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Male–Male Relationships in Lion-tailed Macaques (*Macaca silenus*) and Bonnet Macaques (*Macaca radiata*)

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Abstract Socioecology suggests that female distribution in space is determined by the distribution of food resources and the male distribution is influenced by female distribution. Though studies have traditionally focused on females, males have received increasing attention in recent years. We compared male–male relationships in lion-tailed macaques and bonnet macaques. Because bonnet macaques have a high adult male:female sex ratio and are seasonal breeders whereas lion-tailed macaques have a low adult male:female sex ratio and are largely aseasonal breeders, we predicted that bonnet macaque males would be spatially and socially more tolerant of each other and would have less linear dominance relationships than lion-tailed macaques. We recorded male–male and male–female relationships in 1 group of wild macaques of each species via scan sampling and 1–0 sampling. The results revealed that lion-tailed macaque males largely remained at a distance from each other whereas bonnet macaque males remained in close proximity to one another. Lion-tailed macaque males were more agonistic toward each other whereas bonnet macaque males showed more affiliative interactions. The dominance hierarchy among lion-tailed macaque males was more linear than among bonnet macaque males. Our data support the hypothesis that the study of spatial structuring, temporality of interactions, and linearity of social relationships may contribute to a better understanding of macaque social systems.

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Introduction

The influential concept of primate socioecology suggests that female distribution in space is determined by the distribution of food resources and the male distribution is influenced by female distribution (Emlen and Oring 1977; Sterck *et al*. 1997; van Schaik 1989; Wrangham 1980). During the past few decades, much attention has been paid to study resource use patterns, offspring rearing, and social relationships among females. In recent years, more attention has been paid to primate males, especially to understanding the causes and consequences of variation in number of adult males among groups of primate species (Kappeler 2000). Females are thought to prefer a larger number of adult males in the group to defend their offspring against attacks from males of other groups and the associated risks of infanticide. However, a male's strategy should be to exclude other males and monopolize all females for reproduction because males cannot share fertilization (van Hooff and van Schaik 1994). Getting access to reproductive opportunities is the main force that drives evolution of male sociality (Kappeler and van Schaik 2002). However, a male could also benefit from other males for mate defense or resource defense, especially during intergroup encounters (Cooper *et al*. 2004; Ostner and Kappeler 2004). As a result, primate males may be more agonistic or tolerant toward other males, and be active in reconciliation, retribution, and policing (de Waal 2000; Flack *et al*. 2006). For example, male chimpanzees have been observed to form coalitions and alliances to defend resources (Mitani and Amsler 2003) or to maintain social bonds (Watts 2002). The prevailing theory of male–male relationships, therefore, can be summarized as follows: If a male can benefit from monopolizing female(s), he is expected to be intolerant of other males. This should result in fewer but agonistic interactions among males. However, if a male can gain access to female(s) with the support of a subordinate male (van Hooff 2000), or the males are related to each other by a high degree, or the cost of injury among almost equal sized males is high owing to aggression (Preuschoft *et al*. 1998), males are expected to become more tolerant of other males. The study of male–male interactions may help broaden basic concepts of socioecology (Ostner and Kappeler 2004).

Macaques are a geographically widespread primate taxon with great species diversity, and provide a wide comparative perspective to test hypotheses concerning social organization (Thierry 2004). The ratio of adult males to females varies widely across macaque species (Singh and Sinha 2004). Whereas in bonnet macaques (*Macaca radiata*), the ratio can be as low as 1:1.2 (Singh and Rao 2004), in lion-tailed macaques (*Macaca silenus*), it is as high as 1:9.9 (Singh *et al*. 2000), though this number may become highly variable in groups inhabiting isolated forest fragments (Singh *et al*. 2002). These adult sex ratio differences are linked to a high rate of male migration among lion-tailed macaques (Ananda Kumar *et al*. 2001; Kumar 1987) and low rates of male migration among bonnet macaques (Singh *et al*. 2006b). Because male philopatry is an important factor in male bonding (van Hooff and van Schaik 1994), this predicts that male–male relationships will be different in the 2 species. Bonnet macaques are strictly seasonal breeders, both in free ranging (Sinha 2001) and

captive (Silk 1989) conditions, whereas newborn infants are seen throughout the year in lion-tailed macaques, although there are 2 birth peaks (Krishna *et al*. 2006; Singh *et al*. 2006a). Because female lion-tailed macaques are less synchronous in sexual receptivity, a male may be able to monopolize a receptive female (van Hooff and van Schaik 1994), which would not be the case in bonnet macaques. Because adult sex ratios and seasonality in reproduction are expected to influence social relationships, the study of male–male relationships in these 2 macaque species, which may even be sympatric species in the Western Ghats of south India, will contribute to our understanding of male–male relationships in primates.

Here, we compare the results of 2 independent but comparable studies focusing on wild lion-tailed macaque and bonnet macaque males. Based on differences in adult male:female sex ratio and seasonality of reproduction, we predicted that male lion-tail macaques would be more dispersed and more agonistic toward each other than bonnet macaques. Because of the expected higher agonism among lion-tailed macaques, the dominance hierarchy among lion-tailed macaques is also expected to be more linear than that in bonnet macaques.

Methods

Study 1

Tephillah Jeyaraj studied a group of lion-tailed macaques inhabiting a rain forest fragment in a privately owned coffee/tea garden called Puthuthotam in the Anaimalai Hills, Western Ghats, India in February–March, 2003. The group comprised 72 individuals including 4 adult males (≥8 yr) and 17 adult females (≥6 yr); the rest of the group was immature (males <8 yr and females <5 yr) (Table I). The study area harbored another small group of lion-tailed macaques that always avoided the large study group, and intergroup encounters were almost absent.

We used 1–0 focal animal sampling, scan sampling, and *ad libitum* notes for adult males. During 1–0 sampling, we observed a focal individual continuously for 10 min divided into 30 intervals of 20 s each. We recorded the occurrence of social grooming, social play, threat, chase, attack, and self-groom during an interval (for behavior definitions, see Johnson 1985; Mallapur *et al*. 2005; Skinner and Lockard 1979). We recorded no behavior twice in an interval. We analyzed the occurrence of a behavior as % occurrence in all 20-s intervals. Scan sampling involved observing each male every hour and recording its distance from each of the other males in meters. Later, we converted the distances recorded into 4 categories: <1.5 m, 1.6–6 m, 6.1–9 m, and >9 m. We maintained *ad libitum* of all agonistic interactions between any 2 males and used these data to determine the strength of the dominance hierarchy on a scale of 0–1, calculated using a modification of Landau's (1951) method (Singh *et al*. 2003) in which

$$h = [12/(n^3 - n)] \sum_{a=1}^{n} [d_a - n(n-1)/2]^2$$

wherein $d_a = \sum_{a=1}^{n} P_a$

Table I Age-sex structure of the study groups

Age-sex class	Lion-tailed macaques	Bonnet macaques
Adult male	4	5
Adult female	17	6
Immature	51	11
Total	72	22

P_a is the proportion of encounters (instead of the number of individuals dominated as in Landau) won by the *a*th individual against others and n is the number of individuals. h ranges from 0, indicating a completely nonlinear system, to 1, indicating a completely linear hierarchical system.

We observed each male for 75 focal sessions amounting to a total of 9000 20-s intervals in 50 h of observation. In addition, we made 1096 scans to record interindividual distance.

Study 2

U. Prashanth studied a group of bonnet macaques inhabiting dry deciduous belt of forests in the Anaimalai Hills, Western Ghats, India in February–March, 2003. The group comprised 5 adult males (≥5 yr), 6 adult females (≥3 yr), and immature (males <5 yr and females <3 yr) (Table I). The home range of the focal group overlapped with the home ranges of ≥4 other wild groups of bonnet macaques, and intergroup encounters were frequent. We used the same observation methods as described in the preceding text to observe each of the 5 adult males for 130 focal sessions amounting to a total of 19,500 20-s intervals in 108.3 h of observation. We recorded interindividual distances among bonnet macaque males in 1445 scans.

M. Singh trained the 2 observers T. Jeyaraj and U. Prashanth thoroughly in behavioral observations, and interobserver reliability was >95%.

Data Analysis

We analyzed interindividual distances among males; sociopositive behaviors including social grooming and social play; and socionegative behaviors including agonistic encounters such as threat, chase and attack, and self-groom. We tested the significance of difference in the occurrence of behaviors between species using Mann-Whitney U tests, with a significance level of 0.05.

Results

Intermale Distances

Table II presents the percent occurrence of interindividual distance of males in different distance categories within the focal groups of lion-tailed and bonnet macaques. Bonnet macaques were significantly more likely to be observed in the distance categories of <1.5 m (U=0, p=0.001), 1.5–6 m (U=0, p=0.001) and 6.1–

Table II Mean percent scans in which another individual was within a distance category of focal individual

Distance category	Lion-tailed macaques		Bonnet macaques	
	Mean	SE	Mean	SE
<1.5 m	0.91	0.84	27.00	1.70
1.6–6.00 m	4.62	1.61	54.00	2.46
6.01–9.0 m	4.81	1.62	16.00	1.48
>9 m	89.66	3.51	3.00	0.88

9 m (Mann-Whitney $U=0$, $p=0.001$) than lion-tailed macaques. However, lion-tailed macaques were observed in the distance category of >9 m more often than bonnet macaques ($U=0$, $p=0.001$).

Social and Self-directed Behavior

Table III presents the occurrence of social behavior and self-groom in the 2 species of macaques. Overall, social behavior among males occurred in 32.4% intervals in bonnet macaques, which was much higher than in lion-tailed macaques (1.4% intervals, $U=0$, $p=0.001$). However, self-groom was higher in lion-tailed macaques than in bonnet macaques ($U=0$, $p=0.001$). Sociopositive behaviors were much higher in bonnet macaques than in lion-tailed macaques ($U=0$, $p=0.001$) whereas socionegative interactions did not differ between the two species ($U=5.0$, $p=0.286$). Male to female affiliative interactions in lion-tailed macaques did not differ between the 2 species (Table IV, $U=9.0$, $p=0.286$), but male lion-tailed macaque were more often agonistic toward females than male bonnet macaques were ($U=0$, $p=0.001$).

Dominance Hierarchy

Tables V and VI presents the data on agonistic interactions among males. Both species showed a clear dominance hierarchy among males. The strength of dominance hierarchy among lion-tailed macaque males was 0.88, indicating

Table III Occurrence of different behaviors in percent 20-s intervals in lion-tailed macaques and bonnet macaques

Behavior	Lion-tailed macaques		Bonnet macaques	
	Mean	SE	Mean	SE
Self-groom	10.13	0.42	1.09	0.21
Sociopositive	0.38	0.12	31.72	7.96
Socionegative	1.05	0.24	0.69	0.24

Sociopositive and socionegative behaviors indicate type of male-male interactions.

Table IV Occurrence of sociopositive and socionegative behaviors of males toward females in lion-tailed macaques and bonnet macaques

Behavior	Lion-tailed macaques		Bonnet macaques	
	Mean	SE	Mean	SE
Sociopositive	6.75	0.70	7.03	2.36
Socionegative	0.32	0.01	0.11	0.001

moderately high linearity and 0.76 in bonnet macaque males, indicating a less linear hierarchical system.

Discussion

Male lion-tailed macaques remained distant from each other, whereas male bonnet macaques remained in close proximity. Male bonnet macaques engaged more in social interactions than male lion-tailed macaques, whereas the lion-tailed macaques showed more self-directed behavior. Social interactions among male bonnet macaques were largely affiliative, whereas those among male lion-tailed macaques were more agonistic. Males of both species were almost equally affiliative toward adult females, although male lion-tailed macaques showed more agonistic behavior toward females. Male lion-tailed macaque had a stronger linearity in hierarchy than bonnet macaque males. The results, therefore, confirm our predictions.

Lion-tailed macaques live in a resource-limited environment of mature mountainous rain forests. They are selective feeders (Sushma and Singh 2006), and their food resources are widely dispersed (Ganesh and Davidar 1999). A group usually has a very large home range. Although they show 2 birth peaks (Singh *et al*. 2006a), lion-tailed macaques have offspring throughout the year (Krishna *et al*. 2006), and hence, at any given time, there may be 1 or a few adult females in estrus, leading to permanent competition among males. In contrast, bonnet macaques are habitat generalists (Singh *et al*. 1997) and spend much lesser time in food search as their food comprises a much wider variety of items (Sinha 2001). As a larger number of adult males in a group is expected only if it facilitates male-mate defense (Fashing

Table V Matrix of agonistic interactions among lion-tailed macaque males

Dominant	Number of times dominated			
Males	M1	M2	M3	M4
M1	X	22	6	6
M2	1	X	5	3
M3	1	0	X	2
M4	0	0	0	0

Table VI Matrix of agonistic interactions among bonnet macaque males

Dominant	Number of times dominated				
Males	M1	M2	M3	M4	M5
M1	X	7	12	29	18
M2	1	X	5	8	3
M3	5	1	X	12	6
M4	4	1	0	X	9
M5	0	0	0	0	0

2001; van Schaik *et al*. 1992) or male-resource defense (Rubenstein 1986), additional males are not required for either case of defense in lion-tailed macaques, resulting in a low number of males per group. Bonnet macaques are seasonal breeders (Sinha 2001), and many females come into estrus simultaneously. It would not be possible for a male to monopolize all estrous females, and male raids from other groups also occur (Singh *et al*. 2006b). Both male-mate defense and male-resource defense have been observed in bonnet macaques (Cooper *et al*. 2004), corresponding with the presence of a larger number of adult males in bonnet macaques.

In capuchins, adult males become more tolerant of each other if there are no adult females available (Janson 1984). This may be the case in species with less linear patterns of social interactions but may not be the case in others with a more pronounced linear system of dominance hierarchy. The dominance hierarchy of 0.88 among the wild lion-tailed macaque males was much lower than that of 0.97 in the more despotic Japanese macaques (Singh *et al*. 1992), but higher than the value of 0.76 in bonnet macaques. This agrees with previous work showing that male bonnet macaques are exceptionally tolerant of each other when compared to most other macaque species, remaining spatially closer and frequently grooming, huddling, and supporting others (Silk 1994).

As demographic factors are the most potent factors influencing social relationships (Dittus 2004), differences in adult male:adult female sex ratio should relate to differences in social interactions. In lion-tailed macaques, another male is likely to be a rival whereas in bonnet macaques, additional males are of mutual assistance, at least during the long nonbreeding season. Because bonnet macaques often indulge in intergroup encounters and both adult and subadult males participate in such encounters (Cooper *et al*. 2004), both male-mate defense and male-resource defense may further promote affiliative relationships among male bonnet macaques. High male:female sex ratio and more intertroop encounters result in an increase in male–male affiliative relationships in Japanese macaques (*Macaca fuscata*) (Horiuchi 2007), and Formosan macaque (*Macaca cyclopis*) dominant males mostly groomed subordinate males in the mating season, but this pattern changed in the nonmating season to strike a balance between competition and affiliative relationships (Lin *et al*. 2008). However, lion-tailed macaques and bonnet macaques have similar adult male:female sex ratios and breeding seasonality as our focal groups, despite

inhabiting a variety of habitat types, suggesting that the patterns of male–male relationships in these macaques are species characteristics.

Our observations provide us with a new perspective on macaque social systems. Both lion-tailed and bonnet macaques are female-bonded, as are most macaques (Thierry *et al*. 2004). Males in a bonnet macaque group are spatially close to each other at any given time, maintaining visual contact, and indulging in more social interactions. In contrast, males in a lion-tailed macaque group are spatially widely distributed, often without visual contact, and show fewer social interactions. However, whenever they meet, social interactions among lion-tailed macaque males are more agonistic whereas in bonnet macaque males, social interactions are more affiliative. Males of both species seem to regulate their spatial and social positions differently but still remain integral members of their respective groups. Information on spatial structuring, temporality of interactions, combined with knowledge of predictability of directional outcomes, may point to a "deep structure" (Kummer 1992) underlying the surface established by the frequencies and durations of interactions alone. For example, male lion-tailed macaques are considered to have a less relaxed social system than females. This species has been classified under Grade III of macaques, indicating a relatively relaxed social system (Thierry 2004, 2007). However, our observations and a linearity-based analysis of social interactions among lion-tailed macaque females on an interval scale of 0–1 (Singh *et al*. 2006c) indicate that both male and female lion-tailed macaques have a more aggressively organized social system than previously thought.

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