REVIEW ARTICLE

Affiliative Relationships and Reciprocity Among Adult Male Bonnet Macaques (*Macaca radiata*) at Arunachala Hill, India

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In captivity, male bonnet macaques (*Macaca radiata*) frequently express "friendship" toward one another, including affiliative behavior such as huddling, grooming, coalitionary support, and sitting in close proximity. The purpose of this study was to determine whether wild adult male bonnet macaques also express "friendship" by investigating whether or not (1) adult male bonnet macaques have affiliative social relationships with other males, (2) the strength of social relationships varies among dyads, (3) there is time-matched reciprocity in allogrooming among dyads, and if so, whether the level of reciprocity occurs within a bout of grooming, a day, or over 2 months (the limit of this study), and (4) a correlation exists between the strength of social relationships and dominance ranks among adult males. Focal samples totaling 150 hr on all seven adult males in one study group were conducted to record both agonistic and affiliative interactions. Agonistic interactions were used to construct a dominance hierarchy, whereas affiliative interactions (sitting in proximity to within 1 m with and without grooming) were used to quantify the existence and strength of social bonds within dyads. Results show that adult male bonnet macaques had differentiated affiliative relationships with other males in their group. There was little reciprocity of grooming within a bout of grooming or within a day, but greater reciprocity over the study period of 2 months. There was no correlation between dominance ranking distance and the strength of affiliative relationship within dyads; however, within dyads lower-ranking males groomed higher-ranking males more than vice versa. This study suggests that friendships in male bonnet macaques are characterized not by immediate tit-for-tat reciprocal altruism, but by reciprocity over a longer time span, and that affiliative social relationships may be less constrained by agonistic relationships than is the case in more despotic species of macaques. Am. J. Primatol. 73:1107–1113, 2011. © 2011 Wiley Periodicals, Inc.

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INTRODUCTION

Male mammals typically do not have affiliative or cooperative relationships or form long-lasting social relationships with other males [Silk, 1994]. Several factors may contribute to this pattern. The higher intensity of intrasexual competition among males for mates relative to females discourages affiliative relationships with other males. Similarly prohibitive is the greater mobility of males relative to females. In most mammalian species, males disperse from related conspecifics after reaching puberty, whereas females are more philopatric, remaining nearer or within their natal home ranges and nearer related conspecifics throughout life [Isbell & Van Vuren, 1996; Jack & Isbell, 2009; Pusey & Packer, 1987; Silk, 1994]. Thus, when adult males live in groups, they usually live among unrelated and less

familiar individuals. Notably, cases of strong male affiliative relationships occur in those species in which males either do not disperse or disperse with male relatives, e.g., lions (*Panthera leo*), bottlenose dolphins (*Tursiops aduncus*), chimpanzees (*Pan troglodytes*), and white-faced capuchins (*Cebus capucinus*) [Connor et al., 1992; Jack & Fedigan, 2004; Packer & Pusey, 1982; Silk, 1994; Watts, 2000].

Cercopithecine monkeys are typical of most other mammals in that females are philopatric and

males disperse [Pusey & Packer, 1987]. Such primates are considered female-bonded, because philopatric females tend to form strong, affiliative relationships with other females, and bonds among females are stronger than bonds between males or between females and males [Silk, 1994]. Bonnet macaques (*Macaca radiata*) are unusual in this regard, however. Like many other cercopithecine primates, bonnet macaques live in multi-male, multi-female groups and adult males have agonistic interactions with each other that are sufficient and decided enough to create linear dominance hierarchies [Silk, 1993; Singh et al., 2011; Sinha, 2001]. On the other hand, male bonnet macaques also frequently sit in close proximity, groom, huddle, greet, and support one another in coalitions [DeVore, 1965; Silk, 1994; Singh et al., 2011; Sinha, 2001]. Indeed, partly because of their frequent affiliative behavior, it was once suggested that males do not disperse from bonnet groups [Ali, 1981]. However, several field studies now indicate that males move directly between social groups and are much more likely to do so than females [Sinha, 2001; Sinha et al., 2005]. There is also growing evidence that, in some species, males can form affiliative social relationships with other unrelated males [Langergraber et al., 2007; Schülke et al., 2010; Silk, 2003]. Models for such relationships revolve around reciprocal altruism rather than kin selection, but the time frame for reciprocity seems to be variable. Human primates value balanced reciprocity with friends but avoid keeping careful count of benefits given and received, and are offended when friends reciprocate immediately and directly [Silk, 2003]. In contrast, when female chacma baboons (*Papio ursinus*), blue monkeys (*Cercopithecus mitis*) and gray-cheeked mangabeys (*Lophocebus albigena*) reciprocate grooming, they do so over a very short time frame, within bouts [Barrett et al., 1999; Chancellor & Isbell, 2009; Cords, 2002]. Female white-faced capuchins do not show time-matched grooming reciprocity within bouts, but do show balanced grooming over a year's time [Manson et al., 1999, 2004]. Similarly, female olive baboons (*P. anubis*) in Laikipia, Kenya, do not have evenly balanced grooming within bouts, but do have more balanced grooming across bouts summed over 15 months [Frank & Silk, 2009]. The time frame for reciprocity in male chimpanzees, at least for reciprocity involving meat sharing, seems to be longer than a bout and shorter than two years [Mitani & Watts, 2001].

The purpose of this study is to investigate social relationships among wild adult male bonnet macaques by answering whether (1) affiliative relationships exist within dyads; (2) the strength of affiliative social relationships varies among dyads; (3) there is time-matched reciprocity in grooming within dyads, and if so, what is its time frame; and (4) a correlation exists between strength of affiliative relationships and closeness of dominance ranks among adult males. This latter question arises because in studies of captive bonnet macaques, males with strong affiliative relationships also support each other in coalitions against third parties, and solicited allies are often higher ranking [Silk, 1994]. In Assamese macaques (*M. assamensis*), males with stronger affiliative relationships more frequently form coalitions, enabling them to eventually rise in rank and improve their reproductive success [Schülke et al., 2010]. We predicted that if competition for affiliative partners constrains low-ranking individuals [Seyfarth, 1977, 1980], males of more similar ranks would have stronger affiliative relationships than males of more disparate ranks.

METHODS

Study Site and Subjects

The study was conducted during July and August, 2009, in the foothills of Arunachala Hill, Tiruvannamalai, Tamil Nadu, South India (12°13′0″N, 79°4′0″E), on the grounds of a retreat center. The research complied with legal requirements of the government of India and adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Nonhuman Primates. Its protocol was approved by the Scientific Review Committee of the Intel *International Science and Engineering Fair*.

A group of bonnet macaques that lives in the forest of Arunachala Hill visits the center regularly, sometimes several times per day. The macaques are habituated to humans at the center, as a result of long coexistence with occasional provisioning by locals and visitors to the retreat. Food received from visitors is only a small fraction of the total dietary intake of the group. Seven adult male bonnet macaques belonging to this group were the subjects for the study. They were identified as individuals based on distinctive marks and coloration, the size of the tail, and presence or absence of hair in particular areas of the body. The group also included ten adult females, with associated juveniles and infants.

Focal sampling of all adult males in the group was conducted throughout the day for 600 focal samples and 150 hr of focal sampling (mean = $21.43 \pm$ SD 11.44 hr/male). Before each focal sample, we scanned the group from left to right to determine the next male to be sampled, with the first one found designated as the next focal subject. Within each 15 min focal sample, we recorded all occurrences of grooming, approaches, leaves, and sitting in proximity within 1 m that were initiated by the focal male [Altmann, 1974]. Durations of affiliative interactions, i.e., grooming, and sitting in proximity within 1 m, were also recorded, with the identity of the associated macaque noted. Analyses were conducted on the data from focal samples.

The dominance hierarchy of the adult males in the group was determined on the basis of approach–leave interactions, approach–avoid interactions, supplants, and threats, i.e., stare threats, eyelid threats, open mouth threats, and growl threats [DeVore, 1965]. Males initiating these interactions or performing threats were considered higher-ranking than the males reacting to the initiators. On three occasions, a single portion of food was placed between two males, and their outcomes were consistent with the direction of the naturally occurring agonistic interactions.

Quantitative Analyses

Our analyses included comparing indices that measure sociality and reciprocity of grooming within dyads. For these analyses, values for a given pair of macaques are the same regardless of the order in which the macaques are listed. Thus, although "O-P" indicates that O was the focal animal and "P-O" indicates that P was the focal animal, the value for the dyad "O-P" is equal to that for "P-O" because our measures were not focal animal sensitive.

Two Sociality Indices were created by analyzing the duration and the frequency of affiliative interactions within dyads to quantify and standardize the strength of affiliative social relationships. The strength of the affiliative social relationship based on duration is measured by a combination of grooming and proximity to within 1 m, and is defined here as

of the pair's grooming that was performed by each partner, a score that is 0 for a completely equitable relationship, and 1 for a relationship that is maintained completely by one of the partners, was subtracted from 1

$$I - \left| \left(\frac{Gi \to j}{Gi \leftrightarrow j} \right) - \left(\frac{Gj \to i}{Gi \leftrightarrow j} \right) \right|$$

so that the Grooming Reciprocity Index would be greatest, 1, when the relationship was most equitable, and 0 when it was least equitable [Silk et al., 2006]. These were measured for different time periods: within a bout of grooming, within a day, and over the sampling period of 2 months, to determine the time period over which males were most likely to reciprocate grooming.

To determine whether dyads with stronger affiliative relationships showed greater reciprocity in grooming, we examined the association between the Sociality Index and the Grooming Reciprocity Index over the duration of the study using the Kr test. We also used the Kr test to determine the influence of dominance rank distance on the strength of affiliative social relationships. For each dyad, we measured the difference in dominance ranks and then compared these distances with the Sociality Index.

Finally, we analyzed whether grooming was more often directed up the dominance hierarchy following Manson et al. [1999] in using the Wilcoxon

$$\frac{\text{(Duration of time spent together grooming and being in proximity)}}{\text{(Total sample time of both dyad members)}}$$

The strength of the affiliative social relationship based on frequency of occurrence of affiliative behavior is measured by proximity alone and is defined here as

$$N_{AB}/(N_A + N_B + N_{AB})$$

where N_{AB} is the number of occasions A and B are seen together, i.e., the number of times proximity was initiated; N_A is the number of occasions A is seen without B; and N_B is the number of occasions B is seen without A [Martin & Bateson, 1986].

Macaques with higher Sociality Index scores were considered to have stronger affiliative relationships. We measured whether these two indices were correlated with the Kr test via the software program MatrixTester [Hemelrijk, 2010] with 2,000 permutations. The Kr test is designed to test for correlations between matrices [Hemelrijk, 1990a,b; Kapsalis & Berman, 1996].

We used the Grooming Reciprocity Index to measure how evenly giving and receiving grooming was balanced within dyads [Chancellor & Isbell, 2009]. The absolute difference between the proportion

matched pairs, signed ranks test. We used the Vassarstats statistical computation website [http://faculty.vassar.edu/lowry/VassarStats.html] to run the test.

RESULTS

Table I presents the dominance hierarchy of the adult males. The hierarchy was perfectly linear with no reversals against the hierarchy. There were 21 potential dyads among the males in the group. All but one dyad spent some time either grooming or sitting in proximity during the study. Among the 20 dyads for which we have data, the Sociality Index as measured by the ratio of duration of time spent grooming and being in proximity to total duration of focal samples, ranged from 0.07 to 0.52, with a mean of 0.35 ± 0.13 SD. The Sociality Index as measured by the frequency of proximity events, ranged from 0.10 to 0.48 among dyads with a mean of 0.36 ± 0.13 SD. These two indices of affiliation are significantly

TABLE I. Dominance Hierarchy of the Adult Males in the Study Group

Loser → Winner ↓	Otmin	Caspian	Tumnus	Peter	Edmond	Aslan	Shasta
Otmin		9	6	2	1	8	1
Caspian	0		7	4	6	1	2
Tumnus	0	0		6	5	1	4
Peter	0	0	0		2	4	5
Edmond	0	0	0	0		1	3
Aslan	0	0	0	0	0		2
Shasta	0	0	0	0	0	0	

Values in cells are the number of agonistic interactions the winning male won against the losing male. Winners are in the first column; losers are in the rows.

TABLE II. Sociality and Reciprocity Index Scores for Each of 20 Dyads

Dyad	Sociality index score (duration of grooming and proximity)	Sociality index score (number of times in proximity)	Reciprocity index score
T-P	0.52	0.48	0.80
A-P	0.46	0.55	0.65
E-A	0.49	0.49	0.60
A-S	0.48	0.48	0.60
S-E	0.46	0.51	0.50
O-T	0.44	0.44	0.50
P-E	0.44	0.41	0.43
T-S	0.41	0.47	0.47
P-S	0.46	0.37	0.45
T-A	0.42	0.39	0.42
T-E	0.36	0.41	0.41
C-S	0.36	0.36	0.33
O-A	0.34	0.34	0.40
O-P	0.26	0.38	0.20
E-C	0.32	0.24	0.30
E-O	0.21	0.24	0.24
C-A	0.29	0.28	0.32
O-S	0.16	0.19	0.10
C-P	0.14	0.16	0.10
C-T	0.07	0.10	0.05
C-O	–	–	–

positively correlated with each other (Tau $Kr = 0.74$, $P < 0.01$); for this reason, in other analyses we only use the Sociality Index based on duration of affiliative interactions. The values for reciprocity of grooming within dyads varied over the 2-month study period from a ratio of 0.05 to 0.8, with a mean of 0.39 ± 0.19 SD (Table II). The average duration of grooming bouts was $6.6 \min \pm 5.6$ SD.

Grooming Reciprocity Over Time

The Reciprocity Index was determined for dyads within a bout of grooming, within a day, and over the sampling period of 2 months. Adult males rarely (i.e., 3 of 20 dyads) reciprocated grooming within a bout (Fig. 1A). Reciprocity of grooming within a day increased to 10 of 20 dyads (Fig. 1B). However, reciprocity of grooming over 2 months was much stronger than either shorter period of time. Nearly all dyads participated in reciprocity over a 2-month period, with levels of reciprocity varying among the dyads from 0.8 to less than 0.1 (Fig. 1C).

Sociality Index and Correlations With Grooming Reciprocity and Rank Distance

The Sociality Index and the Reciprocity Index at the 2-month time frame were significantly and positively correlated (Tau $Kr = 0.87$, $P < 0.05$). However, the Sociality Index was not significantly correlated with dominance rank distance (Tau $Kr = -0.29$, $P > 0.05$). This latter finding suggests that males do not necessarily associate with other males preferentially based on relative positions in the dominance hierarchy. On the other hand, within dyads lower-ranking males groomed higher-ranking males significantly more than higher-ranking males groomed lower-ranking
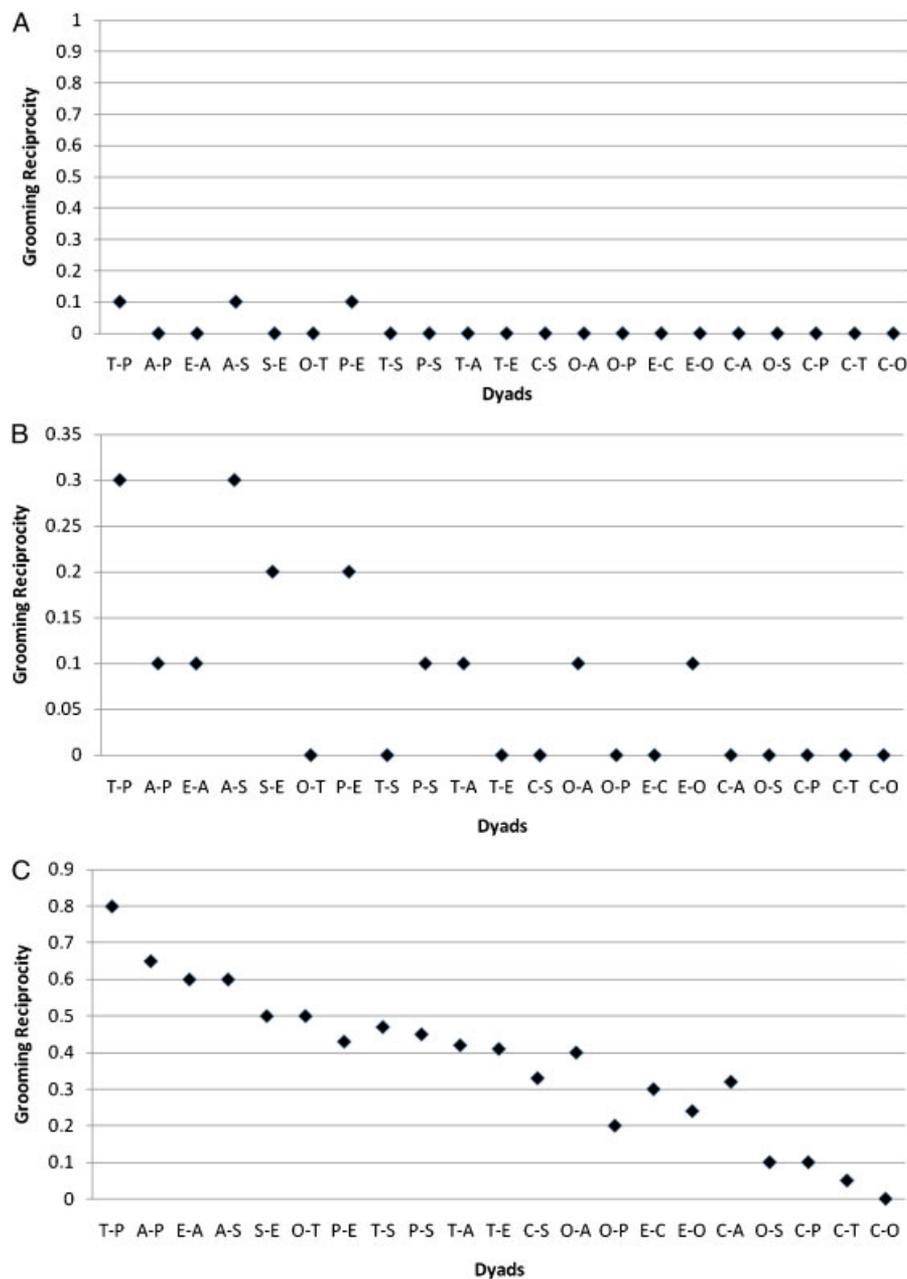
Fig. 1. Reciprocity Index between dyads for grooming. The Grooming Reciprocity Index was used to measure how evenly giving and receiving grooming was balanced within dyads (Chancellor & Isbell, 2009). The Grooming Reciprocity Index is greatest, 1, when the relationship is most equitable, and 0 when it is least equitable. Dyads are represented along the x-axis with letters corresponding to the first letter of their names. (**A**) Reciprocity within a grooming bout. (**B**) Grooming reciprocity within a day. (**C**) Grooming reciprocity over 2 months.

males (Wilcoxon test: $W = -182$, $z = 3.39$, $N = 20$ dyads, $P = 0.0007$, two-tailed). Lower-ranking males groomed higher-ranking males nearly three times more than higher-ranking males groomed lower-ranking males. On average, lower-ranking males spent 91.4 ± 15.15 SE minutes grooming higher-ranking males, whereas higher-ranking males spent 32.4 ± 6.65 SE minutes grooming lower-ranking males.

DISCUSSION

Male bonnet macaques are unusual among Old World monkeys in having frequent affiliative interactions with other males, including grooming one another [Silk, 1994]. Given that animals in affiliative relationships sometimes show reciprocity in grooming [Barrett et al., 1999; Chancellor & Isbell, 2009; Cords, 2002; Manson et al., 1999, 2004], we predicted

that wild male bonnet macaques would also show reciprocity in grooming.

We documented affiliation by the proportion of time males sitting in proximity to within 1 m with and without grooming and labeled this the Sociality Index. We found that there was variation in affiliative social relationships among dyads of males. We also found that reciprocity in grooming occurred among dyads but that, as with the Sociality Index, it varied among dyads. We also found that reciprocity in grooming increased with longer time periods. There was almost no reciprocity of grooming within a bout of grooming within dyads. Within a day, more dyads showed reciprocity of grooming. Over the sampling period of 2 months, there was extensive reciprocity within many more dyads. This suggests that adult male bonnet macaques tend not to indulge in immediate tit-for-tat reciprocity of affiliative behavior; i.e., they do not seem to pay back the grooming immediately, as predicted by biological markets theory [Henzi & Barrett, 1999]. Over a longer period of time, dyads that had stronger social relationships showed higher levels of grooming reciprocity.

When pairs of males groomed each other, the lower-ranking male of the pair spent significantly more time grooming the higher-ranking male. Grooming up the hierarchy has been found in numerous other species [Schino & Aureli, 2008]. Interestingly, the Sociality Index was not significantly correlated with dominance rank distance. In female vervets, grooming occurs more among individuals closer in rank, a pattern that has been interpreted to be a result of competition for access to high-ranking individuals that constrains low-ranking individuals disproportionately [Seyfarth, 1977, 1980]. Silk [1994] found that, in contrast, male bonnets in captivity groomed other males much higher in the dominance hierarchy than themselves, suggesting that low-ranking males were not particularly constrained in their access to males high in the hierarchy. The lack of a correlation with the Sociality Index and rank distance in this study may reflect either relaxation of competition in this particular group of bonnet macaques or a species difference in social tolerance compared with other, more despotic, species. In either case, greater reciprocation of grooming would be expected [Schino & Aureli, 2008].

Bonnet macaques are a sister taxon to Assamese macaques (*M. assamensis*) [Hayasaka et al., 1996]. Like male bonnets, male Assamese macaques form strong social bonds with other males as measured by proximity and grooming [Schülke et al., 2010; see also Cooper & Bernstein, 2008]. However, bonnet macaques are apparently more socially tolerant than Assamese macaques [Thierry, 2007], and this difference might be shown in the outcome of coalitionary support. Among captive bonnets, socially bonded males frequently support each other in coalitions

[Silk, 1994]. Among Assamese macaques, as well, the stronger the bonds, the more frequently males cooperate in coalitions against third parties [Schülke et al., 2010]. However, although coalitions seem not to influence changes in rank among male bonnets, at least in captivity [Silk, 1993], coalitions among male Assamese macaques help individuals rise in rank, and high rank is associated with greater reproductive success [Schülke et al., 2010]. We did not record data on coalitions in our study; we predict that future studies will find a weaker association between coalition formation and male rank in wild bonnet macaques than that found in Assamese macaques.

Interestingly, in Assamese macaques, social bonds seem to be independent of kinship [Schülke et al., 2010], suggesting that philopatry is not required for the development and maintenance of social bonds. The presence of strong affiliative relationships among unrelated male Assamese macaques introduces the possibility that strong affiliative relationships with nonkin can also exist in male bonnet macaques, thus reconciling their behavior with studies reporting that male bonnets, like males in other species of macaques, are the usual dispersers [Sinha et al., 2005].

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