ORIGINAL ARTICLE

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Between-group encounters among bonnet macaques (*Macaca radiata*)

Abstract Socioecological theory suggests that between-group competition is an important factor affecting the nature of primate social relationships. Between-group encounters in macaques may involve female resource defense, male mate defense, and male resource defense. We observed between-group encounters in two groups (a forest group and a temple group) of bonnet macaques (*Macaca radiata*). We observed 102 encounters in 875 h of observation of the forest group (1.40 per 12-h day) and 58 encounters in 907 h of observation of the temple group (0.77 per 12-h day). Aggressive interactions between groups occurred in 32.4% and 29.3% of encounters in the forest and temple groups, respectively. Overall, we found little support for the female resource defense hypothesis. Females in both groups rarely participated aggressively in between-group encounters. We found support for the male mate defense hypothesis. For example, males of the forest group were more aggressive during encounters in the mating season than in the non-mating season. Males were also aggressive to females from their own group immediately following encounters. We also found partial support for the male resource defense hypothesis. Encounters in the forest group occurred in a feeding context more often than expected based on time budgets. Also, males in the temple group were more often aggressive in food-related encounters than in other encounters. The findings of this study suggest that socioecological models of primate social relationships need to distinguish male and female strategies during between-group encounters and integrate the resulting functional outcomes.

Keywords Between-group encounters · Female resource defense · Male mate defense · Male resource defense · Between-group competition

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Introduction

In most group-living species, interactions between groups are antagonistic (Cheney 1987). The level of hostility in between-group encounters can range from mutual avoidance (e.g. *Alouatta seniculus*: Sekulic 1982) to lethal aggression (e.g. *Pan troglodytes*: Manson and Wrangham 1991). Between-group competition is an important factor in numerous theoretical models of primate socioecology (Wrangham 1980; van Schaik 1989; Isbell 1991), and in the gregariousness of social carnivores (Mills 1982, 1989; Packer et al. 1990; Heinsohn and Packer 1995; Gompper 1996). While theoretical interest in between-group competition is growing, empirical data with which to evaluate socioecological models is still limited. The lack of data is due, in part, to the low rate of between-group encounters in the wild, the difficulty in reliably observing group-level interactions under conditions of poor visibility, and the reduced availability of pristine habitat where between-group competition can be studied without direct (e.g. provisioning) or indirect (e.g. habitat destruction) human interference.

In mammals, female reproductive success is expected to be primarily limited by food, while male reproductive success is expected to be limited by access to mates (Trivers 1972). This sex difference results in males and females pursuing different strategies during between-group encounters. Female primates may be inclined, when possible, to defend the food resources in their home range

Table 1 Predictions for male and female behavior during between-group encounters according to three hypotheses. Support for each prediction is shown in *parentheses*. *Y* Yes, *N* no; *E* equivocal. Cells marked with a *dash* indicate that the model makes no prediction for that dependent variable

Predictions	Models		
	Female resource defense	Male mate defense	Male resource defense
1. Rate of encounters	High in dry season (N)	High in mating season (N)	High in dry season (N)
2. Involvement	High for females (N)	High for males (Y)	High for males (Y)
3. Aggressive involvement	High for females (N)	High for males (Y)	High for males (Y)
4. Aggression in food context	High for females (E)	–	High for males (Y)
5. Aggression in dry season	High for females (N)	–	High for males (N)
6. Aggression in mating season	–	High for males (Y)	–
7. Target of aggression	Females and males (N)	Males (Y)	Females and males (N)
8. Rank and aggression	–	Correlated for males (Y)	–
9. Herding by males	–	Present[a] (E)	–
10. Pay back by females	–	–	Present (E)

[a] Especially during the mating season

(female resource defense: Wrangham 1980; van Schaik 1989). Male primates, in contrast, are expected to defend mates. One way males can accomplish this goal is by joining a group of females and preventing other males from gaining access to them. This type of male mate defense has been called female-defense polygyny (van Schaik et al. 1992) or direct mate defense (Fashing 2001). Males may also join a group of females and defend the food resources in the group's home range in exchange for reproductive access to females (male resource defense: Rubenstein, 1986).

Macaques live in multimale–multifemale groups. Females remain in their natal group their entire lives and maintain close bonds with their maternal relatives reflected in kin-biased patterns of affiliation and alliance formation (Thierry 2000). Males emigrate at puberty and may transfer several times during their lives (Pusey and Packer 1987). Males are generally less closely bonded with one another than are females, but in some macaque species males frequently affiliate and support one another in fights (Silk 1994; Paul et al. 1996; Cooper and Bernstein 2000). The different life histories and reproductive strategies of males and females affect their behavior during between-group encounters. Below we briefly review those aspects of female resource defense, male mate defense, and male resource defense relevant to macaques, and make specific predictions for male and female behavior during between-group encounters according to each hypothesis (Table 1).

Wrangham (1980) proposed that female primates should cooperatively defend food resources when they are of high quality and are distributed in patches (i.e. female resource defense). All else being equal, kin should be preferred as coalition partners. Consequently, under these ecological conditions females are expected to remain in their natal group, form strong relationships with kin and respond aggressively to females from other groups (Wrangham 1980). In contrast, strong within-group competition can also pressure females to remain in their natal

group, establish dominance relationships, and affiliate with kin (van Schaik 1989; Sterck et al. 1997). In macaques, within-group competition is strong and appears to have shaped social organization and female social relationships. Variation exists between macaque species in the degree of social tolerance displayed by females, and is expected to depend, at least in part, on the strength of between-group competition (Sterck et al. 1997). Female bonnet macaques have been described as having tolerant social relationships (Silk 1981; Clarke and Mason 1988; Thierry 2000). Therefore, we expected females to be actively involved in between-group encounters, more aggressive in food-related encounters than in other encounters, and more aggressive when food resources are scarce such as during the dry season (Table 1). Females are also expected to target aggression at both females and males during between-group encounters.

While male mate defense likely explains the evolution of territoriality in *Presbytis* (van Schaik et al. 1992), it is not restricted to one-male groups that defend territories (e.g. Cowlishaw 1995; Perry 1996). In multimale groups, males may attempt to prevent copulations between females and extra-group males during periods of close proximity, such as during between-group encounters. Males often do this by chasing away other males (Cheney 1981; Perry 1996; Saito 1998), but they can also chase females from their own group (e.g. Kumar and Kurup 1985; Mehlman and Parkhill 1988; Kinnaird 1992). Herding of females by males typically occurs in one-male groups and appears to function to prevent females from transferring groups (Byrne et al. 1987; Stanford 1991; Sicotte 1993). In species with multimale–multifemale groups, male aggression may function to prevent females from mating with non-resident males during between-group encounters.

In multimale groups, males have the option of cooperatively defending females. Males are expected to form alliances for mate defense only if by doing so they are able to achieve greater reproductive success than if they

do not. This does not imply that fertilizations must be shared evenly, as males may still cooperate when rewards are asymmetrical (Noe et al. 1991). If some males become freeloaders and benefit from the mate defense of other males then a collective action problem will arise and cooperation could breakdown (Nunn 2000). While we expect some cooperation among males during between-group encounters, we do not expect mating to be distributed evenly. In spite of alternative reproductive tactics by low-ranking macaque males (Berard et al. 1994), high-ranking males tend to have greater reproductive success (de Ruiter and van Hooff 1993; Bauers and Hearn 1994; Bercovitch and Nurnberg 1997; Keane et al. 1997). Consequently, high-ranking males have a greater incentive to defend females. We expected high-ranking males to participate in between-group encounters frequently and be aggressive (Table 1). Furthermore, males are expected to be more aggressive during the mating season and specifically target extra-group males.

In macaques, males do not show resource defense polygyny (Emlen and Oring 1977), but they may act as hired guns for females (Rubenstein 1986). Using this strategy, males join a group and defend food resources in exchange for reproductive access to females. Accordingly, males are expected to be most aggressive when between-group encounters are food-related, and when food resources are more limited during the dry season (Table 1). Males are also expected to direct between-group aggression at all non-resident individuals, not preferentially at males or females. Males may cooperatively defend resources but still have the problem of sharing fertilizations (see above). Females benefit from male resource defense and should repay males after males defend resources (Fashing 2001). For instance, females are expected to preferentially mate with and groom males that frequently participate in between-group encounters.

The rate and nature of between-group encounters may differ between macaques living under natural conditions and those living commensally with people. Artificial feeding tends to increase competition for food and within-group aggression (Southwick et al. 1976). Indeed, urban monkeys have a more aggressive behavioral profile than do forest monkeys (Singh 1969). Rhesus macaques (*Macaca mulatta*) that receive food from people, and thus have an extremely clumped distribution of food, live at high densities and have a high rate of between-group encounters (Vessey 1968; Lindburg 1971; Hausfater 1972). Ciani (1986) observed that between-group encounters in a group of rhesus macaques were more likely to involve aggression when those encounters occurred in urban areas than in forest areas. Southwick (1962) also noted that severe between-group fights tended to occur when groups met unexpectedly at blind corners created by buildings or walls.

In the present study we investigated which of the three main hypotheses (female resource defense, male mate defense, and male resource defense) better explained the pattern of between-group encounters in two groups of bonnet macaques (*M. radiata*), by testing predictions derived from each hypothesis (Table 1). One study group had its home range entirely in forest habitat (the forest group) and the other group lived near a temple (the temple group). Although we did not expect habitat to alter female and male strategies, we expected between-group encounters to be more frequent and aggressive in the temple group than in the forest group, which lived under more natural conditions.

Methods

Study site and study groups

We collected data on two groups of bonnet macaques, referred to as the forest group and the temple group. The forest group lived in the Indira Gandhi Wildlife Sanctuary, Anaimalai Hills, Tamil Nadu, India. Bonnet macaques occur in a variety of habitats and mixed primate communities inside the park (Singh et al. 1997a, 1997b). The study group lived in a dry section of forest in a rain shadow area of the Western Ghats. The group ranged over a steep hill that was bisected by a park road and an irrigation canal. The animals relied primarily on the natural vegetation for food. Occasionally they found trash on the roadside. We studied this group for 11 months from July 2000 to May 2001, during which time we collected 875 h of observation. Group size and composition of the forest group, and other neighboring groups, are presented in Table 2. Adult females were defined as those that reached sexual maturity, and adult males as those that had reached full size. Subadult males were at least as large as adult females, but smaller than adult males in body and testicle size. All animals were individually recognizable, and well habituated to human observers. Some adult animals in the neighboring groups were individually recognizable, and some groups were partially habituated.

The temple group lived at Chamundi Temple near Mysore, Karnataka, India. Chamundi Temple is an ancient Hindu temple that was built on top of Chamundi Hill, which itself is a rocky, forested outcrop. A small village and a variety of tourist-related shops surround the temple. The animals received food from tourists and worshippers at the temple, and relied heavily on trash generated by tourists and villagers. They also stole food from houses and fed on some of the natural vegetation. We studied this group for 12 months from November 1999 to October 2000, during which time we collected 907 h of observation. Group size and composition of the temple group, and other neighboring groups, are presented in Table 2. All animals over 1 year of age were individually recognizable, as were some of the adult males in the neighboring groups. All animals in this population were well habituated to humans.

Data collection

We recorded between-group interactions ad libitum while following the study groups (i.e. the forest group or temple group). We defined between-group encounters as those occasions when the study group was within 100 m (for the temple group) or within 150 m (for the forest group) of members of another group. These distances corresponded to the point at which members of different groups typically established visual or auditory contact. Encounters ended when the groups moved apart. A new encounter was recorded when two groups approached each other again 1 h after a previous encounter. We recorded the location of the encounter, the identity of the neighboring group, the group activity prior to the encounter, and the identity and behavior of all animals involved in the encounter when possible. Involvement in between-group encounters consisted of: monitor, approach, avoid, sexual behavior, affiliation, aggression, and flee (Table 3). All responses were recorded individually for participating adults and subadults of the study groups. Age/sex class and behavior were also recorded for those animals from the neighboring group involved in the en-

Table 2 Group size and composition of study groups and neighboring groups

Group	Group size[a]		Adult males		Subadult males		Adult females	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Forest site								
Forest group	19	19–22	2	2	3	3	5	5
B group	50	47–53	10	9–12	4	4–5	12	12
W group	36	35–38	4	3–4	2	2–3	9	9–10
Y group	14	13–16	3	2–3	1	1	4	4–6
M group[b]	–	–	–	–	–	–	–	–
Temple site								
Temple group	42	41–49	5	5–6[c]	6	6	13	13
D group	23	22–25	3	2–3	2	2	10	10
S group	46	44–48	5	5	6	6	14	14

[a] Variation in group counts due to births, deaths, immigration, and emigration
[b] We never got a reliable count of M group
[c] A sixth adult male was with the temple group during the first week of the study and then transferred to D group

Table 3 Description of behavior during between-group encounters

Behavior	Description
Monitor	Orienting toward and directing gaze for at least 5 s at the neighboring group.
Approach	Direct movement toward members of the neighboring group.
Avoid	Movement away from members of the neighboring group as they approach.
Sexual behavior	Males orient toward and may approach a female while teeth-chattering and retracting their ears and eyebrows. Teeth-chattering involves retracting the lips, exposing the teeth, and rapidly protruding and withdrawing the tongue. Also, females may approach a male and present their hindquarters. (Extra-group copulations were not observed.)
Affiliation	Includes groom, embrace, play and a variety of mounting displays (e.g. mount, hindquarters present, and genital touch).
Aggression	Includes aggressive behavior of any intensity (e.g. round-mouth stare, charge, chase, manual contact aggression, and bite).
Flee	Running away from the neighboring group; more vigorous than avoid. May occur with bared-teeth display. Often occurs in response to aggression but may also occur in the absence of aggression from the opponent.

counter. Encounters were recorded regardless of the number of individuals involved. For instance, a few animals might have approached a neighboring group while the rest of the group remained behind oblivious to the encounter. Due to the difficulty of observing all group members, our observation method may have underestimated the number of animals involved in subtle behavior such as monitoring, but was probably accurate at recording more obvious behavior such as approach, aggression, and flee. Differential habituation to humans between the temple group and the neighboring groups was not an issue, as all animals in the area were comfortable around people. Although the neighboring groups at the forest site had seen researchers during our periodic censuses, differential habituation was a concern. Consequently, during between-group encounters at the forest site we remained in the background, keeping our presence and movements as inconspicuous as possible. The forest group was subordinate in many encounters, suggesting that differential habituation was not a major problem.

We categorized encounters for each participating individual by the resources involved. Resources included food, roosting site, and sex. When the resource could not be determined, the encounter was classified as unknown. Food encounters occurred when a group approached another group while the latter was feeding or had recently finished feeding and was resting in the fruit tree. The latter group typically moved away as the former group began feeding. Roosting encounters occurred when groups met while moving toward or away from their roosting site. Sex encounters occurred when at least one male sexually solicited a female from another group prior to or during a between-group encounter. Encounters over sex were recorded for the individuals involved in the sexual activity and the encounter was categorized separately for the other individuals not involved in the sexual activity as food, roosting site, and unknown.

The day range was recorded for the forest group and the temple group. Day ranges were plotted on a map of the study area for each group. The home range was defined as including those locations visited at least twice during the study period. Partial home ranges for the neighboring groups were estimated by periodic sightings and occasional half-day group follows. The forest group had extensive home range overlap with four neighboring groups (Fig. 1a). The temple group had an overlapping home range with two neighboring groups, though the overlap was less extensive than in the forest group (Fig. 1b).

We collected instantaneous scans on adult and subadult individuals in the forest group. Scans were performed at 10-min intervals and for each identified animal we recorded its behavior as passive, locomotion, feeding, self-directed behavior, grooming, and social behavior (other than grooming). If the animal was grooming we recorded the direction of grooming and the identity of the partner. In the forest and temple groups, we also recorded agonistic interactions and copulation ad libitum. We used submissive behavior (e.g. bared-teeth display, avoid, and flee) during dyadic, unidirectional interactions to determine dominance relationships. We used a modified Landau index to determine the best fit to a linear dominance hierarchy (Singh et al. 2003), and used that hierarchy to rank order subjects.

Data analysis

We divided between-group encounters into those that occurred during the mating season and non-mating season. The mating season typically lasts from July to October for bonnet macaques in South India (Sugiyama 1971), and this was confirmed by our own observations. In the temple group, we extended the mating season to include November, as mating activity continued into November and some infants were born the following May. We also categorized encounters according to whether they occurred during the dry or wet season. For the forest group, January to mid-June is the dry season and mid-June to December is the wet season. We defined the dry season and wet season according to rainfall, and based on
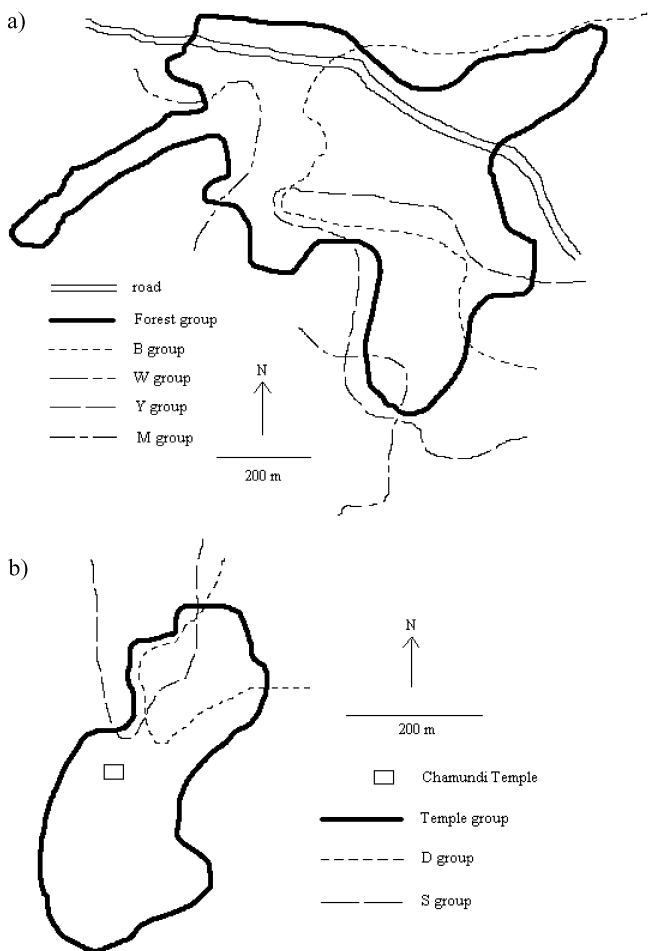
a)

  road
  Forest group
  B group
  W group
  Y group
  M group

N

200 m

b)

N

200 m

  Chamundi Temple
  Temple group
  D group
  S group

Fig. 1 a Home range overlap at the forest site; **b** home range overlap at the temple site. Partial home ranges are estimated for neighboring groups

our previous experience in the region expected reduced food availability during the dry season (Singh 1999). Considerable overlap existed between the mating and non-mating seasons and the wet and dry seasons. To disassociate the influence of mating activity and rainfall, we analyzed one factor while holding the other constant. We compared the mating and non-mating periods of the wet season, and the wet and dry periods of the non-mating season. We did not consider a dry and wet season for the temple group, as the animals did not experience significant seasonal variation in their food supply.

The amount of male aggression against group females during, or immediately following, between-group encounters was compared to the amount of male aggression against females before between-group encounters (i.e. the control sample). Control samples were taken from the data immediately before the corresponding between-group encounter. Control samples were of equivalent duration as the corresponding between-group encounter. When data were not available before a between-group encounter, a control sample was selected from the pool of available samples occurring before other between-group encounters that were not used in the analysis. We selected the control sample by matching group activity and choosing the control sample closest in time to the corresponding between-group encounter.

We used the scan data from the forest group to calculate the proportion of scans that each adult spent feeding. We also used the scan data to calculate for each adult female the proportion of grooming scans that she spent grooming each adult and subadult

male. We divided forest-group and temple-group males into those with high and low participation in between-group encounters based on their position above or below the median. When the number of males was odd, the median male was discarded. We analyzed data using two-tailed non-parametric tests such as Wilcoxon matched-pairs, Mann-Whitney U, Friedman test, and Spearman rank correlations. For comparing two proportions we used a G-test for goodness of fit with the Yates correction for continuity (Zar 1999). The alpha level for all tests was 0.05.

Results

Following the forest group, we observed 102 between-group encounters in 875 h of data collection (1.40 encounters per 12-h day). Following the temple group we observed 58 between-group encounters in 907 h of observation (0.77 encounters per 12-h day). There was a higher proportion of between-group encounters in the forest group than in the temple group (G=14.59, df=1, P=0.001). The proportion of between-group encounters with aggression did not differ significantly between the forest group (32.4%, 33 of 102) and temple group (29.3%, 17 of 58) (G=0.04, df=1, P=0.89).

Female resource defense

In the forest group, between-group encounters often occurred while animals were feeding. Forty-eight percent of between-group encounters occurred in a feeding context (49 of 102), and this was significantly greater than the expected value based on the median percentage of time spent feeding (25.6%, 567 of 2,214 scans) (G=21.4, df=1, P=0.001). The rate of between-group encounters in the forest group did not significantly differ between the wet and dry season (G=0.13, df=1, P=0.84), and correcting for overlap between the mating season and wet season again resulted in no significant difference (G=0.46, df=1, P=0.63) (Table 4).

In the forest group, adult and subadult males participated in more between-group encounters than did adult females (Mann-Whitney, U=0.0, n_1=5, n_2=5, P=0.006) (Fig. 2a). For forest-group males, 88.1% (SD=4.4) of their participation involved monitoring, avoiding, and fleeing from the other group, and for forest-group females, 98.5% (SD=1.0) of their participation involved monitoring, avoiding, and fleeing. Moreover, forest-group males were more often aggressive in between-group encounters than were females (Mann-Whitney, U=0.0, n_1=5, n_2=5, P=0.004) (Fig. 2b). This difference remains when aggression is expressed as a proportion of the total number of encounters (Mann-Whitney, U=0.0, n_1=5, n_2=5, P=0.007) (Fig. 2c). In the temple group, adult and subadult males participated in more between-group encounters than did adult females (Mann-Whitney, U=0.0, n_1=11, n_2=13, P=0.001) (Fig. 2a). For temple-group males, 66.8% (SD=11.0) of their participation involved monitoring and approaching the other group, and for temple-group females, 55.1% (SD=21.9) of their

Table 4 Rates of between-group encounters by season and the proportion of between-group encounters with male aggression

Group	Season[a]	Number of encounters	Observation hours	Rate per 12 h	% Aggression by males (SD)
Forest	Mating	31	213.5	1.74	23.3 (5.6)
	Non-mating	71	661.5	1.29	3.6 (2.0)
	Dry	59	525.0	1.35	4.5 (1.6)
	Wet	43	350.0	1.47	16.8 (4.8)
	Wet part of non-mating	12	136.5	1.05	1.7 (3.7)
Temple	Mating	12	317.0	0.45	0.0
	Non-mating	46	590.0	0.94	13.9 (7.1)

[a] We corrected for overlap between the mating season and the wet season by comparing the mating and non-mating parts of the wet season, and the wet and dry parts of the non-mating season. The mating part of the wet season is the same as the mating season. The dry part of the non-mating season is the same as the dry season. The non-mating part of the wet season and the wet part of the non-mating season are effectively one and the same. See text for significant differences
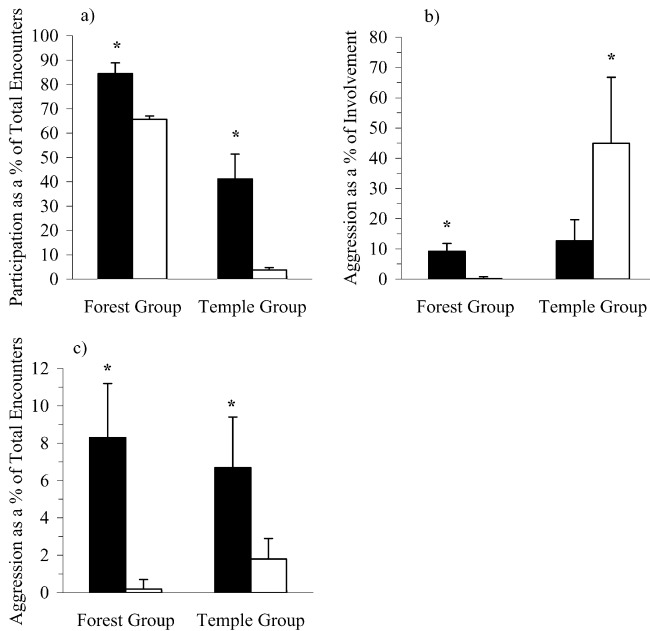

Fig. 2 a Participation in between-group encounters (mean ±SD) is shown as a proportion of the total number of encounters experienced by the study group. **b** Aggression in between-group encounters (mean ±SD) is shown as a proportion of the number of encounters each individual participated in. **c** Aggression in between-group encounters (mean ±SD) is shown as a proportion of the total number of encounters experienced by the study group. *Black bars* represent males, and *white bars* represent females. *Asterisk* indicates a significant difference between opposite-sexed animals in the same group ($P<0.05$)

Table 5 Between-group aggression as a percentage of participation in each encounter context. Table cell marked with a *dash* indicates that animals were not involved in encounters of that context

Subjects	Context		
	Food	Roosting	Unknown
	Mean (SD)	Mean (SD)	Mean (SD)
Forest-group males	8.7 (4.2)	6.9 (2.4)	11.3 (3.0)
Temple-group males[a]	23.9 (13.4)	0.0 (0.0)	7.7 (5.1)
Temple-group females[b]	86.4 (32.3)	–	3.9 (13.9)

[a] Nemenyi post-hoc tests (Zar 1999); food vs unknown: $q=5.52$, $n=11$, $P=0.01$; food vs roost: $q=6.38$, $n=11$, $P=0.01$; unknown vs roost: $q=4.23$, $n=11$, $P=0.01$
[b] Note that temple-group females rarely participated in between-group encounters (see Fig. 2)

than males (Mann-Whitney, $U=1.5$, $n_1=11$, $n_2=13$, $P=0.001$) (Fig. 2c).

In the forest group, a female was once aggressive toward a male during a between-group encounter, and females from neighboring forest groups were not observed to be aggressive during between-group encounters. In the temple group, the majority of between-group aggression by females occurred in a food context (Wilcoxon, $T=1.0$, $n=13$, $P=0.002$) (Table 5). Females directed all of their between-group aggression at males when the target was known (71.4% of 14 cases), whereas we never observed females directing aggression at neighboring females.

Male mate defense

In the forest group, between-group encounters did not occur at significantly different rates in the mating and non-mating season ($G=1.82$, $df=1$, $P=0.39$), and the difference remained non-significant after correcting for overlap with the wet season ($G=2.10$, $df=1$, $P=0.24$) (Table 4). Forest-group males were aggressive in between-group encounters more often during the mating season than during the non-mating season (Wilcoxon, $T=0.0$, $n=5$, $P=0.043$) (Table 4). After correcting for overlap with the wet season, males were still more often aggressive during the mating part of the wet season than during the non-mating part (Wilcoxon, $T=0.0$, $n=5$, $P=0.043$) (Table 4). In contrast to the forest group, be-

participation involved monitoring the other group. Temple-group females never approached other groups during encounters, and the temple-group animals rarely fled. While temple-group females were more often aggressive as a percentage of involvement than were males (Mann-Whitney, $U=21.0$, $n_1=11$, $n_2=13$, $P=0.003$) (Fig. 2b), it should be remembered that the temple-group females rarely participated in between-group encounters. Female aggressive participation at the temple was restricted to females joining males in ongoing aggressive encounters. If aggressive participation is expressed as a proportion of the total between-group encounters experienced by the study group, temple-group females were less aggressive

tween-group encounters in the temple group were more frequent during the non-mating season than during the mating season (G=5.27, df=1, P=0.024) (Table 4). Also, temple-group males were aggressive in between-group encounters more often during the non-mating season than during the mating season (Wilcoxon, T=1.0, n=11, P=0.023) (Table 4). When the target of between-group aggression was known (95.0% of 40 cases), forest-group males directed all of their aggression at males and none at females. Temple-group males also directed all of their between-group aggression at males and none at females when the target was known (97.1% of 35 cases).

Aggressive involvement in between-group encounters was related to male age and dominance rank. Among adult males in the temple-group, aggressive involvement in between-group encounters was significantly correlated with dominance rank (r_s=0.975, n=5, P=0.005). In the temple group, adult males were also aggressive in more encounters (17.9, SD=4.4) than were subadult males (8.4, SD=5.8) (Mann-Whitney, U=2.0, n_1=5, n_2=6, P=0.018). In the forest group, the alpha and beta adult males were aggressive in 12 and 7 encounters, respectively, whereas the lower-ranking subadult males were aggressive 9, 7, and 5 times. We were unable to test the effect of dominance rank among adult males in the forest group because of the small sample size, but aggression did not significantly differ between adult and subadult males (Mann-Whitney, U=1.0, n_1=2, n_2=3, P=0.248).

On three occasions (one in the temple group and two in the forest group) males sexually solicited females during between-group encounters. Mating did not result, and twice resident males chased away the intruder. While the risk of extra-group copulations may not be great during between-group encounters, they can occur at other times. Two males from a neighboring group stayed with the forest group for 7 days during the mating season before returning to their original group. We observed one of the males mating with a forest-group female. Both males were wounded during their stay.

Males did not appear to specifically herd females away from extra-group males during encounters. Rather, adult males periodically chased females upon returning to the group after an encounter. Adult males were aggressive to females significantly more often after between-group encounters than before (Wilcoxon, T=1.0, n=7, P=0.028) (Fig. 3a). We analyzed the males from the forest and temple groups together since we had only seven adult males in total. The trend in each group was the same as the combined result. The mating season did not significantly affect the amount of aggression males directed at females after between-group encounters (Wilcoxon, T=11.0, n=7, P=0.37) (Fig. 3b).

Male resource defense

While forest-group males were more often aggressive in between-group encounters during the wet season than during the dry season (Wilcoxon, T=0.0, n=5, P=0.043),
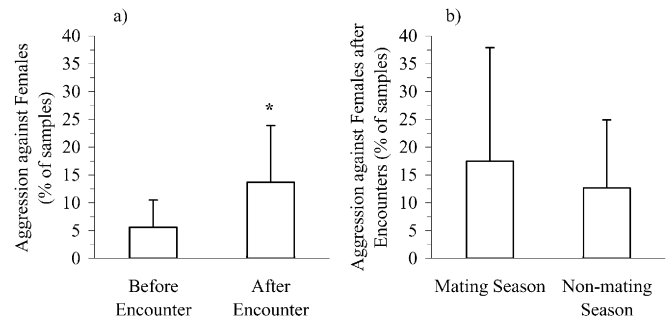

Fig. 3 The amount of aggression (mean ±SD) males directed at females in their own group is shown, **a** as a proportion of samples taken before and after between-group encounters, and **b** as a proportion of samples taken after between-group encounters in the mating and non-mating season. *Asterisk* indicates a significant difference (P<0.05)
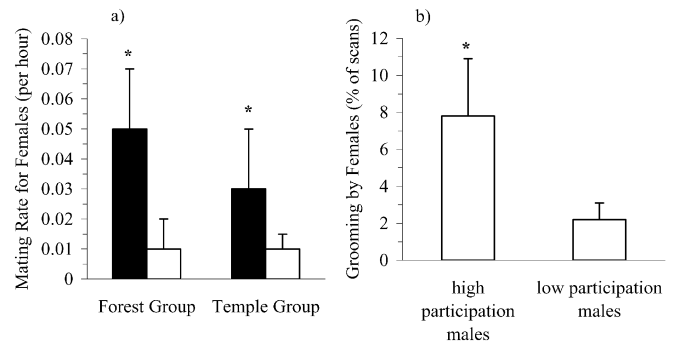

Fig. 4 a The rate per hour (mean ±SD) that females mated with males with high participation in between-group encounters (*black bars*) and low participation (*white bars*) is shown. *Asterisk* indicates a significant difference between males in the same group (P<0.05). **b** The proportion of grooming scans (mean ±SD) that forest-group females groomed males. *Asterisk* indicates a significant difference (P<0.05). Scan data are not available for the temple group

correcting for overlap with the mating season resulted in no significant difference between the wet part of the non-mating season and the dry part (Wilcoxon, T=2.0, n=5, P=0.21) (Table 4). The context of encounters with between-group aggression by males is presented in Table 5. In the forest group, aggression by males was not related to the context of the encounter (Friedman, χ^2=4.8, df=2, P=0.09). In the temple group, males were more often aggressive in food-related encounters than in other encounters (Friedman, χ^2=19.5, df=2, P=0.002, post-hoc tests in Table 5).

If males were defending resources for females, we would expect females to pay back males. Forest-group females mated with males with high participation in between-group encounters more often than they did with males with low participation (Wilcoxon, T=0.0, n=5, P=0.043) (Fig. 4a). Also, forest-group females groomed males with high participation more often than they did males with low participation (Wilcoxon, T=0.0, n=5, P=0.043) (Fig. 4b). Likewise, in the temple group, females mated with high-participation males more often than with low-participation males (Wilcoxon, T=14.0,

n=13, P=0.017) (Fig. 4b). The behavior of males during between-group encounters, however, was influenced by age and dominance rank. While there was no significant effect of age or rank on overall participation, adult and high-ranking males were more often aggressive during between-group encounters than were their younger, subordinate counterparts, at least in the temple group (see Male mate defense section above).

Females did not modify their mating activity in relation to the occurrence of between-group encounters. During the mating season, the rate at which forest-group females mated did not differ significantly between days with food-related encounters, non-food-related encounters, and no encounters (Friedman, χ^2=0.40, df=2, P=0.82). The same was also true for females in the temple group (Friedman, χ^2=0.44, df=2, P=0.80).

Discussion

The nature of between-group encounters differed slightly between the forest and temple groups. Whereas others have found that provisioned groups have higher rates and more aggressive between-group encounters than do wild groups (e.g. Lindburg 1971; Ciani 1986), we found a higher rate in the forest group and no difference in aggression. Lindburg (1971) reported that the density of rhesus monkeys was 44.4 animals per km^2 in the provisioned area, whereas it was at least four times less in the forest. In our case, the density of bonnet macaques was 43.5 animals per km^2 at the forest site (Singh et al. 1997a, 1997b), while it was 26.6 animals per km^2 at the temple site (Singh and Rao, submitted for publication). The reduced density of animals at the temple site was related to the periodic trapping and relocating of pest monkeys. The high density in the forest probably contributed to the high rate of encounters observed and this, along with the relatively low density at the temple, partially explains the inconsistency with earlier studies. But, if density is the critical factor affecting between-group aggression in macaques, as it appears to be in lions (*Panthera leo*) (Heinsohn 1997), then our results are consistent. Previously reported differences between provisioned and wild groups also appear to be related to the distribution of resources. In our case, although the distribution of food was more clumped at the temple than in the forest, and our study group dominated the temple itself, nearby groups were able to find high-quality food around the perimeter of the temple complex in the surrounding village. In addition, home range overlap was much lower at the temple site than at the forest site (Fig. 1), and this probably resulted from temple groups not needing to travel far to find food. We suggest that the groups in the temple population were able to avoid interactions, at least in part, because of the heterogeneous distribution of clumped resources. In contrast, the more scramble-like competition in the forest appears to have forced groups to interact.

The most noticeable difference between the two study groups was in the pattern of female involvement. In the forest group, females often fled from other groups, as did the males. In the temple group, females mainly ignored encounters and occasionally joined males in aggressive encounters. Neighboring groups usually displaced the forest group, whereas the temple group dominated its neighbors. The difference in group dominance status accounted, in large part, for the differences in the behavior of males and females during between-group encounters.

Female resource defense

This study provides little compelling evidence for the female resource defense hypothesis (Table 1). In contrast, the female resource defense hypothesis has received support in a variety of species with female philopatry and strong social relationships among females (e.g. *M. sinica*: Dittus 1986; *Cercopithecus aethiops*: Cheney and Seyfarth 1987; *M. sylvanus*: Mehlman and Parkhill 1988; *Cercocebus galeritus*: Kinnaird 1992; *Presbytis entellus*: Borries 1993). One possible explanation for our failure to support it is that the defense of resources by females can occur at low rates (e.g. Harrison 1983; Perry 1996; Saito et al. 1998; Fashing 2001). Another possibility is that the behavior of males during between-group encounters alters female behavior and makes female resource defense difficult to detect or, in fact, unnecessary.

Van Schaik's socioecological model suggests that strong between-group competition can mitigate the effects of within-group contest competition and produce tolerant social relationships among female primates (van Schaik 1989; Sterck et al. 1997). In macaque species with strong between-group competition all group females are important allies against other groups. High-ranking females are expected to tolerate the presence of low-ranking females at resources in exchange for their support during between-group encounters. Lions are similar to tolerant macaque species in this respect, as the importance of group territorial defense may explain why female lions lack dominance hierarchies and have tolerant, cooperative relationships (Packer and Pusey 1982; Packer et al. 1990; Heinsohn and Packer 1995). Bonnet macaques are normally characterized as having tolerant female social relationships (Thierry 2000). Consequently, we expected between-group competition to be strong, and support for female resource defense. Our results provide mixed support for the hypothesis that strong between-group competition contributes to tolerant social relationships among macaque females. The forest group had a high rate of between-group encounters in comparison with rates reported for other wild populations of macaques (Lindburg 1971; Deag 1973; Kumar and Kurup 1985; van Schaik 1985; Mehlman and Parkhill 1988; Saito et al. 1998; Sugiura et al. 2000; Okamoto and Matsumura 2002). The high rate supports the hypothesis, but the lack of female resource defense does not. Our findings, like those from moor macaques (Okamoto and Matsumura 2002), suggest that

female resource defense is not the mechanism by which between-group competition affects the degree of social tolerance among macaque females.

An alternative to the classic socioecological model is that infanticide risk pressures females to associate with males that provide protection (van Schaik 1996). The infanticide prevention hypothesis has been most widely applied to species with one-male groups where females transfer (Watts 1989; Sterck 1997; Steenbeek 1999; Fashing 2001). Attempts by males to kill infants during between-group encounters, and indirect evidence suggesting infanticide, have also been reported in some species with multimale groups (*Papio anubis*: Collins et al. 1984; *P. cynocephalus*: Tarara 1987; *Cercopithecus aethiops*: Cheney et al. 1988; *Lemur catta*: Hood 1994; *Presbytis entellus*: Sommer 1994). If bonnet macaque females were at risk of infanticide during between-group encounters, we would have expected them to avoid between-group encounters, especially when they had infants. The low rate of active participation (i.e. other than fleeing) by females in the present study supports this prediction, but prevented us from testing whether the presence of infants reduced the probability of female participation. We did not observe any male aggression toward infants that would indicate that females were at risk of infanticide.

Male mate defense

This study provides support for the male mate defense hypothesis (Table 1). The male mate defense hypothesis appears strongest for species in which females transfer between groups (*Papio hamadryas*: Kummer 1968; *Pan troglodytes*: Manson and Wrangham 1991; *Gorilla gorilla*: Sicotte 1993), and has also received support in species living in one-male groups with male and female migration (*Presbytis pileata*: Stanford 1991; *Presbytis* sp.: van Schaik et al. 1992; *P. thomasi*: Steenbeek 1999; *Colobus guereza*: Fashing 2001). However, female transfer is not critical for male mate defense, as varying degrees of male mate defense have been reported in species with multimale–multifemale groups and female philopatry (*Cercopithecus aethiops*: Cheney 1981; *Cercocebus galeritus*: Kinnaird 1992; *Papio* sp.: Cowlishaw 1995; *Cebus capucinus*: Perry 1996; *M. fuscata*: Saito et al. 1998). For example, various studies have found that males play a more significant role in between-group encounters than do females (Lindburg 1971; Mehlman and Parkhill 1988; Cowlishaw 1995; Perry 1996; Matsumura 1998). In baboons and vervet monkeys dominant males are the most aggressive during between-group encounters, which is consistent with their receiving the greatest benefit from defending females (Cheney and Seyfarth 1977; Cheney 1981). In addition, Saito et al. (1998) reported that between-group aggression by Japanese macaque males was greater in the mating season than in the non-mating season. For males in multimale–multifemale groups, male mate defense may reduce the

risk of females mating with non-resident males. Male aggression against other males may also deter the potential influx of males that can occur during the mating season (*M. radiata*: M. Singh, unpublished data).

Male bonnet macaques did not herd females as male baboons and gorillas do (Kummer 1968; Packer 1979; Byrne et al. 1987; Sicotte 1993), but they were observed chasing females from their own group immediately following between-group encounters and occasionally mating with them. Herding appears to be related to the risk of females transferring groups (Stanford 1991). While female philopatry has become the default expectation for macaques (Pusey and Packer 1987), female transfer in bonnet macaques may be more common than previously thought (Kuruvilla 1980; Ali 1981; Moore 1984; A. Sinha, personal communication). Other studies on macaques have reported that males are sometimes aggressive toward females during between-group encounters (*M. silenus*: Kumar and Kurup 1985; *M. sylvanus*: Mehlman and Parkhill 1988). One possible function of this type of male–female aggression is to reduce the chance of females mating with non-resident males during periods of close proximity. While extra-group copulation is rare in macaques, it can occur and occasionally results in pregnancy (e.g. *M. fuscata*: Sprague 1991; Soltis et al. 2001; *M. mulatta*: Lindburg 1969; Berard et al. 1994). Alternatively, males may redirect aggression from between-group encounters at females without affecting mating activity (e.g. Perry 1996).

Male resource defense

This study provides partial support for the male resource defense hypothesis (Table 1). While females often mated with and groomed males that frequently participated in between-group encounters, we could not easily dissociate the influence of age and rank on participation. Aggressive participation in between-group encounters is perhaps one of a constellation of traits that makes older, high-ranking males attractive to females. Furthermore, we could not distinguish between female choice and male–male competition. High-ranking males may have been more aggressive during between-group encounters because they engaged in more copulations, sired more offspring, and had more at stake in group defense. In sum, the relationship between male participation in between-group encounters and mating activity does not distinguish between male mate defense and male resource defense.

Males could benefit from defending resources in three possible ways. First, females might repay males for the service of defending resources (Rubenstein 1986; Perry 1996; Fashing 2001). In species with multimale–multifemale groups such as bonnet macaques, male resource defense with female payback must overcome multiple collective action problems. Some males might cooperate during between-group aggression but not receive payback from females. Similarly, while all females would benefit from resource defense, some might cheat on repayment of

males. Second, males could benefit from resource defense without direct payback from females. For example, capuchin males defend resources during between-group encounters and they benefit by the improved fecundity of the females in their group (Robinson 1988). This is a viable strategy so long as males have a long enough tenure to assure future reproductive access to females. Third, male resource defense may have the added function of defending females. Since males would benefit from their inadvertent mate defense, female payback would be unnecessary. Between-group encounters in bonnet macaques are probably best explained by a combination of male mate defense and male resource defense.

Future studies of between-group encounters need to distinguish male and female strategies and integrate the resulting functional outcomes. For instance, male mate defense may alter female resource defense and ultimately between-group competition among females. Likewise, male mate defense or infanticide protection could be so effective that it might have a profound influence on female behavior during between-group encounters and more generally on female social relationships.

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