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ORIGINAL ARTICLE

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Patterns of participation and free riding in territorial conflicts among ringtailed lemurs (*Lemur catta*)

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Abstract Cooperation in animal social groups may be limited by the threat of "free riding," the potential for individuals to reap the benefits of other individuals' actions without paying their share of the costs. Here we investigate the factors that influence individual contributions to group-level benefits by studying individual participation in territorial defense among female ringtailed lemurs (*Lemur catta*). To control for potentially confounding factors, particularly group size, we studied two semi-free-ranging groups at the Duke University Primate Center. First, we used a combination of experimental and observational methods to investigate the costs and benefits of territorial defense for individual lemurs. We found three indications of costs: physical contact occurred during inter-group encounters, participation in territorial defense was negatively correlated with ambient temperature, and rates of self-directed behaviors increased during encounters. Benefits were more difficult to quantify, but observational and experimental tests suggested that individuals shared the gains of territorial defense by foraging in defended territories. Thus, during experiments in which one of the groups was prevented from defending its territory, the free-ranging group made more frequent incursions into the other group's territory. Second, we examined variation in participation in territorial defense. Individuals varied significantly in their rates of aggression and genital marking during inter-group encounters. The extensive variation documented among individuals was partially accounted for by dominance rank, kinship and patterns of parental care. However, we found no evidence to suggest that participation was enforced through punishment (policing) or exchange of benefits involving grooming. In conclusion, this study provides further insights into cooperative behavior in mammalian social groups by revealing how the costs and benefits of territoriality influence patterns of individual participation in the context of shared (collective) goods.

Keywords *Lemur catta* · Territoriality · Individual participation · Cooperation

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Introduction

Important questions remain concerning the evolution and maintenance of cooperation in large social groups (Heinsohn and Packer 1995; Dugatkin 1997). In such groups, the threat of cheating by "free riders" may reduce overall levels of cooperation. The temptation to free ride emerges when the benefits of one individual's actions spill over to others. Because free riding in social groups involves individual decisions, where the payoffs are affected by other individuals' patterns of participation, cooperation in large groups has been modeled extensively using n-player game theory (Boyd and Richerson 1988; Dugatkin 1990). Many of these models predict that free riding will be common, but they also examine the factors that increase individual participation. For example, computer simulations and analytical models have shown that individual recognition increases cooperation (Crowley et al. 1996; Nowak and Sigmund 1998; Nowak et al. 2000), and a strategy of "raise-the-stakes," in which individuals increase their cooperation incrementally, may explain the development of cooperative relationships among individuals (Roberts and Sherratt 1998).

Despite the promise of theoretical models for understanding the mechanisms that facilitate cooperation, their application to animal social groups has proved difficult. One problem is that the dynamics of individual participation in real social groups are more complicated than most analytical models recognize. For example, Heinsohn and Packer (1995) studied individual responses of female lions (*Panthera leo*) to playbacks of aggressive vocalizations and found that female lions use one of four strategies. Some females always participated (unconditional cooperators), others participated when they were most needed but not at other times (conditional cooperators), and some individuals lagged in their participation (unconditional laggards) or actually participated less when they were most needed (conditional laggards). Heinsohn and Packer (1995) examined whether some cooperative strategies developed in the context of the two-player iterated prisoner's dilemma apply to lion cooperative territoriality (i.e., tit-for-tat and Pavlov; Axelrod and Hamilton 1981; Nowak and Sigmund 1993), but these strategies were insufficient to account for patterns of individual participation.

If we view cooperation as an act by one individual that benefits another, then many cooperative behaviors among conspecifics within social groups probably involve benefits obtained either through kinship or through by-products, in which an animal's action benefits both the actor and other individuals (Connor 1995; Clutton-Brock 2002; Sachs et al. 2004). In either case, conditions may emerge in which individuals are tempted to cheat or free ride, thus receiving the benefits of other individuals' actions without bearing the costs. An important condition that may favor free riding is increased number of individuals (i.e., group size), with the availability of more individuals potentially increasing the benefits obtained but also the opportunity to free ride (Olson 1965; Boyd and Richerson 1988; Dugatkin 1997). An important yet unresolved question concerns the factors that influence patterns of individual participation in these larger groups, particularly the costs and benefits to individuals of participating. In only a few cases have these costs and benefits been examined in the context of individual patterns of participation in cooperative acts (e.g., lions: Heinsohn and Packer 1995; Spong and Creel 2004).

In this paper, we investigate individual variation in territorial defense among female ringtailed lemurs. First, we provide an assessment of the costs of territorial defense for individuals, as well as an initial assessment of the benefits that females within groups gain from this defense. Second, we investigate whether individuals vary in their participation in costly encounters and, if so, whether individual variation correlates with rank, offspring care and kinship. Finally, we test whether individuals punish free riders for their failure to contribute to the benefits of territorial defense (punishment), or whether they reward participants with increased grooming (an incentive for participating).

Methods

Study site and subjects

We studied inter-group encounters between two groups of semi-free-ranging ringtailed lemurs at the Duke University Primate Center (DUPC). Research was conducted in the summers of 1998 (4 May–21 August) and 1999 (6 May–6 July). We observed two groups, Lc-1 and Lc-2 (Fig. 1). These groups have been free ranging during at least part of the year since 1987 (when Lc-2 was formed) and have defended a stable territorial boundary since removal of a fence separating their territories in 1990 (see Pereira 1993; Nunn and Pereira 2000). These groups free ranged virtually the entire year from 1987 to 1996 (see Pereira and Izard 1989; Pereira 1993). Since the fall of 1997, these groups have been detained in indoor enclosures from October until April to protect them from freezing temperatures during the winter.

While free ranging, the animals foraged extensively on the natural vegetation. Their diet was supplemented with fruit and monkey chow, which was provided by the DUPC staff once daily in the early afternoon. We collected data in the period after provisioning and resting, when foraging on natural vegetation resumed and inter-group encounters were more likely to take place (based on previous research on inter-group relationships, C. Nunn, personal observation).

We focused on females during inter-group encounters because females are philopatric and defend stable territorial boundaries, whereas male encounters occur regularly at non-boundary sites and often involve dyadic interactions between resident and transferring males (Jolly 1966; Jones 1983). At the start of the study in 1998, four females in the study had juvenile female offspring from the previous breeding season (two in each group, aged 13 months at the beginning of the study and therefore approaching maturity, but not fully adult). All females in the groups were related, with females

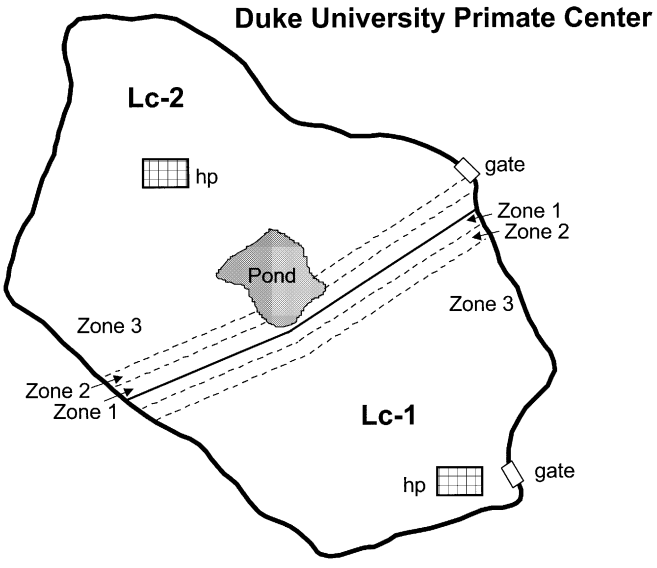

Fig. 1 Natural habitat enclosures at the Duke University Primate Center (DUPC). The fence separating the two groups was removed 8 years prior to the study, allowing the two groups (*Lc-1* and *Lc-2*) access to one another's territories and unobstructed inter-group encounters. Inter-group encounters took place along the territorial boundary on either side (*left* or *right*) of the pond. Each territory was divided into three sections. Zones 1 and 2 represented the first 20 m of each enclosure and were the sites of most inter-group encounters (not drawn perfectly to scale). Zone 3 represented the remainder of the territory. During experimental lockups in 1999, animals were housed in the holding pens indicated by *hp* in zone 3 of each enclosure

Table 1 Individual lemurs studied and their ages and relationships to other animals

Female ID (DUPC code)	Three-letter code	Social group	Date of birth (month/day/year)	Mother
6280f	NIN	Lc-1	3/15/89	COR
5847f	COR	Lc-1	3/16/84	LYS (2543f)
6623f	ALX[a]	Lc-1	3/24/95	NIN
6549f	ATT[a,b]	Lc-1	5/17/93	NIN
6704f	AND	Lc-1	4/9/97	KAT
6708f	CLD	Lc-1	4/11/97	COR
6140f	KAT	Lc-1	3/19/87	THE (5585f)[c]
6159f	CLE	Lc-2	4/15/87	CLI
6276f	DOR	Lc-2	3/15/89	CLI
5984f	CLI	Lc-2	4/9/85	LET (4534f)
6277f	ALI[a]	Lc-2	3/15/89	CLI
6575f	CHA[a]	Lc-2	3/23/94	CLI
6709f	APO	Lc-2	4/11/97	CLE
6711f	SOS	Lc-2	4/13/97	CLI

[a] Female removed during 1999 season
[b] Female mistakenly identified as ADE (6522f) in DUPC records
[c] Daughter of LYS (2543f), ancestor of all females in the group

descended from a common female who was still alive in the group (Lc-2) or a female who was no longer present (Lc-1; Table 1). Lc-1 group ranged on a territory of 3.3 ha, while Lc-2 used a territory of 5.8 ha. These values approximate the size of territories found in wild populations of ringtailed lemurs (e.g., 6.0–23 ha in Richard 1987). Group size and composition (5 females, 3–6 males, and 3–4 juveniles) were also comparable to wild populations (6–30 total animals, Richard 1987), with the exception that there were no infants born in either social group during our study. To obtain detailed information on patterns of participation and its correlates, our research focused on only two groups. We compare our results to patterns of individual participation observed in one of these groups prior to our study, and to other groups of ringtailed lemurs in the wild.

To control the size of the lemur population at the DUPC, female ringtailed lemurs were contracepted for several breeding seasons in the late 1990s, including both breeding seasons preceding our field studies. Contraception was accomplished with injections of Depo-Provera (depo-medroxyprogesterone acetate) every 40 days, beginning in early September and ending in the spring (12 March 1998, and 2 April 1999). Empirical work at the DUPC in prior breeding seasons indicates that Depo-Provera remains in the system for at least 40 days but less than 60 days (C. Williams, DUPC veterinarian, personal communication). Because we initiated our studies 34–53 days after the last injection of Depo-Provera, it is unlikely that the behavior of our subjects was substantially affected by this treatment.

Data collection

Inter-group encounters were operationally defined by the proximity of adult females (Cheney 1987) and were said to begin when two or more adult females from different groups were within 10 m of one another. Occasionally, the groups would separate by more than 10 m and then come back into contact shortly thereafter. If no more than 10 min passed before the two groups re-entered proximity (10 m), we treated the two (or more) episodes as the same encounter in our analyses. From 420 h of observation, we obtained data on 118 inter-group encounters (38 h of total encounter time). The average duration of an encounter was 20 min (range 1–73 min). These encounters ranged in intensity from passive acceptance of the other group to physical aggression exchanged between females of the different groups. Encounters were significantly longer when aggressive behavior was observed (mean of 23 min vs 10 min; $F_{1,85}$=11.5, P=0.001, two-tailed).

We took 10-min focal samples of females in which we recorded all occurrences of aggressive (bite, cuff, chase, lunge, charge and grab), submissive (spat, flee, jump away and cower), and affiliative acts (touch, body–face greet, groom-skin lick, play; Pereira and Kappeler 1997). We also recorded instances of feeding, vocalizing and genital marking (see Kappeler 1998 for a study of scent marking in one of the groups that we studied). To determine dominance relationships, we used only decided agonistic interactions (i.e., only one animal exhibited submissive behavior). All females could be assigned a dominance rank on a linear scale of 1–5 (cf. Pereira 1993), with 1 indicating the highest ranked individual. We sampled animals randomly and collected data during encounters and at other times.

We recorded information on self-directed behaviors in order to investigate if participation in encounters is associated with increased stress. Definitions of self-grooming, scratching, yawning, and grinding teeth were taken from Pereira and Kappeler (1997). Scratching was defined as an animal repeatedly and rapidly moving its hind limb digits over its own pelage. Previous studies of primates, especially macaques and baboons, have demonstrated that increased rates of these correlated behaviors are indicative of stress (Maestripieri et al. 1992; Troisi 2002). In ringtailed lemurs, elevated rates of self-directed behaviors have been observed in agonistic contexts (Jolly 1966; Roeder et al. 1994) and do not cluster statistically with aggressive or submissive behaviors (Pereira and Kappeler 1997), consistent with the idea that such behaviors are indicative of stress. Moreover, Cavigelli et al. (2003) have shown that glucocorticoid levels, a physiological index of stress, can be related to the frequency of within-group aggression initiated and received in ringtailed lemurs. Their study included data on these groups of ringtailed lemurs in 1997, when group composition was largely similar to our study. Thus, using data from Cavigelli et al. (2003), we investigated whether involvement in intergroup encounters in 1998 and 1999 was correlated with measures of fecal corticoids in 1997.

To identify the location of individuals relative to aggressive territorial conflict, we identified three "zones" progressively closer to the territorial boundary (Fig. 1). The boundary was marked clearly by posts for the fence that once separated the two groups, and flagging tape was used to distinguish the zones. Zones 1 and 2 for each enclosure were 10 m wide and closer to the territorial boundary, with the final zone encompassing the remaining portion of the territory. Zone 3 was therefore the largest, but 82% of encounters with at least one aggressive act ("aggressive encounters") took place in zone 1 of one territory or the other (n=82 total encounters).

Some individuals were not present in the zone of aggressive conflict during each encounter. Thus, one of our measures of participation was the location of animals relative to the zones of aggression, examined separately for each encounter. The other two measures of individual involvement in inter-group encounters were the number of aggressive acts committed against members of the

other group during encounters and the number of episodes of genital marking.

Group manipulations and experiments

Group size may influence patterns of individual participation, with free riding thought to be more common in larger groups (Olson 1965; Dugatkin 1997; Boyd and Richerson 1988). For this reason, and because ringtailed lemur groups become unstable as group size increases (e.g., Vick and Pereira 1989; Hood and Jolly 1995; Jolly and Pride 1999), we maintained the number of females at a constant level of five individuals per group throughout the study. Attaining this goal was complicated by developmental changes in two immature females in each group midway through the field season of 1998, when these females began genital marking and participating in inter-group encounters (see Pereira 1993). Thus, to maintain five adult females per group, we permanently removed two other fully adult females from each group halfway through the 1998 field season (with the assistance of the DUPC staff). The removal had no significant influence on overall patterns of territorial behavior in each group in 1998 (e.g., duration of aggressive encounters before and after removal: $F_{1,33}$=0.05, P=0.83, two-tailed; proportion of encounters aggressive: 18 of 21 encounters before removal were aggressive, vs 17 of 24 after removal, chi-square likelihood ratio =1.47, P=0.22, two-tailed).

In 1999, we performed a series of experiments to test whether the lemurs obtained benefits from territorial defense. We did this by retaining one of the two groups in an area within that group's territory far from the territorial boundary (zone 3 "holding pens" indicated on Fig. 1). These lockups were conducted four times over the course of the summer, alternating between groups with 10 days of free ranging by both groups between each lockup. During lockups, animals were housed for 3 full days without rain (always $\leq$5 days total), because rain tended to decrease activity of the free-ranging group. While one group was retained, we monitored the movements of the free-ranging group in order to assess whether incursions occurred more frequently when the territorial boundary could not be defended. We also collected data on the frequency of feeding by interlopers in the usually defended territory. Incursions were identified as one group crossing the border when its neighboring group was not within 10-m proximity. In this paper, we used only "deep" incursions in which females entered zone 3, as this was beyond the majority of observed encounters (see above). Incursions and encounters were most likely to occur after the animals had fed on provisioned food and rested in the early afternoon. Thus, to ensure accurate assessment of the number of incursions per day, we limited the analysis to days with 4 or more hours of observation in the afternoon (n=31 days).

Statistical tests

Analyses were conducted with α<0.05. For many analyses involving the factors that influence individual participation, we tested a priori directional predictions. We therefore used directed tests when investigating these predictions (Rice and Gaines 1994). Directed tests allocate a disproportionate probability under the null hypothesis to the tail of the distribution in the predicted direction (γ), while retaining a smaller probability in the opposite tail to detect unexpected deviations opposite to predictions ($\delta<\gamma$). Directed tests are subject to the constraint that $\delta+\gamma=\alpha$. We followed the guidelines in Rice and Gaines (1994) by setting γ/α to 0.8, giving values of γ=0.04 and δ=0.01. Statistical tests are identified as two-tailed or directed.

Results

Costs of territorial defense

We investigated three potential costs of inter-group encounters: increased risk of injury, increased risk of overheating, and behavioral indicators of stress. Physical contact (bites, cuffs, grabs with one or two hands) between adult females of different groups occurred at a rate of once every 81 min of encounter time during focal samples. Moreover, individuals that were more aggressive during encounters also experienced increased aggression from members of the neighboring group (across focal samples, r_s=0.35, P<0.0001). We observed no injuries that could be directly attributed to inter-group encounters during our two seasons of field research, in part because the animals were often extremely vigilant of non-group members during encounters. However, injuries during territorial encounters have been reported in previous studies of wild ringtailed lemurs (Hood and Jolly 1995).

As predicted if participation entails a thermoregulatory cost, the frequency of encounters per day declined with average daily temperature (Spearman rank order correlation r_s=–0.43, n=32, P=0.008, directed test) and maximal daily temperature (r_s=–0.48, n=32, P=0.003, directed test), which may reflect generally lower levels of activity as temperature increases during the summer months of our observations. Encounter duration was not significantly related to mean temperature (r_s=–0.14, n=31, P=0.28, directed test), but individual rates of aggression during encounters declined with increasing average temperature (r_s=–0.51, n=32, P=0.0018, directed test) and maximal temperature (r_s=–0.43, n=32, P=0.009, directed test). Aggressive encounters and encounters greater than 45 min in duration were observed in all months with more than 15 days of observation across the two study seasons; thus, temperature-related participation was probably not simply an effect of release from wintertime captivity. Moreover, in previous research at the DUPC, M. Pereira (personal communication) observed wrist and palm licking during periods of high temperatures, suggesting that thermoregulatory stress may be a general cost to these lemurs.

In terms of self-directed behaviors, we found that bouts of grinding teeth occurred 14.4 times more often during encounters than outside of encounters (Fig. 2), and yawning was 16.2 times more common (grinding teeth, t_{381}=4.73, P<0.0001, yawning, t_{381}=4.32, P<0.0001, directed tests). Scratching and self-grooming were also elevated significantly (t_{381}=3.93, P<0.0001, self-grooming, t_{381}=5.01, P<0.0001, directed tests). Individuals who displayed higher rates of aggression during inter-group encounters showed higher rates of yawning during encounters (r_s=0.42, n=10, P=0.025, directed test), although this result did not hold for self-grooming (r_s=0.02, n=10, P=0.42), scratching (r_s=–0.16, n=10, P=0.60), or grinding teeth (r_s=0.07, n=10, P=0.28, directed tests). Moreover, among focal samples collected during encounters, samples characterized by at least one aggressive or submis-

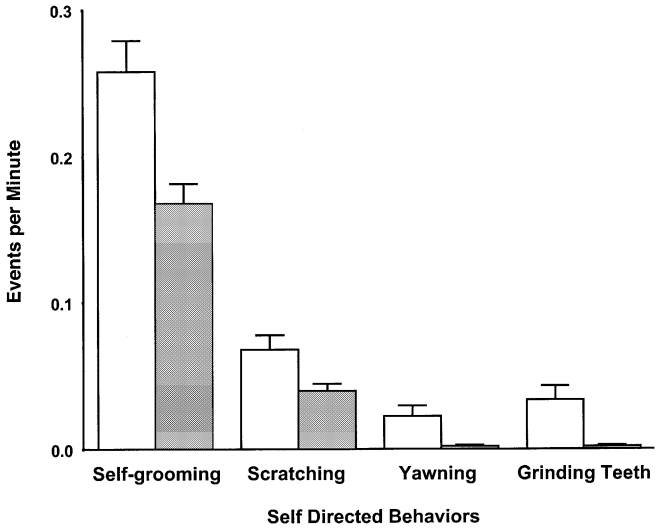

Fig. 2 Self-directed behaviors during inter-group encounters. Plots show the mean rate +1 standard error (SE) of self-directed behaviors during inter-group encounter focal samples (*open bars*) and during non-encounter focal samples (*filled bars*)

sive act had higher combined rates of yawning and grinding teeth than did focal samples without antagonism (t_{147}=2.82, P=0.003, directed test). This result also held when controlling for female identity ($F_{1,137}$=6.02, P=0.008, directed test; focal identification was non-significant, $F_{9,137}$=0.90, P=0.53).

As a final measure of stress, we used data from Cavigelli et al. (2003) to test whether females that were more commonly involved in territorial conflicts exhibited higher levels of fecal corticoids. A significant positive association was found for rates of aggression (t_8=2.40, P=0.03, directed test) and genital marking (t_8=4.81, P=0.0005, directed test), but not for individual location relative to inter-group aggression (t_8=–0.59, P=0.36).

Benefits of territoriality

In the wild, defense varies with habitat quality and population density (Jolly et al. 1993; Sauther and Sussman 1993), suggesting that ringtailed lemurs alter territorial behavior in response to benefits. At the DUPC, groups forage on the neighboring territory when the opportunity arises. Thus, we documented feeding on natural vegetation during 8 of 11 deep incursions with focal data when both groups were free ranging (Lc-1: 9 incursions, 7 with foraging; Lc-2: 2 incursions, 1 with foraging). In addition, each group defended water sources and feeding locations vigorously when they discovered the other group on their territory (n=6), chasing interlopers to the territorial boundary.

These results demonstrate that feeding occurs on neighboring territories during incursions and that incursions are interrupted when detected. However, a critical issue is whether territorial defense reduces the rate of incursions, thus providing benefits to individuals in groups. To address this possibility, we performed an experiment to test whether incursions are more likely when one group is restrained from defending its territory. Deep incursions were more likely on days when one group was locked up (8/13 days, 62%) versus baseline days when both groups were free ranging (4/18, 22%; chi-square=4.99, P=0.016, directed test). Females fed on natural vegetation in the neighboring territory in seven of eight incursions during experimental lockups.

Finally, it is likely that the benefits of territorial defense spill over to other individuals in the group, regardless of whether they participated in obtaining the benefits. Our study provided two indirect indicators that the benefits were shared. First, no individuals were completely excluded from foraging on natural vegetation or provisioned food. Second, only one episode of unambiguous targeted aggression was observed during our two-season study (Lc-2 in 1998, female CHA), and in this case the females did not successfully evict their target (the number of evictions may have been depressed in the study animals due to the absence of births, since most evictions occur during breeding and birth seasons; Vick and Pereira 1989). Targeted aggression, in which one animal is consistently attacked and eventually expelled from the group (Vick and Pereira 1989), is the most obvious form of exclusion in ringtailed lemurs; thus, the absence of this behavior during our study is consistent with the sharing of benefits obtained from territorial defense.

Patterns of participation in territorial defense

Given that territoriality is costly and provides corresponding benefits to individuals, we investigated patterns of individual participation in territorial defense. In each of the two groups, there were striking differences in individual participation. In Lc-1 in 1998, for example, one female (ATT) accounted for a majority of aggressive behaviors documented in inter-group encounters, while the least participatory female (KAT) was not observed to perform a single aggressive act in the context of inter-group encounters (Fig. 3). A similar pattern was found when we analyzed individual location relative to aggressive interactions during encounters (Fig. 4). Over both years, females in Lc-1 differed significantly in their rates of aggressive acts ($F_{6,187}$=15.8, P<0.0001, two-tailed), genital marking ($F_{6,187}$=8.86, P<0.0001, two-tailed) and individual proximity to locations of aggressive acts ($F_{6,157}$=6.66, P<0.0001, two-tailed). When the analysis included only the three females that were followed throughout the two field seasons (KAT, NIN and COR), significant results were obtained for all three measures of involvement (aggressive acts: $F_{2,126}$=7.03, P=0.001, location: $F_{2,104}$=15.5, P<0.0001, genital marking: $F_{2,126}$= 12.2, P<0.0001, all tests two-tailed). Thus, significant differences were not dependent on the one female (ATT) that performed the most aggression in 1998.

Individual differences also were found in Lc-2 in 1998, with one female (CLI) exhibiting a higher rate of ag-

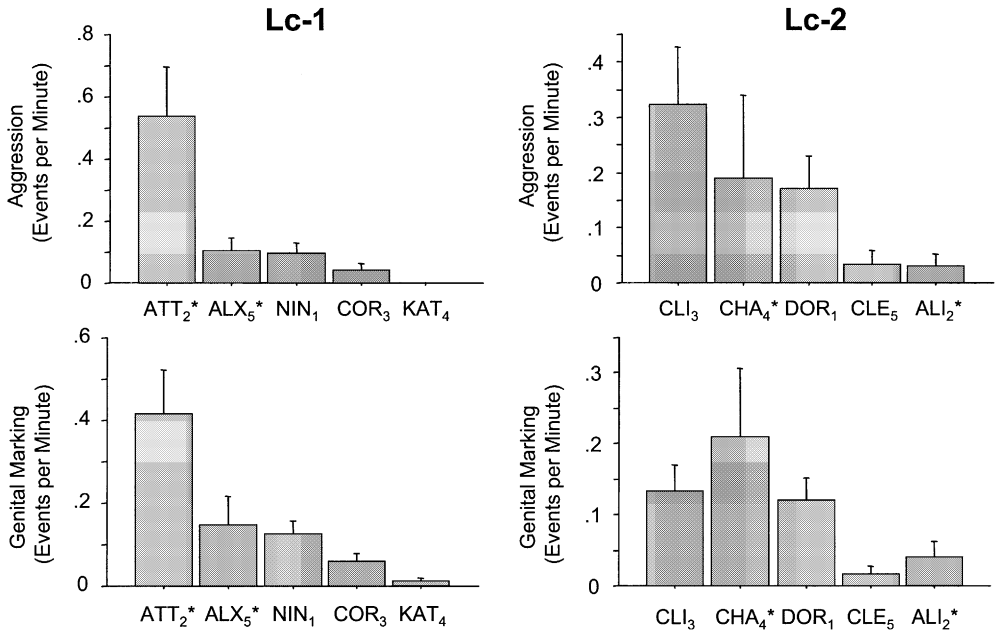

Fig. 3 Individual differences in aggressive interactions and genital marking during inter-group encounters in 1998. *Bars* show mean levels of activity (+1SE) by five females that were fully adult in each of the two groups in the summer of 1998. *Subscripts* indicate dominance ranks. Animals are listed in order of their participation in aggressive interactions, which is likely to be the most risky and energetically costly behavior involved with territorial defense. Individuals with *asterisks* were removed midway during the 1998 season. Only fully adult females are shown. Results for 1998: Lc-1, aggression: $F_{4,110}$=15.4, P<0.0001; Lc-1, genital marking: $F_{4,110}$=12.1, P<0.0001; Lc-2, aggression: $F_{4,129}$=2.45, P=0.049; Lc-2, genital marking: $F_{4,129}$=2.32, P=0.06; all tests two-tailed. See text for other analyses

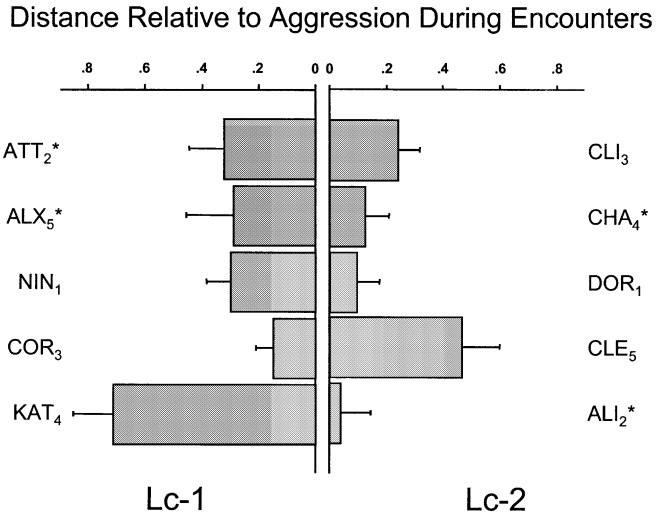

Fig. 4 Individual differences in proximity to aggressive inter-group encounters in 1998. Location was recorded using one of six "zones" (Fig. 1). *Location values* refer to the difference between an animal's zone and the zone(s) where aggressive acts were observed (+1SE), with larger values indicating that an individual is farther from aggressive interactions during encounters. Animals are listed in the same order as Fig. 3 for comparison. *Subscripts* indicate dominance ranks for 1998

gression during inter-group encounters (Fig. 3) and individuals varying in their proximity to aggressive acts (Fig. 4). Across years, females varied in their levels of aggression ($F_{6,175}$=2.71, P=0.015, two-tailed) and genital marking ($F_{6,175}$=2.67, P=0.017, two-tailed), though location relative to aggression failed to reach significance ($F_{6,137}$=2.00, P=0.069, two-tailed). Focusing on the three females in Lc-2 that were observed throughout the 2-year study, significant results were again obtained for aggressive acts ($F_{2,110}$=4.12, P=0.019, two-tailed) and location relative to aggression ($F_{2,83}$=4.77, P=0.01, two-tailed), but genital marking failed to reach significance ($F_{2,110}$= 2.81, P=0.06, two-tailed). Thus, individual differences were less marked in Lc-2 but still significant in most analyses.

The dynamics of individual participation are also expected to change when group composition changes, for example if more active participants emigrate. To maintain constant group size, two females from each group were removed in 1998 (see Methods). In Lc-1, one of these females was the most active participant in inter-group encounters (ATT, Fig. 3). We tested whether the remaining individuals in Lc-1 increased their participation levels in 1999, following housing during the winter and re-establishment in the free-ranging enclosures. A two-way ANOVA, using data on the three fully adult females studied in both years, revealed significant differences in aggression levels among the three fully adult females ($F_{2,103}$=6.24, P=0.003), but not among study years ($F_{1,103}$=0.16, P=0.69, two-tailed). In 1999, however, these three adult females did increase their levels of genital marking ($F_{1,103}$=11.9, P=0.0008). In terms of aggressive behaviors, one of the newly mature females accounted for 54% of observed aggressive interactions (CLD) in 1999,

while the other female (AND) performed 10% of aggressive acts (other females performed 0–29%). Thus, females in this group filled the defensive gap in a variety of ways following removal of the most active participant.

Lc-2 group was less remarkable in that neither of the removed females was the primary provider of territorial defense (Fig. 3). In 1999, however, the two recently matured females together accounted for 41% percent of the aggressive acts observed during encounters. As with Lc-1, there was no significant change in aggression by the three fully adult females from 1998 to 1999 ($F_{1,82}$=2.24, P=0.14, two-tailed). Non-significant results were also obtained in analyses of genital grooming rates and location relative to aggression during encounters for Lc-2.

Factors that influence participation: dominance rank, offspring care and kinship

These results demonstrate that individuals vary in their participation in inter-group encounters. Variation in participation, however, does not equate to free riding if individuals experience either differential costs in performing defensive behaviors, or differential benefits from defending a territory. The net benefits are likely to vary among individuals and are difficult to quantify directly, but the extremely low levels of participation by some females suggests that some free riding occurs in these social groups. A female in Lc-1 provides the best example. In 2 years of data collection, this female (KAT) was never observed to participate aggressively in inter-group encounters (for 1998, see Fig. 3), even outside of focal samples, and she was consistently far from the zones of aggressive activity (Fig. 4). A similar pattern was found in independent research involving this female from 1989 to 1995 (M. Pereira, personal communication). During our study, KAT was not targeted for eviction by her group mates. Hence, she acquired benefits from others' territorial defense, but she was never observed to bear the costs.

Variation in the individual benefits of territorial defense may explain patterns of participation, with individuals that benefit to a greater extent from territoriality more likely to participate. We investigated the effects of asymmetrical net benefits using information on dominance rank because dominant individuals are able to displace subordinates from resources, thereby obtaining a larger share of the defended resources (personal observation; see also Pereira 1993). Dominant females may also experience improved physical condition, which would lower the costs of participation (and thus raise the net benefits). High-ranking females showed higher rates of aggressive acts during encounters ($F_{1,374}$=3.48, P=0.032, directed test), genital marked more commonly ($F_{1,374}$=13.5, P=0.0002, directed test), and were closer to the zones in which aggression took place during encounters ($F_{1,306}$=5.67, P=0.011, directed test). As indicated by Fig. 3, however, rank explained remarkably little of the variation in aggressive participation, genital marking and location (r^2<0.05 in all cases).

Offspring care is an additional variable that may account for individual patterns of territorial defense, with increased offspring care reducing the energy available for territorial defense and thus raising the costs of participation. Females did not breed during our study, but at the start of research in 1998, five females had juvenile offspring from the previous breeding season. During the 1998 season, females with juvenile offspring were not significantly less aggressive (no offspring vs singletons or twins: $F_{1,251}$=0.21, P=0.41, directed test) and did not exhibit reduced genital marking ($F_{1,251}$=1.54, P=0.13, directed test), but they were farther from the zone of aggressive inter-group interactions ($F_{1,195}$=3.11, P<0.05, directed test). In a multivariate model that included offspring care and dominance rank, both variables were statistically significant for location relative to aggression, while only dominance rank explained significant variation in patterns of aggression and genital marking (restricted to 1998 data, when dependent offspring were present). However, the r^2 remained below 0.10 for all analyses.

Finally, kinship appeared to play a role in differences between the two groups. In Lc-1, where there was greater variance in participation (Fig. 3), females were less closely related through their maternal lineage than females in Lc-2 (see Methods), and the major free rider in Lc-1 (KAT) was least closely related to the other members of her group. Aside from her juvenile daughter, KAT was related to the other members of Lc-1 through her grandmother, who was not in the group at the time of the study (Table 1). By comparison, all females in Lc-2 are direct descendents of a female that is still present in the group. This matriarch, CLI, was the most aggressive participant during inter-group encounters (Fig. 3).

Because females are philopatric, we predicted that the number of living daughters in the group would account for patterns of individual participation if kinship plays an important role. We compiled data on the number of living daughters for each female using group composition in 1998, with values ranging from 0 to 5. Using non-parametric tests to deal with the highly skewed distribution of values (most females had no daughters), we found that the number of daughters explained significant variation in individual aggression during encounters (r_s=0.092, n=376, P=0.048, directed test), but not for the rate of genital marking (r_s=0.075, n=376, P=0.09, directed test) or location relative to aggression (r_s=0.03, P=0.86, directed test).

We also examined individual participation in a multivariate model, taking into account dominance rank, offspring care (zero dependents vs one or more dependents), and number of daughters. Dominance rank was a statistically significant predictor of rates of genital marking and location relative to aggression, while number of daughters explained significant variation in aggression and genital marking (Table 2). Offspring care provided significant results opposite to the predicted effect, possibly indicating a strong association between this variable and the number of daughters. This collinearity caused some instability in the statistical model when run with

Table 2 Individual participation in inter-group encounters. Table shows *F*-statistic (for overall model) or *t*-statistics, with sign of the *t*-statistic indicating the direction of the effect. All results were in the predicted direction except for those involving offspring care (i.e., females with more offspring exhibited higher rates of genital marking and were in closer proximity to aggression when examined in this multivariate model; see text). Number of observations varies from 308 (proximity to aggression) to 376 (rates of aggression, genital marking)

Measure of participation	Overall model	Dominance rank	Offspring care	Number of daughters
Aggression	5.12**	−1.01	1.70	3.38***
Genital marking	7.73***	−3.16**	3.05**	1.93*
Proximity to aggression	4.56**	2.00*	−2.81*	−1.42

* $P<0.05$, ** $P<0.01$, *** $P<0.001$

different variables; thus, results must be interpreted cautiously, but it appears that dominance rank and the number of daughters best accounted for variation in measures of participation in this model. The variance explained by this model (r^2) remained below 0.06, as compared to $r^2>0.15$ for a model that included only focal identification as a predictor variable.

Policing and private incentives

Additional unexplained variation may be accounted for by patterns of policing, in which free riders are punished for failing to participate in territorial defense (see Clutton-Brock and Parker 1995; Frank 1995). During inter-group encounters, however, within-group aggression among females was uncommon, with only four aggressive acts observed among individuals of the same group. The rate of aggression appeared to increase slightly in the 30 min after encounters ended (Fig. 5), but it was not significantly different from the rate of aggression in the 30 min before encounters started (Table 3). On an individual basis, we found no statistical association between rates of aggressive acts to the other group during encounters and rates of aggressive acts toward group mates (r_s=–0.08, n=14, P=0.76, directed test) or received from group mates (r_s=0.01, n=14, P=0.64, directed test) following encounters. Rates of genital marking and location during encounters also were uncorrelated with aggression received following encounters.

Individuals may also provide incentives, such as grooming, to encourage other animals to participate in territorial defense. Affiliative behavior varied relative to the timing of encounters (Fig. 5), but there was no significant difference before and after the encounter (Table 3) and no significant association between individual affiliative interactions given to group members during encounters and involvement in inter-group encounters (aggressive acts: r_s=–0.31, P=0.67; genital marking: r_s=–0.21, P=0.96; mean location: r_s=0.08, P=0.49, directed tests, n=14). Similarly, individuals that participated in aggressive inter-group interactions were not more likely to receive affiliative acts from group mates during encounters (r_s=–0.09, n=14, P=0.90, directed test), and the affiliative acts that a female received were not significantly related to her rate of genital marking in inter-group encounters (r_s=–0.52, n=14, P=0.96, directed test).

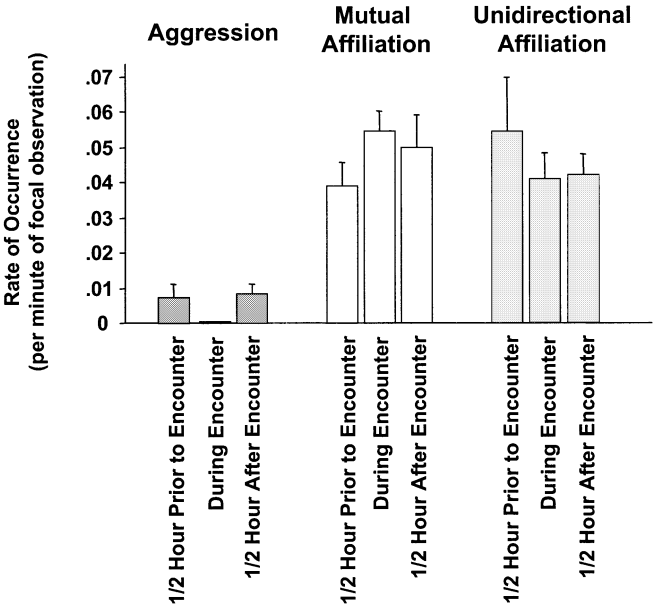

Fig. 5 Aggression and affiliation before, during and after encounters. Rates of affiliative and aggressive behaviors are measured as events per minute during focal samples of females (+1SE). During encounters, aggressive interactions among females of different groups were excluded

Table 3 Individual rates of affiliation and aggression within groups. Statistical tests two-tailed, ANOVA, dependent variable: rate of aggression or affiliation; independent variables: before or after encounter and focal ID

Focal (measure)	30 Min before encounter	30 Min after encounter	*F* statistic (overall model)	*F*-statistic (before or after encounter)	*F*-statistic (focal ID)
Aggression given	0.0071	0.0084	$F_{14,426}$=2.68***	$F_{1,426}$=0.43	$F_{13,426}$=2.88***
Mutual affiliation	0.039	0.050	$F_{14,426}$=1.86*	$F_{1,426}$=0.32	$F_{13,426}$=1.95*
Affiliation given	0.055	0.042	$F_{14,426}$=0.65	$F_{1,426}$=0.77	$F_{13,426}$=0.64

* $P<0.05$, ** $P<0.01$, *** $P<0.001$

Because animals that are involved in territorial defense may have less time available for performing affiliative acts during encounters, we also investigated whether more participatory animals give or receive more affiliative acts in the 30 min after encounters. However, there was no statistical association between overall rate of involvement in aggressive encounters and post-encounter affiliation given (r_s=−0.11, n=14, P=0.81) or received (r_s=−0.03, n=14, P=0.68, directed tests). Similar results were obtained for analyses of genital marking and location relative to encounters.

Discussion

Territorial behavior in ringtailed lemurs entails individual costs and benefits. The increased frequency of self-directed behaviors during territorial encounters, especially during periods when aggression was more likely to occur, suggests that these encounters cause substantial stress to the individuals involved. Chronic exposure to such stress can have negative effects on growth, reproduction, and disease resistance (Henry 1982; von Holst 1985; Lloyd 1995). In addition to measures of individual stress, encounter frequency correlated negatively with temperature, suggesting that the animals face heat stress in the context of territorial defense.

In terms of benefits, incursions by the other group were more likely when a group was restrained from defending its territory. Within groups, individual lemurs were not obviously restricted in their access to resources defended from other groups. These results suggest that when one individual participates in territorial defense, other individuals in the social group benefit. Thus, ringtailed lemur territoriality is consistent with "cooperation" through by-product benefits, in which selfish acts (territorial defense) benefit the actor as well as other individuals (Connor 1995; Sachs et al. 2004). Moreover, females with more daughters in the group participated to a greater extent, suggesting that kin selection may play a role in accounting for individual participation. Additional costs and benefits influenced patterns of individual behavioral patterns. In particular, dominance rank was a significant predictor of participation in encounters, although the overall amount of variation explained was low. More dominant individuals may play a greater role in territorial behavior if they are in better physical condition (and therefore experience fewer costs), or if they obtain a greater share of the benefits from successful territorial defense. In addition, females with more juvenile offspring tended to be farther from the zones of aggressive conflict, although this effect was less robust than the effect of dominance rank or kinship and was probably driven in bivariate tests by the least active participant (KAT), who had two offspring during this time period. Finally, policing has been proposed to influence patterns of participation in cooperative acts (Frank 1996), yet we found no evidence for policing in our study. It remains possible that a more subtle form of policing occurs in these lemurs, reducing the statistical power of our test, or that such behaviors occur over longer periods than our study covered.

Several factors may account for the small amount of variation in participation that was accounted for by individual traits. Our measures of benefits and costs of territorial defense may have been too indirect to account for more variation. Future studies could use a more quantitative measure, such as amount of body fat or levels of parasitism, to investigate the correlates of individual participation in social groups. In addition, some aspect of the captive situation, such as provisioning, may have influenced our results. For example, if the top-ranking female monopolizes provisioned resources, lower-ranking females may have more at stake in defending natural vegetation. Provisioning may also have also altered patterns of range use and the energy available for territorial defense, or it may have disrupted seasonal patterns of territorial defense. Finally, each of the groups in our study had only a single competing group, whereas groups in the wild may have several neighbors (Jolly et al. 1993). If wild animals have limited energy available for defending boundaries, an increase in the number of neighbors might increase the number of encounters but reduce levels of aggression observed during encounters. Similarly, incursions may occur more frequently in the wild than in our captive setting, because wild groups must typically defend several borders, rather than focusing their effort on only one.

The captive setting of our study provided several important advantages, including the ability to maintain constant group size throughout the study and to experimentally limit ranging behavior and territorial defense. This setting also limited the interaction to a single intergroup relationship, whereas interactions among different groups may be influenced by patterns of kinship among groups (Spong and Creel 2004), and by variation in the distribution of resources. Group composition and ranging behavior in this captive population was largely similar to patterns observed in wild populations, as shown in previous studies of ringtailed lemurs at the DUPC (e.g., Kappeler 1993; Pereira 1993; Pereira and Kappeler 1997). Studies of wild ringtailed lemurs have also documented individual differences in involvement in territorial encounters (Jolly et al. 1993; Nakamichi and Koyama 1997), further suggesting that our results do not reflect artifacts of captivity.

In addition to the traits that influenced patterns of participation in our study, three other factors may account for variation in individual participation in territorial defense and/or the absence of detectable policing in our study. First, a form of interchange may exist in which individuals provide different beneficial acts and exchange the benefits over time. Such a system of interchange and reputation has recently been shown to increase participation in human cooperation, with interaction in one game influencing interaction in other games (Milinski et al. 2002; Semmann et al. 2004). KAT and others who participated at low levels did not provide higher levels of

a probably less costly benefit to the group, genital marking, during encounters. Instead, marking rates during encounters were highly correlated with the rate of aggressive acts in Lc-1 (for 1998, see Fig. 3). However, analysis of other potential cooperative acts, such as vigilance against predators, may support the hypothesis that ringtailed lemurs exchange different costly activities. The timescale of exchange may also be important, with animals participating to a greater or lesser extent at different times of year, or at different stages of life.

Second, females may benefit from participation if it serves as an honest signal of competitive ability (Zahavi 1977; Nakamichi and Koyama 1997; Nowak and Sigmund 1998; Roberts and Sherratt 1998). An honest signal of female quality may be important for lower-ranking female ringtailed lemurs as they vie for the top-ranking position (Pereira 1993; Nakamichi and Koyama 1997), possibly accounting for the weak (but statistically significant) association between rank and aggressive participation in encounters. By signaling their quality, participation may be used by females to avoid being targeted for expulsion from the group. This might account for the increased participation of maturing females in 1999, as these young females may be at greater risk of eviction (Vick and Pereira 1989; Nakamichi and Koyama 1997). Arguing against this hypothesis is the fact that animals in stable social groups should have ample opportunities to evaluate one another's competitive ability. Moreover, a recent study found no support for this handicap model in the species for which it was originally proposed (Arabian babblers, *Turdoides squamiceps*: Wright et al. 2001).

Finally, individuals may use inter-group encounters to assess dispersal or breeding opportunities in neighboring groups (Lazaro-Perea 2001). Such assessment is likely to be most relevant to the dispersing sex, and so is unlikely to be a factor in female inter-group encounters in ringtailed lemurs, in which females are philopatric. However, females that face eviction through targeting aggression need to assess breeding opportunities outside the group (e.g., Hood and Jolly 1995), and inter-group encounters may provide a means to do this. Consistent with this hypothesis, the one female that was targeted during our study (CHA) was not particularly aggressive during inter-group encounters, but was relatively close to the areas where aggression took place during encounters (Fig. 4), as would be expected if she was evaluating dispersal options. In an earlier study, Pereira (personal communication) observed that low-ranking females who had recently been targeted for aggression commonly undertook incursions deep into the other group's territory. A larger sample of targeting events will be required to assess whether risk of eviction changes patterns of individual participation in inter-group encounters.

We assumed that aggressive acts, genital marking and proximity to aggressive acts indicated involvement in territorial defense. In most encounters, however, individuals that were not in immediate range of the aggressive acts, and therefore were not the most active participants, were close enough to monitor the encounter. If one group had begun to dominate or over-run the other group, these individuals may have been able to gauge this shift and increase their levels of participation. Thus, even non-participants may have provided some benefits to other individuals that were more active participants, effectively serving as "threat of backup" for situations in which their help may be needed. In other words, the absolute number of individuals in the group may be important, consistent with benefits obtained through group augmentation (Clutton-Brock 2002). Although Jolly et al. (1993) found no support for an effect of group size on the outcome of encounters in an observational study of wild lemurs, this hypothesis could be tested experimentally by removing non-participants (free riders) from one group; if the presence of non-participants does contribute to territorial defense, then their removal should affect the outcome of encounters and/or frequency of the opposing groups' incursions into the territory. Similarly, the number of males in a group may have an effect on the outcome of encounters. Based on our initial observations, we focused on females and their defense of stable territorial boundaries involving resources (see also Jolly et al. 1993). But it may be interesting in future research to investigate whether males have any influence on inter-group encounters among females, in this case by experimentally manipulating the number of males in social groups.

The results that we obtained are consistent with a framework of by-product reciprocity and shared genes (see Connor 1995; Clutton-Brock 2002; Sachs et al. 2004). Although shared genes (kin selection) have received much attention from biologists interested in cooperation, by-product benefits have been given less consideration (Clutton-Brock 2002). A conceptual framework from economics involving "collective action" (Olson 1965; Hardin 1982; Taylor and Ward 1982; Ostrom 1990, 2001; Sandler 1992) may shed light on by-product benefits and patterns of individual participation in animal social groups (van Schaik 1996; Nunn 2000; Nunn and Lewis 2001). These issues are closely related to the "tragedy of the commons" problem in humans (Hardin 1968; Frank 1995), and collective action frequently involves use of resources that are costly to produce and difficult to monopolize, similar to by-product benefits in animal societies. The concept of collective benefits is not entirely distinct from previous approaches in biology, but this framework offers a more comprehensive cost–benefit framework for formulating hypotheses about individual participation in large social groups, a topic which has attracted much recent attention in behavioral ecology (e.g., Heinsohn and Packer 1995; Clutton-Brock et al. 1999, 2000; Watts and Mitani 2001; Wilson et al. 2001). Moreover, the collective action problem has been investigated more extensively in economics than in biology. Thus, this economic framework may offer a blueprint for future empirical and theoretical research on cooperation in animal social groups.

In conclusion, our study of female ringtailed lemurs provides insights to the costs and benefits of territorial defense, and to patterns of individual participation in

social groups. Our results suggest that individuals adjust their contributions to "collective" goods in accordance with the costs and benefits. At least one female in our study appears to have benefited from territorial defense without obviously bearing the costs. However, our estimates of the costs and benefits explained only a small proportion of the variance in individual participation. Individuals may exhibit differences in participation that are not directly linked to the costs and benefits that we considered, a form of interchange may take place, or there may be other costs and benefits that have not yet been identified. Future research on this topic should investigate how benefits spillover to other group members, as represented through by-product benefits. Fruitful advances may also come from applying collective action models as a conceptual framework to understand the mechanisms that facilitate cooperation in animal groups.

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