Do males bond? A study of male-male relationships in Nicobar long-tailed macaques *Macaca fascicularis umbrosus*

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In primates, males compete for a mate, which is a non-sharable resource. This makes the conditions less conducive for males to have stable relationships. One such special kind of relationship is a bond where the interactions are reciprocated, equitable and differentiated. Bonds in macaque societies are based on the degree of within-group contest competition for mates which is dependent on the synchronization of female fertile phase and reliability of fertility signals. Species of the *Fascicularis* group, including Nicobar subspecies, show intermediate reliability in the signals with mild peaks, and studies have shown reciprocity but no differentiation. We conducted a study on a group of wild Nicobar long-tailed macaques *Macaca fascicularis umbrosus* to understand the existing patterns of male-male relationships. We examined whether there is reciprocity in affiliation among the individuals and whether the rate of affiliation is balanced. We also measured the dominance linearity and steepness in the group to understand the monopolizability of females. We used social network analysis to understand whether the relations are differentiated based on hierarchical position and whether the high-ranking individuals are the most central individuals in the distribution of grooming in the group. We found that there is reciprocity among the males although that is not equitable. There was no rank-related differentiation of affiliation among the males of the group. Instead, the identities of individuals influenced affiliation patterns. Our results correspond to the existent strong relationships but lack of social bond otherwise found in the *Fascicularis* group of macaques.

Keywords. Great Nicobar Island; *Macaca fascicularis umbrosus*; male–male relationships; mate competition

1. Introduction

Affiliation and cooperation, when favored between specific individuals, lead to social relationships (Ostner and Schülke 2014). When such interactions are reciprocal, equitable and stable over time, and differentiated among the individuals, the relationships usually are defined as social bonds (Hinde 1976, 1987; Silk 2002). The unifying theory of social relationships in a matrilineal multi-male multi-female society proposes that distribution of females will depend upon the availability of food, and for males, it depends upon the availability of females (Wrangham 1980; van Schaik 1989; Sterck *et al.* 1997). Females, therefore, are expected to have strong kin-based groups due to sharable nature of the resource. In contrast, males compete to maximize their fitness by monopolizing fertilizations and the resource in fertilizations cannot be shared. Thus, the strategy employed by males is to exclude other males from accessing females, leading to decreased sociality and increased aggression among them. Under certain conditions when having more males does not decrease the share of individual fertilizations, and when a higher number of males can be

useful during extra-group conflicts, sociality and affiliation has been observed in primate males (Silk 1994; Singh *et al.* 2010; Adiseshan *et al.* 2011; Kaumanns and Singh 2012). However, presence of affiliation does not necessarily give rise to strong social bonds among individuals when the conflict is against a common enemy and the bonds would be more circumstantial and mostly kin-biased (Ostner and Schülke 2014). In other words, interactions and affiliations need to be differentiated i.e., specific individuals should be more favored in the distribution of affiliation and not all the relations in a group are the same, which is also known as homophily (Lazarsfeld and Merton 1954). Homophily has been found in primates with high differentiation under the conditions of high between-group encounters with high affiliation towards kin (Cords 2002; Silk 2002; Port *et al.* 2009; Sosa 2016; Sosa *et al.* 2017; Ostner and Kappeler 2004).

However, it is the within-group competition for access to receptive females which influences male-male affiliation irrespective of kin relations (Nunn 1999b; Carnes *et al.* 2011; Willems *et al.* 2013, Ostner and Schülke 2014). Access to receptive females will depend on the number of fertile females which may vary based on the synchrony of the fertile phase (Nunn 1999b; Carnes *et al.* 2011). Thus, in a species where there is high synchrony in the fertile phases of females at a particular time of year, the monopolizability of females is lower by the dominant individuals leading to low contest potential and high male-male affiliation. Thus, different patterns of male-male affiliation are seen in primates with differences in female fertile phase synchrony and also the identification of reliable fertility signals by males (Nunn 1999b).

Studies on the genus *Macaca* have revealed contrasting patterns in the male-male affiliation due to the variation in the social structure (Ostner and Schülke 2014). Macaques can be classified into three groups: (a) *Silenus-sylvanus* group, (b) *Fascicularis* group, (c) *Sinica-arctoides* group (Thierry 2007; Ostner and Schülke 2014). Studies have shown that male dominance, female fertile phase, and reliable female fertility signals influence social bonding in males which differ amongst these species groups (for review, Ostner and Schülke 2014). The contest competition among males increases in a system where breeding is aseasonal and the reliability of female signals is high (Ostner and Schülke 2014). For example, in the *Silenus-sylvanus* group, the reliability of sexual swellings in females is high and the breeding is aseasonal leading to strict dominance relationships, paternity skew and low affiliation among males (Aujard *et al.* 1998; Krishna

et al. 2006; Thierry 2007; Singh *et al.* 2010; Kaumanns and Singh 2012). The exception to this, however, is the Barbary macaque where the breeding is seasonal and consistent pattern of differentiated male bonding has not been seen (Berghänel *et al.* 2010, 2011; Young *et al.* 2013). Macaques of *Sinica-arctoides* group breed seasonally, do not have reliable signals and have relaxed dominance relationships and thus males show differentiated and equitable affiliative behaviours (Nunn 1999a; Fürtbauer *et al.* 2010; Singh *et al.* 2010; Ostner and Schülke 2014). Macaques of *Fascicularis* group follow an intermediate pattern where affiliative behaviours have been seen among the males but no evidence of differentiated bonds with reciprocity and balance has been found (Hill 1994; Higham and Maestripieri 2010). This is consistent with the findings that the seasonality of breeding in a group has milder peaks than in *sinica* although still more seasonal than *Silenus-sylvanus* group with dominance relationships moderately strong (Engelhardt *et al.* 2004; O'Neill *et al.* 2004; Maestripieri and Roney 2005; Dubuc *et al.* 2009; Ostner and Schülke 2014).

Macaca fascicularis umbrosus located on three islands of Nicobar in the Andaman and Nicobar Archipelago, India, is a subspecies of long-tailed macaques (Umapathy *et al.* 2003). This subspecies of *Macaca fascicularis* has three isolated populations since 0.65 mya on three islands, viz., Great Nicobar Island, Little Nicobar and Katchal in Andaman and Nicobar Islands, India (Fooden 1995). A recent study on the reproductive behaviour in a population at Great Nicobar Island found that there is low synchronicity in the fertile phases in this population i.e., there was a low number of receptive females at a particular season (Pal 2018). Besides, female fertility signals were not reliable in the population (Pal 2018). Under these conditions, it is expected that the patterns of affiliation will follow the prediction, that, males will show affiliation among themselves although it may not be reciprocated and balanced. Besides, these affiliative relationships are not expected to be differentiated based on rank as the monopolizability of fertile females by the dominant individuals is low. To verify if these predictions are followed in the Nicobar long-tailed macaque, we studied a group of *Macaca fascicularis umbosus* at the Great Nicobar Island.

2. Materials and methods

2.1 *Study area and study group*

We selected a wild group of Nicobar long-tailed macaques, TR, at Campbell Bay, an eastern settlement

in Great Nicobar Island (93° 8′ 05.6″–93°57′13.7″ E and 6° 44′7.8″–7°13′46.6″ N). The habitat characteristics have been explained by Velankar *et al.* (2016). The group was chosen due to the ease of following and observing it for long durations as other groups spent a considerable time in restricted military areas and/or in very dense evergreen forests. The individuals were identified based on the facial patterns ("knowing by face") and body markings. The age of individuals was determined by their body size. The size of the study group changed during the study period and varied between 15 and 19, as we recorded 5 deaths/disappearances (3 adult males and 2 adult females) and 8 births (7 males and 1 female). The mean group size during the study period was $16.67 \pm 1.70_{SD}$ with 5 adult males, 4 sub-adult males and 6 females residing throughout the study period (Pal *et al.* 2018). Data were collected for all the 5 adult males residing in the study group throughout the study period. Kinship was not known among the group members.

2.2 *Data collection*

The study was conducted between October 2013 and November 2015. Behavioural data were collected for a total of 1,660 h of observation. The group was followed from 05:00 to 17:00 h and the data were collected by maintaining a distance of 2–5 m from the group. Because the group spent considerable time either in the bushes or thick vegetation with cane and Pandanus, they could not be kept in eye contact continuously for a long period of time. Thus, to record individual activities, we used 5 min focal animal sampling (Altmann 1974). The activities were divided as frequency-based (self-directed behaviours: scratching, yawning; affiliative behaviours: muzzle contact, genital touch, silent bared-teeth display, sitting in contact, inspection, embrace, active and passive touch, lip-smacking; agonistic and submissive behaviours: slap, bite, lunge, chase, charge, flee, canine flash, open-mouth threat, tail-raise), and duration-based (explore, feed, object/food manipulation, movement, infant carrying, resting/sleeping, vigilance, social and non-social play, grooming) (Aureli 1992) (Appendix 1). For each dyadic interaction from a focal sample, we recorded the identities of actor and receiver. We collected focal samples of each individual from 05:00 to 17:00 h by dividing it in blocks of 2h. When the focal individual could not be followed or it moved out of sight, an attempt was made to track it for the next 5 minutes and the duration of disappearance was recorded. If the

individual was not found, we resumed sampling for the next randomly selected individual and the incomplete sample was not considered for analysis. A total of 63.08 h of focal data were collected for the adult males (Mean $\pm$ SD = 12.62 $\pm$ 7.74 h).

We also used ad libitum sampling in addition to focal sampling to record the agonistic behaviours mentioned above which were used to construct the dominance hierarchy in the group.

2.3 *Analysis*

From the focal sampling data, we found 41 affiliative interactions among the males. We calculated the overall rate of affiliation (dividing total number of affiliative interactions by total focal hour) and mean affiliation among males (total affiliation among males divided by the number of males) considering the same residency period for the 5 males as they stayed in the group throughout the study period. Data are reported as mean and standard error unless stated otherwise.

We used 85 aggressive encounters from ad libitum and focal samples to construct a dominance hierarchy structure using normalized David's score values (David 1987, 1988; de Vries *et al.* 2006). The hierarchy was constructed based on the proportions of wins which is corrected for chance events. The analysis was performed with DomiCalc software (de Vries *et al.* 2006; Schmid and de Vries 2013). Both decided and undecided interactions were recorded and direction for each interaction was noted. Each possible outcome was coded as 1 (win), −1 (loss), (0.5) ties/undecided and (0) observational zeroes/non-interacting dyads (0) for calculation of dominance rank in DomiCalc. Dyadic scores were transformed and further analyzed by the software.

We calculated hierarchical linearity using DomiCalc software using unbiased Landau's Index (Landau 1951; de Vries 1995). We also calculated steepness of the hierarchy using linear regression with the rank position of each individual as an independent variable and David scores as a dependent variable. The analysis was performed using "compete" package version 0.1 (Curley 2016) on R 3.4.3 (R Core Team 2017).

To investigate whether the rate of affiliation given was dependent on the rate of affiliation received, we performed Kendall's TauKr matrix correlation between the matrices of affiliation given and affiliation received (Hemelrijk 1990a, b, 2003, 2005, 2008).

2.3.1 *Rank-related differentiation:* To check whether the affiliation distribution was differentiated and

skewed towards the high-ranking individuals, we performed double Dekker semi-partialing multiple regression quadratic assignment procedure (MRQAP) which corrects for the autocorrelations between the variables, viz., rank and affiliation (Dekker *et al.* 2007). To test whether the rate of affiliation was biased towards rank or identities of the individuals, we performed a linear mixed model (LMM). We ran two sets of the model: (a) full model with identities of actor and receiver, as well as of dyad considered as random effects with affiliation rate and normalized David's score values being the dependent variable and the response variable respectively; (b) A null model considering only random effects to see whether affiliation was influenced by random effects only. We then compared the full model with the null model using ANOVA to explain which model fits better to explain distribution of affiliation. To estimate the effect size, regression coefficient values were used with 95% confidence intervals. LMM was performed using the package "lme4" version 1.1–2 1 (Bates *et al.* 2015) on R 3.4.3.

2.3.2 *Network analysis:* To understand differentiated interactions among the individuals, we investigated two network measures for each individual. We calculated in-degree and out-degree of affiliation using UCINET version 6 (Borgatti *et al.* 2002) using the affiliation rates given and received by the males. We then compared these values across the males to find out whether affiliation was distributed according to the rank. To further understand homophily in the group, we determined the eigenvector centrality for each individual. An individual with high eigenvector centrality is well-connected to other well-connected individuals and thus depicts its influence on the distribution of affiliation in the group. To further examine whether a high-ranking individual is the most connected individual, we performed Pearson's correlation between the individual eigenvector centrality scores and normalized David's scores. We also constructed a sociogram based on affiliation rate and rank for an overview of how affiliation is distributed among the males in the group. The calculations were performed on UCINET version 6 and NetDraw 2.158 (Borgatti 2002) was used to construct the sociogram.

3. Results

The mean affiliation rate among the males was found to be $0.946 \pm 0.718_{SE}$/h (N = 5). The rate of affiliation given was related to the rate of affiliation received (Linear regression: $R^2 = 0.882$, $P = 0.018$, N = 41),

although, the rates were not equitable in nature (Matrix correlations: TauKr = 0.30, Pr = 0.071, Pl = 0.95, N = 5, perm =10000).

There were moderate linearity and steepness values among the males with two individuals having more wins than losses (Fy and Ku) (table 1).

3.1 *Affiliation and rank*

The affiliation was not favored towards the high-ranking individuals thus showing a lack of differentiated interactions based on rank (Double-Dekker MQRAP: R=0.002, P=0.40, N=5, perm=2000). Affiliation rate given was not dependent on rank (normalized David's score) (table 2).

Additionally, the high-ranking male did not have the highest eigenvector centrality showing that affiliation was not biased towards the high-ranking individuals (table 3) which was also depicted in the sociogram (figure 1).

Also, the out-degree and in-degree values of affiliation was not highest for the high-ranking individuals providing additional support that rank did not influence affiliation in the males. There was no correlation between the nDS values and eigenvector centrality values (Pearson's correlation coefficient = −0.259, $P = 0.643$, N = 5). However, the results are considered with caution as the sample size is very small and finding a relationship for small sample size is difficult.

Table 1. Dominance hierarchy in the males of the study group TR

| Individuals	Rank position	David score (nDS)	Linearity	Steepness
Fy	1	3	0.65	0.79
Ku	2	0.98		
Be	3	−0.31		
Hk	4	−0.94		
Ai	5	−2.73		

Table 2. A linear mixed model to test whether affiliative interaction was dependent on rank or identities of the individual (random effects)

Variables	Estimate± standard error	t	P
Intercept	0.246 ± 0.078	3.17	0.001
Rank (Normalized David's Score)	−0.004 ± 0.015	−0.317	0.751

Null Model vs. Full Model : $\chi^2 = 0.098$, p = 0.755, df = 5.

Table 3. Eigenvector centrality values for the males in the study group

Rank	ID	Eigenvector centrality
1	Fy	0.132
2	Ku	0.551
3	Be	0.463
4	Hk	0.632
5	Ai	0.255
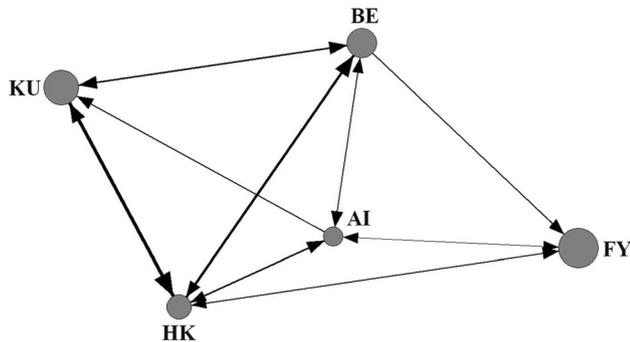
Figure 1. Affiliation network for the males in the study group TR. Size of the nodes is proportional to the rank of the individual. Arrowheads and width of the edges (connection between the nodes) are proportional to the rate of affiliation among the nodes.

4. Discussion

Our study showed that the affiliations among males in the Nicobar long-tailed macaques were reciprocated although the bonds may not be balanced. Hinde (1976) mentions that if there is a sense of recognition among the individuals, then every interaction may influence how future interactions may take place between the individuals. We found that the rate of affiliation given by the males was influenced by the rate at which they received affiliation. However, we found that this reciprocity was not balanced. We also found that the preference for individuals was not dependent on their ranks as the affiliative interactions were not directed towards the high-ranking males. This result was further substantiated when the high-ranking males did not take the central positions in the affiliation network or did not give and receive higher affiliation. Instead, centrality values were slightly skewed towards the lower-ranking males. Thus, we did not find either rank-related social bonding among the males in the group or differentiated relationships based on rank.

A bond is a special kind of relationship which should be reciprocal, balanced, stable over time, and differentiated (Silk 2002). Differentiation is perhaps the most important component as it suggests that some

relationships are more important for an individual than the others, and thus can be defined as special bonds (Silk 2002). Thus there is a gradation of bonding among the individuals based on whether the conditions mentioned by Silk (2002) are followed or not. The strongest bonds are the ones which follow all the conditions and there will be no bond if there is no differentiation. In our study, we found that there was a differentiation among the individuals regarding the identities of the individuals as some of the relations were stronger than the others. However, there was no equality in the payoffs between the interactions in these relations. In our study population, the females show low breeding synchronicity although they have mild peaks and lack reliable fertility signals, and so, under these circumstances, the contest potential is high as it is easier to monopolize the females (Pal 2018). This resembles the patterns found in the *Fascicularis* group (Engelhardt *et al*. 2004; O'Neill *et al*. 2004; Maestripieri and Roney 2005; Dubuc *et al*. 2009). Under such circumstances, it has been seen that males have frequent affiliative interactions and coalitions; however, no differentiation or equitability has been found (Hill 1994). Our results showed that the affiliation rate is high $0.946 \pm 0.718_{SE}/h$ (N = 5) and males favor certain individuals for interactions. Although, as seen in the previous study (Hill 1994), there was no balance in the affiliative interactions in this study as well. *Fascicularis* group species are expected to show male-male bonding which will be intermediate to the *Silenus-sylvanus* group and *Sinica-arctoides* group (Ostner and Schülke 2014), where the former does not form strong affiliative bonds because of high synchronicity in the fertile phases but the latter group has been seen to maintain strong affiliative bonds due to the low synchronicity (Ostner and Schülke 2014). This is in congruence with the moderate linearity (0.65) and steepness values (0.79) compared to lion-tailed macaque (*Macaca silenus*, linearity = 0.88) and bonnet macaques (*Macaca radiata*, 0.76) (Singh *et al*. 2010) which suggests that the hierarchy is not strong and opportunities for affiliation are high, as the high rate of affiliation was found in our study $(0.946 \pm 0.718_{SE}/h)$.

We acknowledge that the results found in the group are restricted to 5 males of a group and thus attempts have not been made to compare the findings with other species or subspecies. We also found that in LMM the confidence interval is large but the t value of rank was in the confidence interval showing that although the model has sufficient power. A larger sample size will decrease the confidence intervals and increase robustness of the model. However, the study is important to

understand the patterns of affiliation in an isolated population and provides the baseline for male-male affiliation and bonding patterns. In conclusion, our study delineates relationship among males in a group of Nicobar long-tailed macaques and attempts to understand the social and ecological constraints that underpin these relations. We found that the results are in partial agreement with the predictions as there was a differentiation in the interactions but they were not balanced which is consistent with the previously found results in the *Fascicularis* group of macaques (for review, Ostner and Schülke 2014). Hence, it seems that the pattern of affiliation is conserved among different classes of macaques. Further studies across and between groups as well as populations will further enlighten the underpinnings of male-male affiliations in the Nicobar long-tailed macaques and to have a detailed understanding of male bonds in *Macaca fascicularis* in specific and in macaques in general.

Acknowledgments

Appendix 1

Description of the affiliative behaviours:

Muzzle contact	Muzzle contact is defined as touching the muzzle of another individual by its own muzzle. This behaviour is irrespective of the sex of the individuals
Genital touch	This behaviour is defined as touching or holding the penis of another male by an individual. This is an exclusive behaviour between males
Silent bared-teeth display	In this behaviour, an individual retracts its lips upwards exposing its teeth to the other individual as a sign of affiliation. This behaviour is also irrespective of the sex of the individuals
Sitting in contact	This involves the individuals sitting in close proximity to each other with parts of their bodies touching each other. Although this behaviour is mostly seen among the females, males have been observed to sit in close proximity as well
Inspection	This behaviour involves touching and sniffing the genitals of another individual for mating. This behaviour usually involves a male touching and sniffing the sexual swellings of a female
Embrace	Embracing is defined as wrapping the forelimbs around another individual while facing it. This behaviour is prevalent in both the sexes
Active touch and Passive touch	Active touch involves an individual to intentionally touch another individual using any part of the body. Where, passive touch involves accidental touch by one individual to the other using any part of the body
Lip-smacking	Lip-smacking involves pursing of lips with the lower jaw moving up and down in rhythm producing a soft sound audible only at short distances (Micheletta *et al.* 2012)

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