of year usually associated with high food availability (Sauther, 1998). During the "typical" birth/lactation season, all groups could exploit fruiting *Tamarindus indica* trees within their ranges. For 2 months during this period, all groups foraged heavily on *Rinorea greveana*, which was also found within the typical ranges of all groups. During the "food-scarce" weaning season (February–April 2000), *Azadirachta indica* was the only fruiting tree and was found only within the typical range of one group (A2). Figure 13.1 shows the location of the fruit trees exploited by these groups and the typical ranges of these groups.

The atypical food scarcity can be attributed to a tornado in late 1999 that had destroyed one-third of the forest canopy trees, severely damaged another third of the trees, and blown most of the fruit and leaves off the trees (Jolly et al., 2001) such that the *Tamarindus indica* fruit commonly exploited by *L. catta* was almost entirely absent by February 2000; a concurrent drought may also have lowered

TABLE 13.1. Size and composition of study groups.

Group	Total group size	Adult males	Adult females
A2	26 (26)	9	10
A1	19 (19)	6	6
D1	14.5 (13–16)	4–6	6–8
CX	9 (8–10)	1–3	4
SB	9 (9)	2	4
SE2	5.5 (4–8)	1–4	3

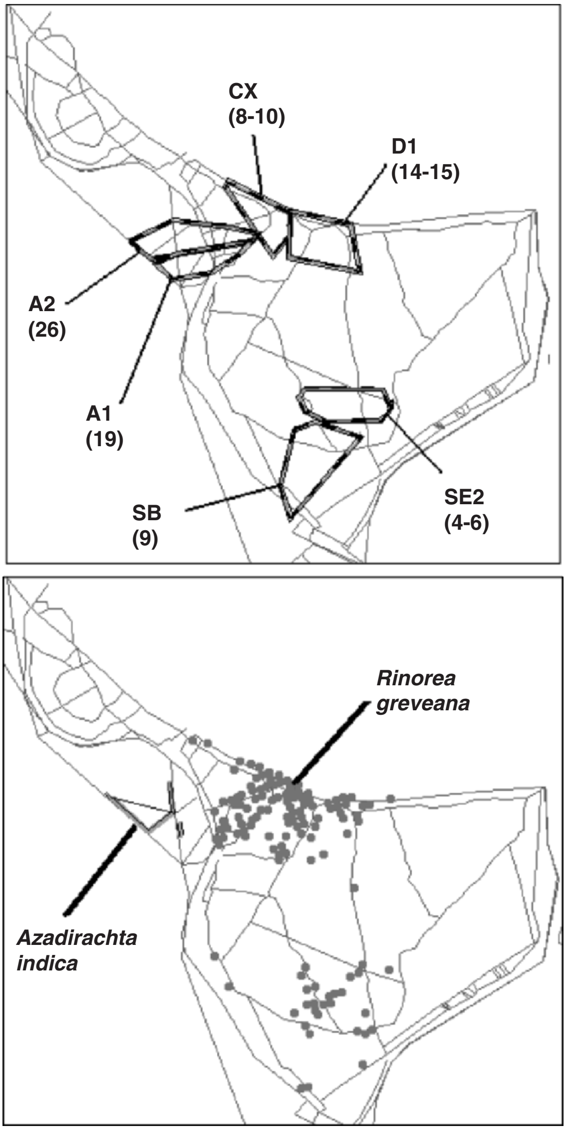


FIGURE 13.1. The top panel shows the sizes and typical ranges of the six study groups. Ranges shown are minimal convex polygons of the 85% most commonly used grid squares. The bottom panel shows the location of *R. greveana* trees exploited by these groups (the principal fruit source for 2 months in the "typical" season), and the location of the *A. indica* plantation (the only fruiting tree in the "food-scarce" season). Although all groups had access to *R. greveana* within their typical ranges, only the largest group maintained a range with *A. indica* trees.

productivity. Because high-quality food resources were scarce and female energetic demand was high, competition for food was likely to be intensified at this time.

13.2.1.1. Ranging

For each group, we recorded its location in the reserve (using a 25-m grid coordinate system) every 30 minutes during full-day follows (6:00 a.m. to 6:30 p.m.). We conducted 22 full-day follows for each of five groups (A2, A1, D1, CX, and SB); we conducted 13 full-day follows for the sixth group (SE2) under "typical" conditions but could not conduct follows in the "food-scarce" season because the group was ranging extensively outside of the reserve. We defined typical ranges for each group as the central 85% of locations recorded during full-day follows. We compared ranging in normal and food-scarce conditions by plotting day-ranges observed in normal conditions (N = 19 per group: August–November 1998, August–November 1999, May–July 2000) and food-scarce conditions (N = 3 per group: February–April 2000) using the range determination program Map (Williams, 1999). We then compared these to the distribution of available fruit trees in each season to determine the relative quality of ranges. Because food-scarce conditions were a brief aberration, only 3 day-ranges per group are available from this time period, and extent of ranging is likely to be underestimated at this time. However, *ad libitum* observation of troop locations during the food-scarce season (an additional 3–12 days per group) support the characterizations of each group's ranging determined from these day-range data.

13.2.1.2. Intergroup Conflict

We estimated intergroup conflict rates by recording all occurrences of intergroup encounters during full-day follows (typical season: August–November 1999; Food-scarce season: February–April 2000). We noted location, duration, which individuals participated at the maximum level of aggression for that encounter (displacement, lunges, physical contact), and which group withdrew/lost. We also determined the escalated defense rate, as this was found to correlate with high cortisol levels, and *L. catta* females may be particularly sensitive to this stressor (Pride, 2005a). Escalated defense encounters are those in which neither group immediately withdrew and which occurred inside the group's typical range. We then calculated these same rates at the individual level. We also calculated individual participation as the proportion of a group's observed conflicts in which a given individual participated at the maximum level for that encounter.

To determine if membership in large groups increases competitive ability, we compare proportion of conflicts won in large and small groups, indicating greater success, as well as individual participation per conflict in large and small groups, indicating lower *per capita* agonism costs. We considered number of adult females as well as group size as the independent variables in my analyses, because it is primarily the adult females that participate in intergroup agonism (Sauther, 1993). In each season, we determined each group's total intergroup conflict rate.

13.2.1.3. Food Intake

Feeding data are available on three adjacent groups (CX, A1, A2). We measured individual intake rates for two food items: *Rinorea greveana* fruit and *Azadirachta indica* fruit. *Rinorea greveana* was the primary fruit source exploited by *L. catta* for 2 months during the typical season (October–November: 165/580 feeding occurrences based on half-hourly scan samples); at this time, all groups had access to fruit-bearing trees within their typical ranges, as *R. greveana* was densely distributed throughout the gallery forest (Figure 13.1). *Azadirachta indica* was used heavily for 2 months in the food-scarce season (February–March: 228/574 feeding occurrences based on half-hourly scan samples); at this time, it was the sole fruit-bearing tree species. Most *L. catta* groups did not have fruiting trees within their typical ranges, as *A. indica* was planted only along roads as an ornamental tree near the hotel bungalows (Figure 13.1); among groups studied here, only the largest group (A2) had fruiting trees within its typical range at this time. *R. greveana* and *A. indica* provide good measures of individual differences in intake because the trees of both species are relatively small (~3–5m crown diameter), facilitating observation, and the fruit are small (1–2 cm) discrete items, consumed one at a time, so it was possible to obtain accurate fruit intake counts on the most heavily-used high-energy food items in both normal and food-scarce conditions.

For each individual, we calculated intake rates during foraging bouts on each species (the number of fruit consumed per unit time foraging on that species). During focal animal observations (Altmann, 1974), we recorded foraging duration by measuring the focal animal's start and stop times of active searching for fruit and counted the total number of fruit ingested during that time period. Because focal samples were taken randomly throughout the animals' entire daily active period, not exclusively while animals were foraging on these food sources, duration of foraging observations varied across individuals, and not all individuals or groups are evenly sampled (*A. indica* median: 16 minutes; range: 8.5–36 minutes; *R. greveana* median: 7 minutes; range: 4–16.2 minutes). However, there was no relationship between intake rate and duration sampled for *A. indica* (linear regression: $F_{1,20} = 0.073$, $r^2 = 0.00$, $p = 0.790$) or *R. greveana* (linear regression: $F_{1,9} = 0.292$, $r^2 = 0.04$, $p = 0.606$), and visual inspection of the data did not suggest that variance changed substantially with sample duration.

We estimated time spent foraging per day by recording behavior with instantaneous scan samples taken every 30 minutes from 6:00 a.m. to 6:30 p.m., one day per group per month, for the 2 months in which each fruit was eaten (*R. greveana*: October–November; *A. indica*: February–March). In a previous field season, it was determined that daily time spent foraging estimated from half-hourly scans correlate highly with that calculated from scans taken every 10 minutes ($r = 0.89$), and therefore give a fair estimate of daily time spent foraging.

For each individual in each season, we estimated food intake per day by multiplying fruit eaten per minute of foraging time times minutes spent foraging per day. We then compared food intake rates of animals in groups of different size in normal and food-scarce conditions to determine if animals gained foraging advantages through membership in larger groups in each condition.

13.3. Results

13.3.1. Are Group Sizes Proportional to Intergroup Conflict Rates?

Group size is directly proportional to intergroup encounter rate (linear regression: $F_{1,5} = 17.854$, $r^2 = 0.82$, $p = 0.013$). However, as number of adult males and offspring are likely to depend on the number of adult females in a matrifocal social system, and females are responsible for most intergroup conflicts, a comparison of number of females is more appropriate. Number of adult females per group increases with daily intergroup encounter rate (linear regression: $F_{1,5} = 17.631$, $r^2 = 0.82$, $p = 0.014$). Based on this regression, the number of adult females is predicted to be $1.5 + 2.5^*$(daily intergroup encounter rate). The relationship is similar if only escalated intergroup conflicts are considered (linear regression: $F_{1,5} = 19.679$, $r^2 = 0.83$, $p = 0.011$). Intergroup conflict rates from typical conditions may be more representative than the aberrant conditions of the atypical food-scarce season; if data from the atypically harsh weaning season are excluded, the relationship based on the 19 remaining appears non-linear (Figure 13.2).

Differences in intergroup conflict rates among Berenty's three habitat regions (Tourist = 2.7/day, Gallery = 1.7/day, Scrub = 0.4/day) parallel differences in group size among these regions observed in longterm demographic studies (Tourist = 14 to 16, Gallery = 13, Scrub = 9) (Jolly et al., 2002; Koyama et al., 2002). Similar variation in intergroup conflict rates among these regions have been noted in prior studies (Jolly et al., this volume).

13.3.2. Does Membership in Large Groups Increase Chances of Winning Intergroup Conflicts?

Proportion of conflicts won does not vary with group size (linear regression: $F_{1,5} = 0.058$, $r^2 = 0.01$, $p = 0.821$) or with number of adult females in group (linear regression: $F_{1,5} = 0.011$, $r^2 = 0.00$, $p = 0.920$), as shown by Table 13.2.

For the 188 observed conflicts in which the number of adult females in both rival groups is known, the larger group won in 103 instances, which was not

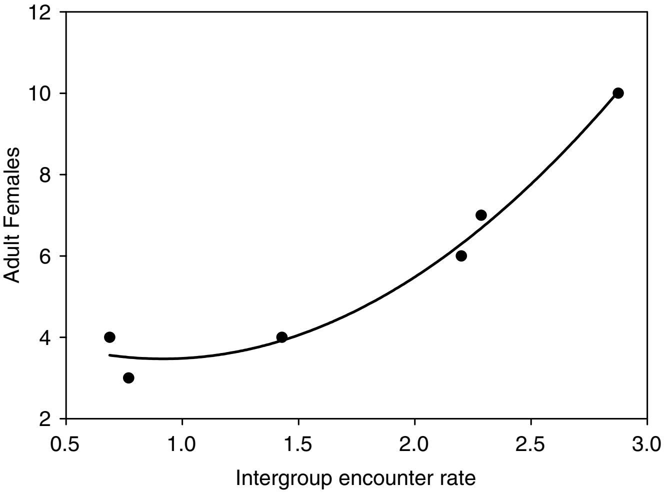


FIGURE 13.2. Number of adult females in a group is an increasing function of the intergroup conflict rate (encounters per day). Each point represents one of the study groups; intergroup conflict rate represents the average daily rate observed in typical seasons (August–November 1999; May–July 2000). The curve shows number of adult females predicted from a regression of number of adult females on daily intergroup encounter rate squared ($F_{1,4} = 73.605$, $r^2 = 0.95$, $p = 0.001$).

significantly greater than expected by chance (chi-square test: $\chi^2= 1.785$, $p= 0.182$). These results agree with prior studies (Jolly et al., 1993). A group's probability of winning an intergroup conflict did not vary with the difference in number of adult females between it and its opposing group (logistic regression: $N= 188$, $\chi^2 = 1.068$, $r^2 = 0.00$, $p = 0.302$).

Outcome of intergroup conflicts depended not on group sizes but on location, with groups tending to win conflicts within their typical ranges (Figure 13.3). Groups won 92/141 conflicts observed within their typical range, but only 28/103 conflicts observed outside of their typical range (chi-square test: $\chi^2 = 35.520$, $p = 0.0001$). When location (inside or outside of typical range) and relative group

TABLE 13.2. Outcome of intergroup conflicts.

Group	Size	Females	Percent of conflicts won
A2	26	10	52% (43/83)
A1	19	6	42% (26/62)
D1	14.5	6–8	56% (18/32)
CX	9	4	54% (21/39)
SB	9	4	31% (5/16)
SE2	5.5	3	62% (8/13)

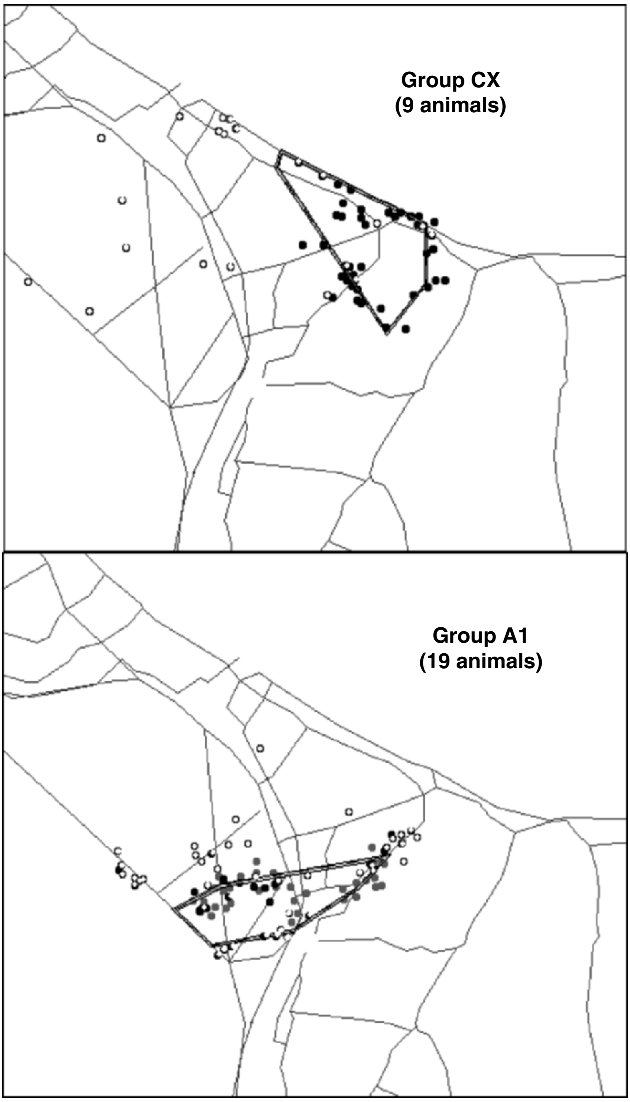


FIGURE 13.3. The outcome of intergroup agonism is spatially determined. Open circles indicate losses, closed circles indicate wins. Groups tended to lose conflicts outside their range, particularly in the high-quality habitat (A1, A2, CX) where conflicts were common and ranges were consistent. The two groups foraging on low-quality habitat (SB, SE2) exhibited less consistent ranging patterns, so typical ranges displayed here should be taken as approximations. They also had few intergroup encounters, possibly due to the poor quality of the habitat (supporting few groups at low density and few resources worth defending).

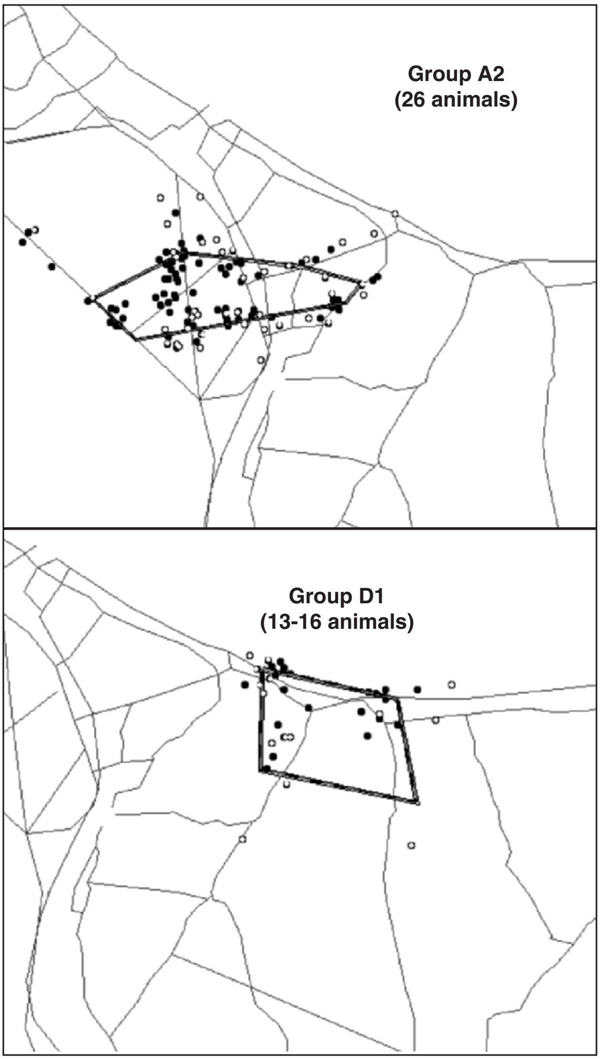
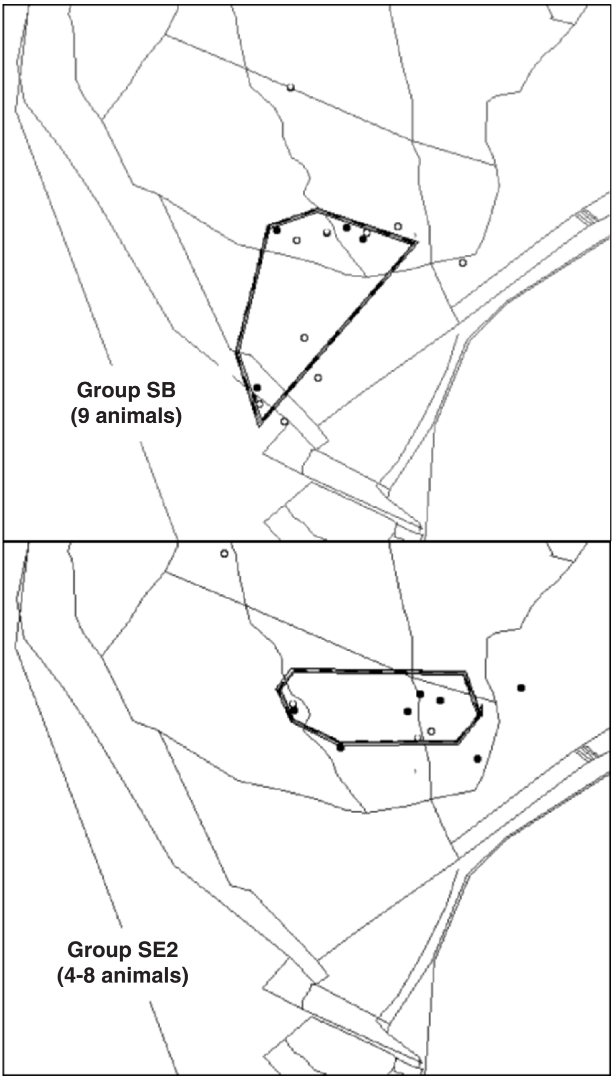


FIGURE 13.3. Cont'd.

size (larger or smaller than opponent) are both included as predictor variables, only location significantly predicts conflict outcome (nominal logistic regression: $N = 188$, $\chi^2 = 42.193$, $r^2 = 0.16$, $p = 0.0001$; location $\chi^2 = 35.28$, $p = 0.0001$; size $\chi^2 = 2.48$, $p = 0.115$). Large groups will only tend to supplant smaller groups from food patches if the food patches are contained with large groups' typical ranges.



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13.3.3. Does Membership in Large Groups Reduce Costs of Intergroup Conflicts?

Although outcome of conflicts is independent of group size, the costs of attaining a given outcome are lower in large groups. Individual participation per intergroup conflict declined with group size in both typical and food-scarce seasons, indicating a lower cost per conflict for individuals in large groups (linear regressions; typical season: $F_{1,29} = 6.922$, $r^2 = 0.26$, $p = 0.014$; food-scarce season: $F_{1,19} = 9.286$, $r^2 = 0.33$, $p = 0.007$). Median individual participation (proportion of conflicts an individual participated in) is inversely related to the number of females in the group (linear regression of each group's median participation rate onto the reciprocal of number of females: $F_{1,5} = 88.922$, $r^2 = 0.95$, $p = 0.001$, Figure 13.4).

Participation in intergroup conflicts is not shared evenly among groupmates. Dominant females participated in a greater proportion of their group's encounters than subordinate females in both the typical season ($\text{mean}_{\text{dom}} = 63\%$, $\text{mean}_{\text{sub}} = 21\%$) and in the food-scarce season ($\text{mean}_{\text{dom}} = 61\%$, $\text{mean}_{\text{sub}} = 23\%$) (ANOVAS: typical season: overall $F_{6,29} = 7.194$, $r^2 = 0.51$, $p = 0.0001$; group $F_5 = 2.581$, $p = 0.048$; dominance $F_1 = 16.561$, $p = 0.0003$; food-scarce season: overall $F_{3,17} = 6.931$, $r^2 = 0.47$, $p = 0.003$; group $F_2 = 2.308$, $p = 0.130$; dominance $F_1 = 7.120$, $p = 0.015$). If participation in intergroup conflicts is costly, these costs are borne more heavily by dominant than subordinate females:

13.3.4. Do Large Groups Gain Advantages Through Resource Defense?

Large groups gained advantages through maintaining access to higher quality habitat. As noted previously, the largest group (A2) was the only group whose typical range contained fruiting trees even in the atypically harsh weaning season. Even in a typical weaning season, A2's habitat may be more productive than neighboring areas, due to the rows of contiguous *A. indica*, with their briefly

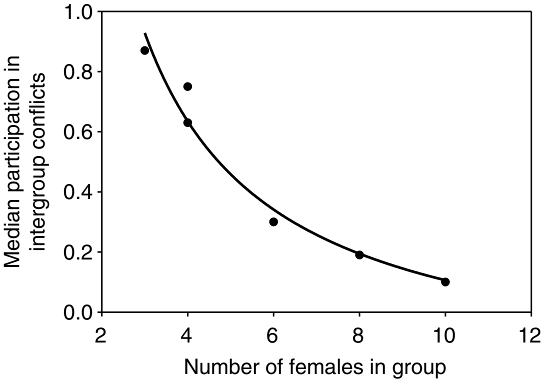

FIGURE 13.4. Individual participation per intergroup conflict is inversely proportional to the number of females in the group. The black line is a first-order inverse regression, and suggests that females can lower costs of intergroup agonism by grouping, as they may participate less often in intergroup conflicts.

TABLE 13.3. Participation in intergroup conflicts.

Group (no. of females)	Mean individual participation in intergroup conflicts	
	Dominant	Subordinate
A2 (10)	0.46	0.25
D1 (6–8)	0.34	0.15
A1 (6)	0.51	0.24
CX (4)	0.70	0.35
SB (4)	0.96	0.29
SE2 (3)	0.94	—

abundant clusters of fruit. More generally, though, the range size *per capita* decreases linearly with the size of the group (Figure 13.5), suggesting that the ranges of large groups are more productive, as less land is required to support each animal.

However, benefits of resource defense are expected to accrue only when resources are defensible as well as worth defending. Ranging data suggest that groups were able to exclude rivals from their habitats under typical conditions, leading to a territorial dispersion pattern; however, during the atypical food-scarce weaning season, groups ranged widely and ranges overlapped considerably (Figure 13.6). Resource defense could provide benefits to larger groups in the typical season if the groups they excluded were relegated to foraging on lower quality food patches, and in the food-scarce season if rival groups' foraging time within their range was reduced even when they did not have exclusive access to their food resources.

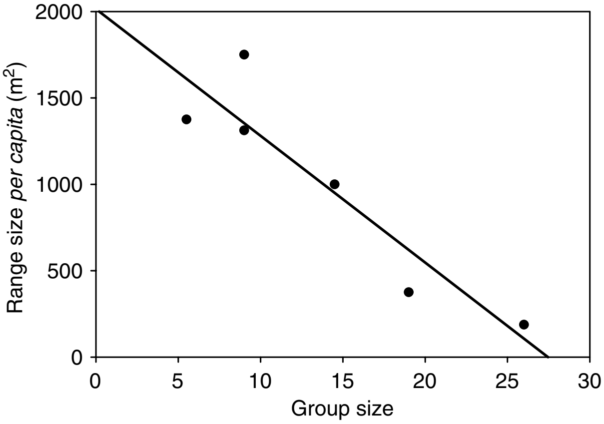

FIGURE 13.5. Range size per capita decreases with group size, suggesting that habitat of larger groups is more productive. Range size was calculated as the area of a minimal convex polygon of all grid squares in which a group was recorded during 22 observation days.

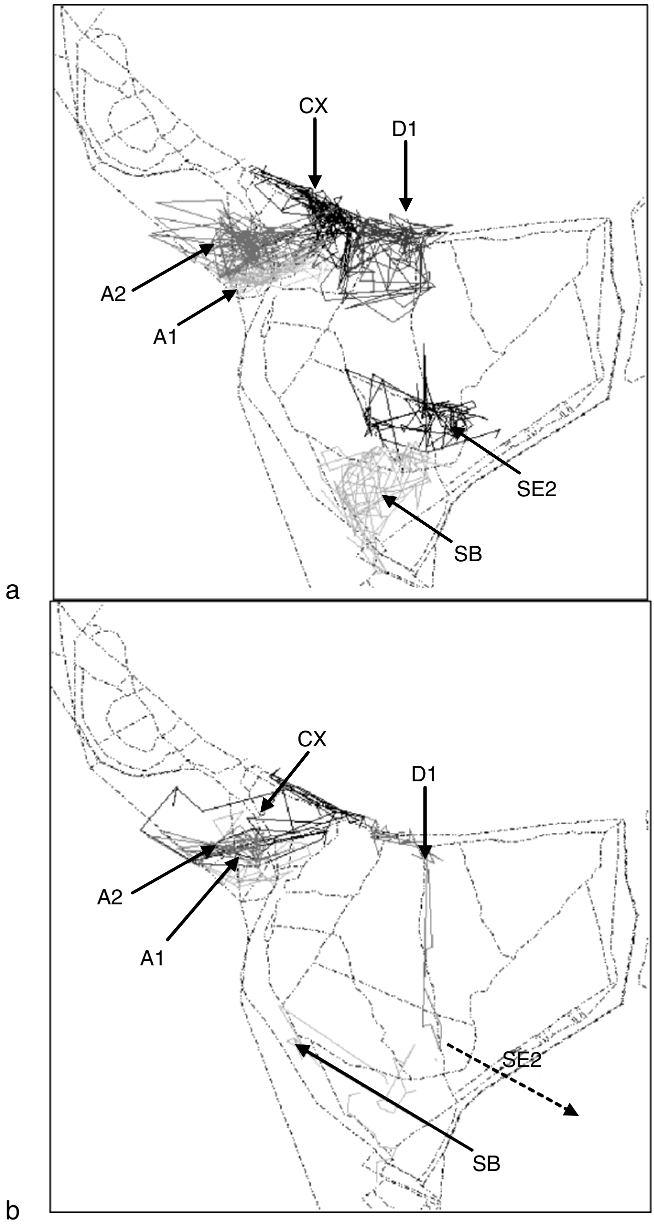

FIGURE 13.6. Ranging patterns in (a) typical conditions and (b) food-scarce conditions. When all groups have access to high-quality food sources, range overlap is minimal. When food is scarce, the large group (A2) with high-quality habitat defends the same range, while all other groups make excursions from their typical ranges (raid).

While foraging on *R. greveana* fruit (in the typical birth/lactation season), large groups attained greater intake rates. Females in the small group (CX; 9 animals) ingested 3.4 ± 1.1 *R. greveana* fruit per minute while foraging (mean ± SE) while those in larger groups ingested more (A1; 19 animals: 6.1 ± 0.8 and A2; 26 animals: 6.6 ± 1.0). If the larger groups are pooled, females in the smaller group obtained significantly fewer fruit per minute of foraging time (Student's t-test: N = 9, t = 2.42, p = 0.046). Proportion of time spent foraging did not differ among different groups (ANOVA: $F_{5,25} = 1.637$, $r^2 = 0.10$, p = 0.187). Estimated daily fruit intake of females in the small group (254 ± 122 fruit/day) was considerably lower than the estimated intake of females in the larger groups (452 ± 100 and 420 ± 100 fruit/day), suggesting that large groups did obtain foraging advantages at this time (Figure 13.7a). However, this result should be taken with caution, as this possible advantage is too small to detect statistically given the low sampling intensity (ANOVA: $F_{2,5} = 1.142$, $r^2 = 0.31$, p = 0.390).

In contrast, while foraging on *A. indica* (in the food-scarce weaning season), large groups had lower intake rates. Females in the small raider group (CX; 9 animals) ingested significantly more *A. indica* fruit per minute while foraging (mean ± SE: 3.9 ± 0.32) than those in the larger groups (A1 (19 animals): 2.8 ± 0.22; A2 (26 animals): 2.6 ± 0.20) (Tukey–Kramer: $F_{2,19} = 6.54$, $r^2 = 0.43$, p = 0.008). This may have been due to crowding, as there were more animals per tree in larger groups (CX: 1.8 ± 0.2; A1: 1.6 ± 0.2; A2: 2.5 ± 0.2) (Tukey–Kramer: $F_{2,141} = 0.368$, $r^2 = 0.04$, p = 0.697), and a lower proportion of animals eating at any given time during foraging bouts (CX = 78%, A1 = 70%, A2 = 56%) (Tukey–Kramer: $F_{2,141} = 3.376$, $r^2 = 0.05$, p = 0.037), based on 144 *A. indica* trees in which foraging was observed during instantaneous scan samples. The large defender group (A2) maintained presence in or near fruit patches slightly longer than the raider groups (A2: 8 hours/day; A1 and CX: 6.5 hours/day, based on half-hourly scans of group location). However, this did not translate into differences in proportion of time spent foraging (means ± SE: A2: 18 ± 1%; A1: 19 ± 1%; CX: 18 ± 1%) (ANOVA: $F_{2,17} = 1.532$, $r^2 = 0.15$, p = 0.244). Females in the small raider group had a significantly higher daily fruit intake than those in the large defender group (Tukey–Kramer: $F_{2,17} = 3.914$, $r^2 = 0.32$, p = 0.040), with females in the large raider group having intermediate intake (large defender: 378 ± 31; large raider: 442 ± 36; small raider: 535 ± 47). The animals in the large groups that did not attain high intake rates may not have been meeting their daily energy requirements. Assuming a typical caloric value for *A. indica* fruit of ~67 calories per 100 g (Wu Leung et al., 1972), and assuming each fruit pulp ingested is approximately 1.5 g, then according to the general mammalian mass-metabolism equation in which FMR (kJ/day) = $4.82\ \text{mass}^{0.73}$ (Nagy et al., 1999), a 3- to 3.5-kg lemur would need to eat 400–450 *A. indica* fruit per day to meet its daily energy requirements. Females in the largest groups (subordinates in A1 and both dominant and subordinate females in A2) had intake rates lower than 400 fruit/day (Figure 13.7b). Although their diet also included foliage (*Cordia* and *A. indica* leaves), and their actual field metabolic rates are unknown, it is quite possible that these animals faced an energy deficit at this time.

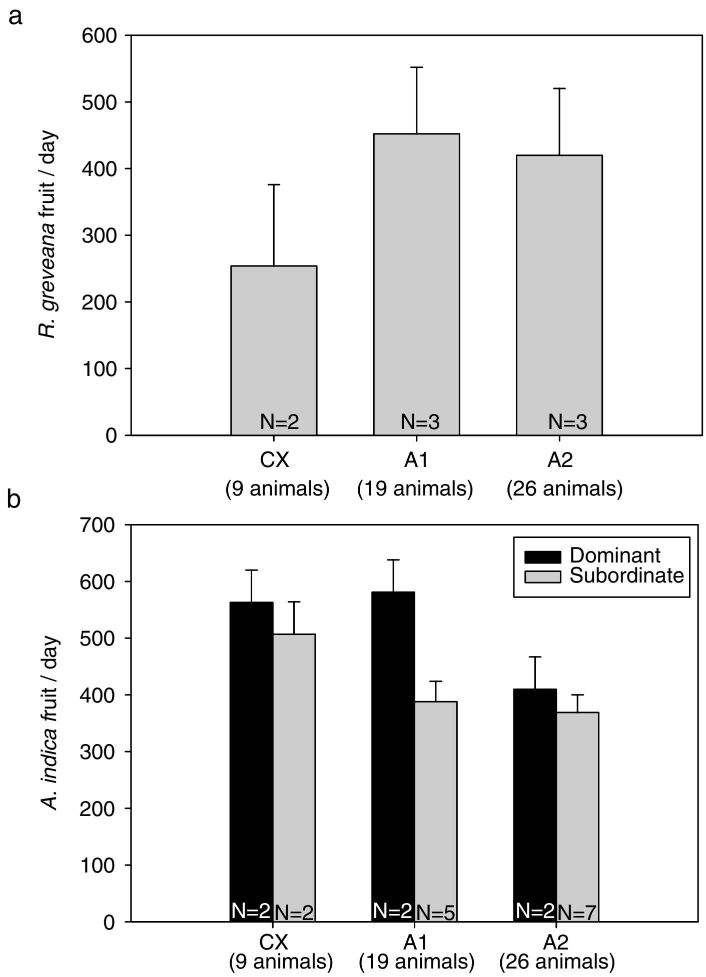

FIGURE 13.7. (a) Food intake rates for females in groups CX (9 animals), A1 (19 animals), and A2 (26 animals) foraging on *R. greveana* in the typical birth/lactation season. (b) Food intake rates for these same groups foraging on *A. indica* in the food-scarce weaning season. Although the *A. indica* exploited by all three groups was located within A2's typical range, and A2 evicted rival groups from this area, females in this group did not gain greater food intake by doing so.

13.4. Discussion

Intergroup competition for food resources is one factor that may promote larger group size in female-bonded primates such as *L. catta*. The importance of this factor in explaining variation in group size within the Berenty population is suggested by the remarkably close correlation between group size and intergroup conflict rate shown here. This relationship is predicted by the Wrangham (1980) model, which suggests that animals remain in larger groups because doing so enhances their ability to defend food resources from rival groups. The predicted values for group size based on a simple linear regression suggest that groups of four females should be found where intergroup conflict rate is low (e.g., <1/day) but can increase to eight females when conflict rates are high (3/day), which adequately reflects differences in Berenty's three habitat regions. Indeed, long-term differences in group size among the three regions (Jolly et al., 2002; Koyama et al., 2002) parallel differences in daily intergroup conflict rates observed in this and prior studies (Jolly et al., this volume). Smaller groups of ~4 adult females are typical at Beza Mahafaly Reserve (Gould et al., 2003), suggesting that intergroup competition for food resources may be less important there, as one may expect given the lower observed conflict rates (Sauther, 1992).

The benefit of membership in larger groups appears to be that a female's participation in intergroup conflicts decreases as she has more groupmates to share the burden of defense, lowering costs of attaining a given level of success in intergroup competition. Large groups' ability to maintain ranges in the most productive and stable habitats may be facilitated by the lower costs of defense *per capita*. Under typical conditions, the two largest groups maintained greater food intake rates than a smaller rival (since no animals in the larger groups had intake rates as low as those in the small group), suggesting that the spatial exclusion of rival groups observed in these conditions provided foraging benefits. Concurrent study shows that females in these large groups also exhibited lower cortisol levels at this time, suggesting lower stress and mortality risk (Pride, 2005b, 2005c).

However, results from the food-scarce weaning season highlight the importance of resource defensibility in determining the payoffs associated with group size, showing that benefits of being in a large group are eroded when resources cannot be monopolized. At this time, differences in food resource quality across ranges were extreme, and these conditions are expected to favor large groups (Wrangham, 1980), provided that they can monopolize the scarce resources. Females in the largest group (A2) were unable to prevent smaller adjacent groups from gaining access to the food resources, and they foraged less efficiently than their smaller rivals. Since they could not completely exclude rivals, benefits to defense depended on defenders limiting the raiders' foraging time enough to overcome the costs of their own relatively inefficient foraging, which they did not do. Females in large groups had highest cortisol levels at this time (Pride, 2005c).

Defensibility typically depends on the defender's ability to patrol resources in its day-range (Mitani and Rodman, 1979), the defender's sensory abilities to detect invaders (Lowen and Dunbar, 1994), and the aggregation of the resources (Rubenstein, 1981). In this case, the defending group's range was small relative to the distance it traveled in a typical day (range diameter = 375 m, daily path = 1250 m, based on 21 full-day follows), suggesting high defensibility on Mitani and Rodman's (1979) defensibility index (D = 3.33). Ability to detect intruders was likely to be greater in the *A. indica* plantation than in the forest, as tree density was much lower. However, the resources to be defended were not sufficiently aggregated to be continuously guarded against multiple groups that simultaneously made incursions to exploit them. Because defense behavior did not result in exclusive use of the resources in a range, and raiders were more efficient at harvesting resources because of their smaller group size, defense did not provide net foraging benefits.

The failure of resource defense to provide benefits may be understood in the framework provided by theoretical models showing that territoriality and resource defense are expected when there are intermediate levels of habitat variation (Carpenter and MacMillen, 1976; Pride, 2003). When habitat variation is low, resources are not worth defending because the gross benefit is too low, but when habitat variation becomes too pronounced, resources are not worth defending because gross costs of defense are too high. When the alternative habitat becomes poor enough, as in the food-scarce weaning season, many groups may raid the scarce high-quality food patches, and overwhelm the ability of the resident groups to mount effective defense. Thus even though females in large groups maintain access to high-quality habitats, have lower costs per conflict, and can evict rivals from resources within their typical range, they can be at a disadvantage because they are unable to repel multiple small raider groups, and have lower food intake than those small groups that gain access.

Given that, in the food-scarce season, large groups did not gain exclusive access to food resources from defense behavior, and may have suffered lower foraging efficiency as a result of their size, we must ask (1) why defense behavior was maintained at all; (2) why foraging time was not extended to compensate for the lower intake rate in large groups; and (3) why large groups did not fission, when doing so would give them greater foraging efficiency.

13.4.1. Why "Defend" When It Does Not Result in Foraging Advantages?

The defender group continued to allocate effort to resource defense even though doing so did not result in foraging advantages over raider groups, while defense costs could have been avoided by tolerating the presence of rivals. Three possible explanations for this can be made:

13.4.1.1. Resource Defense Is Maladaptive in Current Conditions, but Not Under Those in Which *L. Catta* Evolved

Although maladaptive behavior would be discouraged both by learning and natural selection, it is possible that the conditions in which resource defense was maladaptive are sufficiently uncommon that neither of these forces have shaped its expression. The conditions seen here are unlikely to have been prevalent throughout *L. catta*'s evolutionary history for several reasons. First, the habitat structure in the defender group's range was atypical. The defended resources were rows of exotic fruit trees planted along roads, and this contiguous fruit-tree monoculture would be uncharacteristic of most *L. catta* habitats prior to human arrival in Madagascar. Second, the invasion pressure the defending group faced was atypically high. Population density of *L. catta* at Berenty is much higher than anywhere else in Madagascar, possibly due to the high quality food and water usually available (Jolly et al., 2002). Where the habitat quality is lower, and population density is lower, fewer neighboring groups can attempt to exploit a defender group's resources. If groups are more widely dispersed across the landscape, a defender group will have to defend its resources far less often, and a fixed strategy of defense can be practical. While defense may not have been beneficial in this atypically harsh season in this atypical environment, a fixed strategy of resource defense—or antagonism toward all rival groups—could be the response best suited to the range of ecological conditions under which *L. catta* evolved. Characterizing behavior of *L. catta* outside of high-density gallery forest, that is, in most places this species is currently found (Sussman, this volume; Goodman, this volume), is an important next step towards understanding the costs and benefits of the behaviors previously found.

However, there are differences in *L. catta* intergroup agonistic behavior across seasons and among groups in different habitats (Jolly et al., 1993), which suggests that the effort devoted to resource defense is conditional rather than fixed. For example, at Beza-Mahafaly, a site with lower *L. catta* population density and little human modification of food supply, groups exhibit greater tolerance of rival groups (L. Gould, pers. comm.), at least in some seasons, and maintain overlapping typical ranges (Sauther and Sussman, 1993). If resource defense is not a fixed strategy, then its occurrence suggests that it was either less costly than alternative behavior in the short term, or actually provided net benefits over a longer term.

13.4.1.2. Resource Defense Is Less Costly Than Permitting Rivals to Deplete Resources

In the immediate or short-term timescale, the large defending group A2 had lower daily food intake than the smaller raider groups during the food-scarce months. However, it is not known what their food intake would have been if they had not exerted effort to evict raiders. If incursions by neighboring rival groups were not repelled, the resident group would face lower food availability as rival groups depleted the food supply. With no defense effort, costs to raiders will decrease, and more groups are expected to invade the highest quality food patches. Furthermore, since *L. catta* maximize food intake during the wet season (Pereira, 1993b), the expected depletion of food resources by unchallenged raiders can be substantial, particularly given the relatively efficient foraging of small raider groups. If this exploitation competition lowers the foraging efficiency of the resident group more than the cost of defense, then defense behavior is beneficial (Gill and Wolf, 1975). The large defender group faced at least 8 rival groups whose typical ranges were close to the *A. indica* plantation (comprising >100 animals), and it was observed evicting at least 5 of these groups in the food-scarce season. Assuming that these animals ingested food at a comparable rate to the observed groups (3–4 fruit/individual per minute), this represents a loss of 18,000–24,000[CE2] fruit per hour, which is approximately twice the observed daily intake the large group. Given the high potential depletion of food resources, the large defender's response can be seen as "the best of a bad situation," choosing to pay high defense costs instead of even higher costs of food scarcity, a strategy of converting exploitation competition to interference competition. If the payoff of raiding is greater than the payoff of defending, and this in turn is greater than the payoff of tolerating rivals, this will result in a "quasi-territoriality" (Sauther et al., 1999) in which territorial behavior is observed but exclusive range use is not.

13.4.1.3. Maintaining Spatial Dominance Is Less Costly Than Establishing It

Even if paying greater defense costs is not beneficial in the short term, there may be long-term consequences to permitting invasion that make it more costly than maintaining defense efforts. When the cost of maintaining spatial dominance is much lower than the cost of establishing it, for example, then greater investment in evicting rival groups even at times when it is not immediately advantageous will be favored. As shown here and in prior studies (Sauther and Sussman, 1993), *L. catta* maintain spatial dominance relationships in which the resident group wins intergroup conflicts; when far from their core areas, raiding groups often retreat immediately from residents without contest, suggesting a "resident wins" convention. This strategy reduces costs of intergroup agonism by eliminating escalation when challenges are unlikely to change the *status quo* (Davies, 1978). By maintaining a "resident wins" convention, costs of maintaining spatial dominance are kept low, and *L. catta* intergroup encounters rarely escalate to physical contact (Jolly, 1966). However, if two (or more) rival groups acquire familiarity with habitat such that residency is contested, both groups may value the resources more highly, conflicts would escalate, and the original resident would have to pay high costs to reestablish its spatial dominance, or lose its dominance status (Tobias, 1997). It may be cheaper to exert small effort to continuously evict rivals through periods when defense does not provide immediate net benefits than to exert great effort to displace fellow residents only when it does. In this study population, high *escalated* intergroup defense rates were associated with high cortisol levels (Pride, 2005a), while overall conflict rates were not, suggesting that the costs of establishing spatial dominance when contested may be higher than routine displacement of subordinate raider groups that immediately retreat. If reestablishing spatial dominance is stressful and maintaining it is not, then the duration for which nonbeneficial defense should be maintained may be quite high, presuming that defense benefits accrued at other times will ultimately make defense worthwhile. Given that periods food scarcity of the magnitude seen here occur as seldom as once in an animal's lifetime, even a slight benefit conferred by spatial dominance in typical conditions may outweigh the substantial costs accrued to maintain it through these atypical periods.

13.4.2. Why Did Large Groups Not Compensate for Lower Intake Rates by Foraging Longer?

Large groups could have compensated for their lower foraging efficiency if they had foraged longer, which is one way in which resource defense could provide benefits to large groups. Given that the small raider group obtained 50% more fruit per minute foraging than the larger groups, however, the two larger groups would have needed to forage 50% longer to compensate. Time individuals spent actively foraging on *A. indica* was small (e.g., 3 hours/day), but this figure does not include waiting for access to food patches, or movement among or within patches other than when directly searching for food, so actual time required to meet food requirements was considerably greater.

One possibility is that all groups were already foraging as much as was energetically feasible. *L. catta* maximize food intake in the rainy season, when resources are usually most abundant, and ingest up to 50% more food than they do in other seasons (Pereira, 1993b). At this time, the large defender group A2 devoted less time to resting than it did in the rest of the year (food-scarce season: 4.75 hours/day; other seasons: 6–7 hours/day; based on half-hourly scan samples of modal group activity during monthly full-day follows), suggesting that they were already maximizing active time. Active time may have been constrained due to thermal limitations, an important factor shaping time budgets in many taxa (Porter et al., 1973; Dunbar, 1996). The period of food scarcity occurred in the hottest season (daytime shade temperatures commonly >40°C), and foraging activity in the middle of the day (particularly in the exposed roadside *A. indica* plantation) could have been more costly than the expected gain from foraging, rendering extension of foraging time unfavorable.

Comparison with other groups supports this interpretation, as the groups that foraged on lower quality food sources at this time (i.e., foliage, dry fallen tamarind fruit) took longer midday siestas (A2, A1, CX: 2–2.5 hrs/day; SB, D1: 4–4.5 hrs/day). This would be expected because having a lower foraging payoff lowers the threshold temperature at which foraging payoff exceeds metabolic costs of being active, lengthening siestas. If large groups could not reduce their midday "siestas" beyond a certain threshold due to thermal constraints, then their foraging time would be limited. This could impose a cost on groups that are least efficient foragers, as they must either suffer low food intake or diminish other activities. Alternatively, the longer siestas taken by groups foraging on lower quality food sources may be considered a mechanism for coping with lower energy or moisture intake by reducing metabolic demand. Even if these groups obtained less food, they would be able to maintain positive energy balance by sleeping more (they also travelled less: A2, A1, CX: 1.1–1.7 km/day; SB, D1: 0.7–1.0 km/day). This option may not have been available to the groups foraging on *A. indica*; given the potential for depletion of resources by multiple groups, there may have been strong benefits to harvesting resources as fast as possible. Regardless of whether siestas limited foraging time of large groups or provided a way for groups foraging on uncontested resources to lower their demand, it is clear that large groups did not forage long enough to compensate for their lower intake rate.

13.4.3. Why Did Animals Stay in Large Groups?

Although large group size may provide benefits in typical conditions, this does not explain why large groups do not fission when large group size becomes unfavorable. Although *L. catta* do actively constrain the size of their groups (Vick and Pereira, 1989; Koyama, 1991; Hood and Jolly, 1995), they do not attempt to match short-term environmental fluctuations that alter optimal group size (Pride, 2005c). A likely explanation is that costs associated with the process of evicting rivals from a group (or establishing one's own group after being evicted), as well as costs of reassessing and reestablishing dominance relationships within and among unstable groups, exceed costs of being suboptimally large for a short time period. In other primate species, periods of dominance assessment and changes in group composition are accompanied by increases in glucocorticoid levels and agonism rates (Sapolsky, 1983; Alberts et al., 1992). In *L. catta,* establishment of dominance relations within and among groups can involve intense or sustained fighting (Vick and Pereira, 1989; Hood and Jolly, 1995), and therefore can be energetically costly and involve risk of injury. While group fissions sometimes are gradual processes of increasingly segregated ranging by subgroups—as is usually observed at Beza Mahafaly (R. Sussman, pers. comm.)—they are not always so, with very high intergroup conflict rates following a fission (Hood and Jolly, 1995; pers. obs.). Given that the food-scarce season when large groups were disadvantageous was atypical and brief, the benefit of reducing group size to match it could be less than the "energy of activation" associated with the reduction.

Due to these potentially high costs, group size modulation could be constrained to occur only in certain times of the *L. catta* annual cycle, when they are least likely to interfere with competing demands such as lactation or seasonal replenishment of fat reserves. Fissions that have occurred during early lactation have resulted in infant deaths (Jolly et al., 2000), suggesting immediate fitness costs in addition to energetic burdens that may constrain fissions. No large groups split during the food-scarce season (even though this was when the penalty for being in a large group was greatest due to low food intake); however, two groups (A2 and D1) did eventually fission at the end of this study. This occurred during the typical dry season, when variation in habitat quality was minimal, intergroup competition was likely to be low, and group size would not be expected to greatly affect food intake. It has been argued that seasonal patterns in targeted aggression (intragroup dominance reversals that can result in evictions) result from seasonal differences in intensity of competition (Pereira, 1993a); the timing of fission here provides anecdotal support for this idea, but suggest that the events are either (1) constrained by fixed annual cycles (like much of *L. catta* physiology (Pereira et al., 1999) such that fissions are unlikely to occur at certain times of year even if atypical conditions make them favorable, or (2) constrained to times when costs of eviction are borne most easily, not simply at times when eviction would be most favorable. If these or other constraints limit the ability of groups to modulate group size, then observed behavioral strategies may be considered “the best of a bad situation.”

13.4.4. Extensions and Other Considerations

Other factors not examined here, such as predation and infanticide avoidance, can promote larger primate group sizes. The importance of one factor—intergroup competition for food resources—does not diminish the potential importance of other selection pressures. When the resource distribution causes lower variation in intergroup conflict rates, the capacity of intergroup conflict to explain group size variation may be negligible. This is expected to occur when there is little variation in resource availability among groups (Pride, 2003). Furthermore, intergroup conflict rates depend not only on the distribution and abundance of resources in groups’ habitats, but also on group history (Jolly et al., this volume). Recently fissioned groups may have higher conflict rates as they modulate their ranging patterns or establish spatial dominance relations with their former groupmates and neighboring groups [e.g., A1/A2 (Hood and Jolly, 1995), D1A/D1B (Mertl-Millhollen et al., 2003), CX/SH and T2/U2 (Koyama et al., 2002)]. Group history may interact with resource patchiness to produce “high-confrontation pairs” (Jolly et al., 1993) as former subgroups contest resources worth defending. Thus we would expect to find variation in the conflict-groupsize relationship, but mainly when dominance relationships among groups are perturbed by changes in group composition or the resource base. Finally, it should be noted that modulations of conflict rate and group composition offer two solutions, but by no means the only solutions, to ecological problems associated with sharing habitat with conspecifics.

13.5. Conclusion

Large group size conferred resource defense advantages by allowing members to participate in a smaller proportion of intergroup conflicts, and large groups maintained access to the highest quality habitat in all seasons. This may lead to foraging advantages and promote membership in larger groups in conditions where intergroup conflict is common. The correlation between group size and intergroup conflict rate is consistent with the idea that intergroup competition for food resources drives increases in group size, and therefore may explain the longterm differences in group size observed among Berenty’s different habitat regions. However, defense behavior does not always allow groups to maintain exclusive access to food resources. As a result, large groups do not always gain foraging benefits in spite of their occupying the highest quality habitat and exerting spatial dominance over rivals. Alternative strategies for large groups (tolerance of rivals, increasing time spent foraging, or fissioning) were not adopted. Defense behavior may be maintained because it diminishes the impact of the raiders and provides long-term advantages, across seasons and possibly generations.

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