Chapter 4

Social behaviour of a pure-species troop of bonnet macaques
Chapter 4  

Social behaviour of bonnet macaques

4.1 Introduction

The bonnet macaque, a medium-sized, Old World cercopithecin primate is typically characterised by a long tail, a whorl of long crown hairs radiating outwards and backwards to form a small cap, and with a distinct central parting in the front (McCann 1933; Pocock 1939; Sinha 2001). Although endemic to peninsular India, the species has a wide distribution and is presently thought to consist of more than 10,000 mature individuals (Molur et al. 2003), making it one of the few “Least Concern” primate species in India (IUCN Red Data Book, 2010). Recent surveys and evaluation of population trends in several parts of its range, however, indicate a decline in distribution and population of the species, calling for a reassessment of the conservation status of the macaque (Singh and Rao 2004; Kumara et al. 2010; Kumar et al. 2011; Singh et al. 2011; Chapter 2). Two subspecies of this macaque has been recognised (Ellerman and Morrison-Scott 1951; Fooden 1981): the narrowly distributed southern subspecies *Macaca radiata diluta* and the more common northern subspecies *M. radiata radiata*.

Bonnet macaques typically live in multimale multifemale societies, with sizes ranging from 5-75 individuals (Roonwal and Mohnot 1977; Kurup 1981). Smaller unimale groups with a single male, a few adult females and their dependent young have occasionally been reported to varying extent (10-52 %) in some populations (Simonds 1965; Kurup 1981; Datta Roy and Sinha 2001; Sinha et al. 2005; see Chapter 3). Group sizes generally tend to be smaller in natural habitats but become significantly larger around human habitations, especially with provisioning (Simonds 1965; Krishnan 1972; Pirta et al. 1981; Singh et al. 1984; Fooden 1986; Datta Roy and Sinha 2001; see also Chapter 3).

Bonnet macaques, like most cercopithecines, live in female-bonded societies wherein female philopatry and male dispersal are general rules (Wrangham 1980; Melnick and Pearl 1987). These dispersal patterns directly lead to a female-centric social structure although exceptions to these rules exist, either in the form of males who fail to emigrate (Ali 1981; Sinha 2001) and subsequently became alpha males (Sinha 2001) or in the form of extensive female emigration (Sinha et al. 2005), with concordant changes in social structure. Female philopatry and the development of kin relationships amongst closely related females also result in stable, culturally
inherited, matrilineal dominance ranks within the group with youngest daughters attaining ranks just below their mothers, also referred to as youngest ascendancy (Hill and Okayasu 1995). The male dominance hierarchy, in contrast, is much more an outcome of the physical attributes and fighting prowess of individuals (Darwin 1871; Clutton-Brock et al. 1977; Alexander et al. 1979), coupled possibly with an inner temperamental drive and the ability to form successful alliances, particularly in this species (Sinha 2001). Rank positions of individual males in the hierarchy are, thus, much more unstable and could even change within weeks (Silk 1993; Sinha 2001) unlike those of the females, which tend to remain stable over years.

4.1.1 Nepotistic and egalitarian species

Sterck et al. (1997) classified hierarchical relationships among individuals in primate groups on the basis of within-group competition into four classes of nepotistic and despotic organisations, varying from highly nepotistic, tolerant to egalitarian societies (see de Waal and Luttrell 1989). Later authors described these as a continuum, ranging from nepotistic to egalitarian systems, but emphasising the relevance of species-typical behavioural features, based mostly on captive studies (Matsumura 1999; Thierry 2000). Egalitarian macaque species were described to exhibit a relatively lower frequency of aggression, higher frequency of counter-attacks, higher frequency of reconciliation after agonistic interactions, and higher rates of affiliation (Aureli et al. 1993, 1997; Chaffin et al. 1995). Moreover, in egalitarian macaque species, kinship and dominance rank tend to have little influence on the distribution of allogrooming among individuals (Defler 1978; de Waal and Luttrell 1989; Thierry et al. 1990; Cooper and Bernstein 2000).

4.1.2 Effect of dominance rank and kinship on social relationships between adult females

Dominance rank, kinship, age and sex are some of the parameters that can influence the social relationships of individuals (Silk 2001), depending on which an individual may adjust her behavioural patterns and life history strategies, ultimately resulting in better survival and reproductive fitness. In typically multimale multifemale macaque societies, the reproductive fitness of adult females depend on the ability of
individuals to garner resources as well as the access of males to receptive females. Both these processes are strongly influenced by the hierarchical dominance relationships that typically exist between macaque females with priority of access to dominant individuals (see, for example, Dittus 1979, 1986; Cheney et al. 1981; Wrangham 1981; Whitten 1983).

There are various advantages offered by high dominance ranks. A dominant female can monopolise resources (Whitten 1983; Harcourt 1987), supplant a low-ranking female from feeding sites, preferred resting places, potential mating partners (Sinha 2001) and from allogrooming dyads (Sinha 1998; Silk 2001). Dominance rank may also influence the health and reproductive status of females as food and fertility are strongly correlated (Koford 1965; Masui et al. 1975; Dittus 1979, 1980; Altmann and Alberts 2003, 2005). Many primates, including macaques, rely on foods, many of human origin, that occur in monopolisable clumps, making competition over access to food sites quite profitable (van Schaik 1989; Isbell 1991; van Hooff and van Schaik 1992).

4.2 Aims and objectives of the study

Classical studies have emphasised the strong influence of dominance ranks on the nature and pattern of social relationships among adult macaques, typically females; most of these studies, however, are based on a few captive groups of species broadly classified as despotic or nepotistic and egalitarian. Wild troops of these species could, however, be expected to be more finely nuanced and vary in the nature of their social relationships depending on the prevailing ecological conditions. Dominance hierarchies could thus be expected to have variable effects on inter-individual social interactions exhibited by these troops. The aim of this chapter is to assess the flexibility shown by free-ranging bonnet macaque females in their affiliative and agonistic interactions, especially in the context of their dominance ranks. The specific questions addressed in this chapter are:

1. Do dominance ranks affect the affiliative relationships exhibited by adult female bonnet macaques?
2. Do agonistic interactions displayed by these females directly reflect their rank relationships?

3. What is the nature of the relationship between the affiliative and agonistic behaviours displayed by the macaque females in a free-ranging troop?

4.3 Methods

4.3.1 Study area

This study was conducted on a troop of bonnet macaques in the Sanjay Gandhi National Park in Mumbai (19.21° N and 72.90° E), on the western coast of India; this reserve was selected due to the presence of both bonnet and rhesus macaque troops as well as their mixed-species troops within the same area (Fig. 4). The Park lies in the northern section of Western Ghats and receives heavy rainfall (over 1000 mm) during the monsoons (June to September).

The home range of the study troop included a rocky hill (Kanheri Caves) surrounded by thick forest dominated by bamboo and moist deciduous to semi-evergreen vegetation. This hill, with Buddhist caves dating back from the 1st century BC to 9th century AD, was an important tourist site and thus had a thick inflow of tourists even though it is located within a National Park. Thus, although the troop fed on natural resources, depending on the phenology of their food species, they were also continuously provisioned by the tourists visiting the Caves. The undulating topography of the National Park supports the catchment of two lakes and water is plentiful in seasonal streams, holes, rock cuts and ditches during the wet season; in summer, the troop used artificial rock tanks and, occasionally, the lakes in the Park.

Other than natural troops of bonnet macaques, the Park also harbours rhesus macaque troops, which have descended from individuals released here during World War II (Serrao and Amlady 1979) and again in 1972-1973 (Wildlife Management Plan 2000). The other primate species present in the Park was the
Study Area

Figure 4. Study area: Sanjay Gandhi National Park
northern subspecies of Hanuman langur (*Semnopithecus dussumieri*). The predators of the bonnet macaque in the Park were leopards and raptors (particularly on juvenile individuals). Dogs maintained by villagers in the fringes of the Park were another threat to the macaque troops; the species thus invariably gave alarm calls on seeing these dogs.

### 4.3.2 The study troop

The Kanheri Caves area was home to two troops of bonnet macaques and one of rhesus macaques, and one of the former was selected for this study. This troop, with a home range of approximately 0.4 km², consisted of 30-35 individuals with eight adult females, nine mature adult males, two young adult males, 12 subadults and juveniles and five to six infants of both sexes.

The troop was initially habituated over a period of a month and all adult individuals identified with the help of their unique morphological features and various permanent injury marks on their bodies. Adult individuals were defined as those with fully developed canine teeth; additionally, the females regularly displayed an oestrous cycle and had completely developed nipples. Subadult males were sexually, but not socially, mature and had developing canines while subadult females could be distinguished as being primiparous. Offspring, typically less than a year old, which were completely dependent on their mothers and had not yet been weaned, were defined as infants, while juveniles were less dependent on their mothers, foraged independently and were usually one to four years of age. The absolute age of the individuals was not known and hence, they were assigned to six arbitrary, but discrete, age classes: Primiparous/Very Young, Young, Intermediate, Middle-aged, Old and Very Old, on the basis of various aging parameters such as the presence of wrinkled and loose skin, facial freckles (particularly in females), tooth decay (particularly of the canine teeth), wrinkling of the nipples (in females) quality of body hairs and their movement characteristics. Matrilineal kinship between females was primarily inferred from their age and respective positions in the dominance hierarchy, and additionally from their affiliative associations and agonistic support provided, as well as the occasionally striking resemblance in facial features.
4.3.3 Behaviours observed

The social behaviour included in this analysis comprises affiliative, agonistic, and neutral behaviours. Neutral behaviours have been defined as those that did not include any overt affiliative, agonistic or sexual behavioural components associated with them and the function of which remain largely unclear.

I classified all the displayed behaviours of the study troop into behavioural states and behavioural events.

Behavioural states refer to long-lasting behaviours that occupy significant time durations and whose duration can be measured in terms of the proportion of time spent in particular behavioural states relative to the total time observed. These proportions, taken together for a particular individual, constitute the time-activity budget of that individual.

Behavioural events refer to instantaneous behavioural acts that do not occupy any significant time duration and which can be measured in terms of their frequency or the number of events performed per unit time. During this study, the frequency of behavioural events have been analysed in terms of either the overall frequency of particular behaviours displayed by a particular individual over a certain period of time or the frequency of that behaviour displayed towards another individual during dyadic interactions.

The behaviours that have been considered in the present analysis include foraging, allogrooming, affiliation, total aggression, non-contact aggression, contact aggression, aggressive approach, retreat, affiliative approach, and moving away.

Allogrooming (used interchangeably with grooming) refers to the manipulation of the fur and skin of an individual by another with the fingers, mouth, or teeth in order to remove bits of dirt, dead skin, ectoparasites or dried blood from wounds. Allogrooming has been considered as both a behavioural state and event, measured in terms of the proportion of total observed time spent allogrooming any or a
particular member of the troop and the frequency of initiated allogrooming
teractions with any or a particular member of the troop per unit time.

Affiliation, measured as behavioural events, is a composite behaviour of 20
affiliative behaviours including bite gently, cheek-touch, follow, friendly approach,
grapple, grunt, hold, huddle, hug with lip-smacking, hug without lip-smacking,
nibble, nuzzle, pat, pull close, raise eyebrows, seek grooming, seek support, sit in
contact, sleep together and touch.

Total aggression is also a composite behaviour, measured as events and constituted
by agonistic interactions of two kinds. Contact aggression, involving actual physical
contact between the adversaries, includes the more severe acts of bite hard, chase,
hold down, pinch, pull roughly, push, and slap. It must be noted here that although
chase does not strictly involve physical contact, it is usually employed during
intense aggression and has, therefore, been considered in this category. Non-contact
aggression, in contrast, consists of agonistic interactions at a distance that do not
involve any physical contact; these include the relatively milder acts of aggressive
scream, bared-teeth display, eye-flash, ground-slap, head-jerk, lunge, open-mouth
threat, stare, and warning growl.

Aggressive approach refers to an approach made by an individual towards another,
which is followed by the former displaying any of the acts of non-contact and
contact aggression listed above. Retreat, on the other hand, consists of the moving
away or fleeing of an individual from another in response to an act of non-contact
and contact aggression shown by the latter. Both these behaviours have been
measured as events.

Affiliative approach consists of any approach made by an individual towards
another, which is followed by the display of allogrooming or any affiliative
behaviour listed above. Moving away refers to the moving away of an individual
from another, terminating a bout of allogrooming or any other kind of affiliative
interaction in the process. Both these behaviours have also been measured as
events.
The frequency of affiliative approaches and moving away between pairs of individuals have also been analysed in terms of Hinde’s Index (HI), which evaluates the strength of the social bond between a pair of individuals by measuring the interest displayed by an individual in maintaining spatial proximity to another (Hinde and Atkinson 1970). For this analysis, the Index has been calculated as:

\[ HI = \frac{CM_{ij}}{CM_{ij} + CM_{ji}} - \frac{MA_{ij}}{MA_{ij} + MA_{ji}} \]

where,

- \( CM_{ij} \) = frequency of affiliative approach displayed by individual i towards individual j,
- \( MA_{ij} \) = frequency of moving away displayed by individual i towards individual j,
- \( CM_{ji} \) = frequency of affiliative approach displayed by individual j towards individual i, and
- \( MA_{ji} \) = frequency of moving away displayed by individual j towards individual i

### 4.3.4 Data collection

Data collection for the troop started in October 2006 and continued until June 2007. Initial observations ad libitum allowed for the habituation of the troop, the identification and naming of all adult members of the troop and the mapping of its home range. An ethogram of the troop was also prepared during this period to identify all the displayed behavioural acts and interactions. Individuals were uniquely identified on the basis of their facial features, as well as cut and marks on the body. Bonnet macaques have a clear triangular forehead patch, the pattern of which varies between individuals and this too helped in identifying individuals.

The study troop was active from about 0730-0800 h in the morning until 1730-1800 h in the evening and the troop was observed during this period, whenever possible. Structured, random focal animal sampling without replacement (Altman 1974; Sinha 1998) was used to study the social behaviour of the eight adult females of the troop; in this method, focal animal samples were conducted for a duration of 10 min on individuals that were randomly chosen from a pool not including the individuals previously sampled in that round of observations.
The dominance hierarchies among the individuals were determined on the basis of approach-retreat (or supplant) interactions observed during *ad libitum* observations or focal animal sampling. This social interaction was a much better predictor of social ranks than were aggressive or agonistic interactions and led to the clear identification of the rank orders, which are typically linear and transitive in bonnet macaques. The dominance ranks in males and females have both been represented numerically in this analysis with higher numerical values denoting relatively higher positions within each rank hierarchy.

### 4.3.5 Sampling effort

Approximately 195 hours of focal animal sampling data were collected on both adult males and females, with a mean (± SE) of 12.81 (± 0.41) h for females and 11.54 (± 0.68) h for males.

As the emphasis of the chapter is on female social relationships, the behavioural data on adult females alone have been analysed further. In addition to individual behavioural profiles, dyadic interactions between females have also been used to assess their social relationships and strategies with respect to the prevailing dominance hierarchy.

### 4.3.6 Data analysis

The overall frequency of different behaviours displayed by a particular individual over the observation period and the frequency of behaviours displayed towards another individual during dyadic interactions were analysed using the custom-made programs FOCANS and PAIRINI, respectively (A. Sinha, *unpublished*). The statistical analyses of all social interactions employed primarily non-parametric tests including the Mann-Whitney U-test, Wilcoxon’s matched-pairs signed-rank test, Kendall’s rank correlation and Spearman’s rank correlation. All tests were two-tailed and examined for statistical significance at 0.05, as described by Sokal and Rohlf (1995).
4.4 Results

The results have been divided into five sections. The first section deals with the general patterns of affiliative and agonistic behaviour displayed by the adult females in the troop. The second section examines patterns of affiliative behaviour with respect to the dominance ranks of individual females. The effect of the dominance hierarchy on agonistic behaviour constitutes the third section while the fourth one investigates the possible relationship between affiliative and agonistic behaviours. Finally, the fifth section deals with individual-specific patterns of behaviour displayed by certain females in the troop.

4.4.1 General patterns of affiliative and agonistic behaviour

4.4.1.1 Distribution of allogrooming and affiliative behaviours

Affiliative behaviours were initiated by each bonnet macaque female towards a majority of the other females in the troop. Each female thus directed affiliation to a mean (± SE) of 6.9 (± 0.2) females out of the total seven possible affiliation partners in the troop while allogrooming was initiated towards a mean (± SE) of 6.3 (± 0.5) females.

4.4.1.2 Patterns of affiliative behaviour

The major affiliative behaviours analysed here include affiliation frequency, allogrooming frequency, allogrooming time, affiliative approach and Hinde’s Index, which represents the interest of a female in initiating affiliative behaviours and thus maintaining social relationships with the other females of the troop. Affiliation was expressed at a higher frequency than was allogrooming and affiliative approach while allogrooming time constituted approximately 0.5% of the total observation time (n = 56 dyads, Table 4.1).

The consistent nature of the affiliative relationships developed by the study females was made apparent by the strong positive correlation observed between initiated affiliation frequency, allogrooming frequency and allogrooming time, on one hand,
and between the received levels of these behaviours, on the other (Table 4.2). Individual females thus appear to express comparable levels of these different affiliative behaviours towards their favoured social partners.

A different picture was, however, observed when the reciprocity of these behaviours was examined. Initiated and received frequencies of affiliation, for example, were strongly correlated to one another (Table 4.2) indicating the reciprocal nature of this behaviour as displayed by the troop females. There was, however, no correlation at all between initiated and received allogrooming, both in terms of frequency and time; allogrooming was, thus, not reciprocated between the females in this particular troop (Table 4.2).

### 4.4.1.3 Patterns of agonistic behaviour

Agonistic behaviour was classified into total aggression – a sum of contact and non-contact aggression, aggressive approach and retreat. Agonistic interactions were relatively rare among the study females, with only 10 out of the possible 56 dyads displaying any kind of agonistic behaviour. More ritualistic aggressive approach and retreats were, however, observed among 23 dyads. Females also initiated agonistic interactions at low frequencies though, surprisingly, contact aggression was displayed at higher levels than was non-contact aggression; aggressive approach and retreat by females were, however, shown at comparable levels (Table 4.1).

There were no consistent patterns of initiated or received agonistic behaviour as the frequencies of non-contact aggression, contact aggression, aggressive approach and retreat, both initiated and received respectively, were not correlated to one another (data not shown).
<table>
<thead>
<tr>
<th>Behaviours</th>
<th>Allogrooming frequency</th>
<th>Allogrooming time&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Affiliation frequency</th>
<th>Affiliative approach frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.221 ± 0.025</td>
<td>0.005 ± 0.001</td>
<td>0.752 ± 0.073</td>
<td>0.304 ± 0.036</td>
</tr>
</tbody>
</table>

**Affiliative approach**

<sup>a</sup>Allogrooming time has been expressed as mean (± SE) proportion of total observed time spent in the behaviour.

<table>
<thead>
<tr>
<th>Behaviours</th>
<th>Total aggression</th>
<th>Non-contact aggression</th>
<th>Contact aggression</th>
<th>Aggressive approach</th>
<th>Retreat</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.014 ± 0.005</td>
<td>0.005 ± 0.002</td>
<td>0.009 ± 0.004</td>
<td>0.045 ± 0.009</td>
<td>0.046 ± 0.010</td>
</tr>
</tbody>
</table>

*Standard error

All behaviours, except allogrooming time, have been expressed as mean (± SE) frequency of the initiated behaviour per h.

<sup>a</sup>Allogrooming time has been expressed as mean (± SE) proportion of total observed time spent in the behaviour.
The strictly linear dominance hierarchy leading to the virtual absence of any agonistic behaviour directed by a subordinate female towards a dominant counterpart ensured that there were no reciprocity in aggressive interactions, as indicated by an absence of any correlation between any of the aggressive behaviours initiated and received. The only exception was the significant positive correlation between the frequency of aggressive approach initiated by a female and the frequency of retreat received by her from her subordinate partner (Kendall’s rank correlation, \( \tau = 371, n = 28 \) dominant to subordinate dyads, \( p = 0.03 \)).

### 4.4.2 Relationship between affiliative behaviours and dominance rank

The dominance rank of the study females strongly influenced the number of other adult females groomed by them with dominant individuals grooming a relatively greater number of females (Kendall’s rank correlation, \( \tau = 0.617, n = 8, p = 0.04 \)). Dominance rank, however, was not correlated to any affiliative behaviour initiated by a female or received by her; there was also no obvious pattern to the way affiliative behaviours were distributed along the dominance hierarchy.

Although the frequency of affiliation and allogrooming initiated by the study females do not show any obvious trends (Fig. 4.1a and c), the received frequency of these behaviours exhibited a declining trend with increasing dominance rank (Fig. 4.1b and d); relatively lower-ranked females in the study troop, thus, tended to receive higher frequencies of affiliation and allogrooming that decreased with increasing dominance rank of the receiver. Allogrooming time initiated and received, however, did not show any such trend with dominance rank (Fig. 4.1e and f).

The frequency of affiliative approach initiated by females again did not yield any relationship with dominance rank (Fig. 4.1g). The study females, however, received more affiliative approaches as their dominance rank decreased, as was indicated by the negative relationship between rank and the received levels of this behaviour (\( \tau = -0.258, p = 0.01 \); Fig. 4.1h). Hinde’s Index of affiliative interest increased with increasing rank of the actor (\( \tau = 0.208, p = 0.031 \); Fig. 4.i) but, interestingly, also increased with decreasing rank of the target females (\( \tau = -0.208, p = 0.03 \); Fig. 4.1j).
### Table 4.2 Correlations between the different affiliative behaviours initiated and received by the study adult females

<table>
<thead>
<tr>
<th>Behaviours Given / Received</th>
<th>AF Initiated</th>
<th>AF Received</th>
<th>AG Initiated</th>
<th>AG Received</th>
<th>AGT Initiated</th>
<th>AGT Received</th>
<th>CM Initiated</th>
<th>CM Received</th>
<th>HI Initiated</th>
<th>HI Received</th>
</tr>
</thead>
<tbody>
<tr>
<td>AF Initiated</td>
<td>0 (\tau = 0.186, p = 0.047) (\tau = 0.675, p = 0.000)</td>
<td>(\tau = 0.173, p = 0.080)</td>
<td>(\tau = 0.497, p = 0.000^*)</td>
<td>(\tau = 0.147, p = 0.116)</td>
<td>(\tau = 0.744, p = 0.000^*)</td>
<td>(\tau = 0.158, p = 0.099)</td>
<td>(\tau = 0.295, p = 0.002)</td>
<td>(\tau = -0.295, p = 0.002)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>AF Received</td>
<td>(\tau = 0.173, p = 0.080)</td>
<td>(\tau = 0.675, p = 0.000^*) (\tau = 0.148, p = 0.113)</td>
<td>(\tau = 0.496, p = 0.000)</td>
<td>(\tau = 0.158, p = 0.099)</td>
<td>(\tau = 0.744, p = 0.000)</td>
<td>(\tau = -0.295, p = 0.002)</td>
<td>(\tau = 0.295, p = 0.002)</td>
<td></td>
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</tr>
<tr>
<td>AG Initiated</td>
<td>(\tau = 0.166, p = 0.112)</td>
<td>(\tau = 0.540, p = 0.000^*) (\tau = 0.106, p = 0.283)</td>
<td>(\tau = 0.501, p = 0.000)</td>
<td>(\tau = 0.127, p = 0.209)</td>
<td>(\tau = 0.153, p = 0.118)</td>
<td>(\tau = -0.153, p = 0.118)</td>
<td>(\tau = 0.153, p = 0.118)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AG Received</td>
<td>(\tau = 0.107, p = 0.276)</td>
<td>(\tau = 0.539, p = 0.000) (\tau = 0.127, p = 0.209)</td>
<td>(\tau = 0.501, p = 0.000)</td>
<td>(\tau = -0.153, p = 0.118)</td>
<td>(\tau = 0.153, p = 0.118)</td>
<td>(\tau = 0.153, p = 0.118)</td>
<td>(\tau = 0.153, p = 0.118)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AGT Initiated</td>
<td>(\tau = -0.017, p = 0.854)</td>
<td>(\tau = 0.333, p = 0.001)</td>
<td>(\tau = 0.117, p = 0.227)</td>
<td>(\tau = 0.333, p = 0.001)</td>
<td>(\tau = 0.119, p = 0.200)</td>
<td>(\tau = 0.370, p = 0.000)</td>
<td>(\tau = -0.370, p = 0.000)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AGT Received</td>
<td>(\tau = 0.117, p = 0.227)</td>
<td>(\tau = 0.333, p = 0.001) (\tau = 0.122, p = 0.212)</td>
<td>(\tau = 0.370, p = 0.000)</td>
<td>(\tau = -0.370, p = 0.000)</td>
<td>(\tau = 0.332, p = 0.001)</td>
<td>(\tau = 0.370, p = 0.000)</td>
<td>(\tau = 0.332, p = 0.001)</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>CM Initiated</td>
<td>(\tau = 0.122, p = 0.212)</td>
<td>(\tau = 0.370, p = 0.000) (\tau = 0.370, p = 0.000)</td>
<td>(\tau = 0.370, p = 0.000)</td>
<td>(\tau = 0.370, p = 0.000)</td>
<td>(\tau = 0.332, p = 0.001)</td>
<td>(\tau = 0.370, p = 0.000)</td>
<td>(\tau = 0.332, p = 0.001)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CM Received</td>
<td>(\tau = 0.370, p = 0.000)</td>
<td>(\tau = 0.370, p = 0.000) (\tau = 0.370, p = 0.000)</td>
<td>(\tau = 0.370, p = 0.000)</td>
<td>(\tau = 0.370, p = 0.000)</td>
<td>(\tau = 0.332, p = 0.001)</td>
<td>(\tau = 0.370, p = 0.000)</td>
<td>(\tau = 0.332, p = 0.001)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HI Initiated</td>
<td>(\tau = -0.144, p = 0.221)</td>
<td>(\tau = 0.370, p = 0.000) (\tau = 0.370, p = 0.000)</td>
<td>(\tau = 0.370, p = 0.000)</td>
<td>(\tau = 0.370, p = 0.000)</td>
<td>(\tau = 0.332, p = 0.001)</td>
<td>(\tau = 0.370, p = 0.000)</td>
<td>(\tau = 0.332, p = 0.001)</td>
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</table>

Kendall's rank correlation, \(\tau\): Kendall's tau, \(n = 56\), significance at \(p \leq 0.05\) (bold letters)

AF: Affiliation frequency; AGT: Allogrooming time; AG: Allogrooming frequency; CM: Affiliative approach; HI: Hinde's Index
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**Fig. 4.1a** Affiliation frequency initiated by females of increasing dominance rank

**Fig. 4.1b** Affiliation frequency received by females of increasing dominance rank

**Fig. 4.1c** Allogrooming frequency initiated by females of increasing dominance rank

**Fig. 4.1d** Allogrooming frequency received by females of increasing dominance rank
Fig. 4.1e  Proportion of allogrooming time initiated by females of increasing dominance rank

Fig. 4.1f  Allogrooming time received by females of increasing dominance rank

Fig. 4.1g  Affiliative approach initiated by females of increasing dominance rank

Fig. 4.1h  Affiliative approach received by females of increasing dominance rank
Fig. 4.1i Hinde's Index of affiliative interest initiated by females of increasing dominance rank

Fig. 4.1j Hinde's Index of affiliative interest received by females of increasing dominance rank

(Boxplot: Each rectangle shows the interquartile range—from the first quartile to the third quartile while the central line represent the median. The whiskers represent the lowest and highest frequency. If the values are more than 1.5 times the interquartile range, the whiskers extend to the smallest value in the 1.5 interquartile range. The points represent outliers.)
4.4.2.1 Affiliative behaviour of dominant and subordinate females

The distribution of affiliative behaviours shown by adult females towards their dominant and subordinate counterparts were next examined separately. The levels of affiliative behaviour initiated by dominant females towards their subordinates did not correlate with the rank of either the actor or the target. Dominant females of increasing rank received relatively less affiliation from subordinate females (Kendall’s rank correlation, $\tau = -0.292, n = 28$ dyads, $p = 0.04$). Affiliation frequency was the only behaviour reciprocated by dominant females towards their subordinate coordinates ($\tau = 0.302, p = 0.02$).

4.4.2.2 Relationship between rank difference and affiliative behaviours

Affiliative behaviours like affiliation and allogrooming tend to be distributed more among closely ranked females in primates. The distribution of these behaviours in relation to differences in dominance rank was thus assessed in the study troop. It should be noted that positive values along the axis of rank difference indicate behaviour directed towards subordinate females while negative values represent behaviours targeting dominant partners of increasing rank difference.

Taken along its entire range, no obvious relationship could be detected between rank difference and frequency of affiliation (Fig. 4.2a) or allogrooming (Fig. 4.2b) given. There were, however, strong positive correlations between rank difference and frequency of affiliative approach ($\tau = 0.272, n = 56$ dyads, $p = 0.006$; Fig. 4.2c) as well as Hinde’s Index of affiliative interest ($\tau = 0.311, p = 0.001$; Fig. 4.2d). Females, therefore, initiated increasing levels of affiliative approach and expressed greater affiliative interest towards subordinates of increasing rank difference while both these interactions decreased significantly towards dominant partners of increasing rank difference.

When increasing rank difference towards dominant and subordinate individuals were considered separately, there appeared to be no discrimination in the initiated frequency of affiliation, frequency of allogrooming or allogrooming time towards subordinates of varying rank difference (Fig. 4.2a and b; data not shown for allogrooming time). Females, however, initiated significantly less affiliative
Fig. 4.2a  Affiliation frequency initiated towards dominant (negative abscissa values) and subordinate (positive abscissa values) females of increasing rank difference

Fig. 4.2b  Allogrooming frequency initiated towards dominant (negative abscissa values) and subordinate (positive abscissa values) females of increasing rank difference

interactions towards dominant individuals of increasing rank difference; these included affiliation frequency \( (\tau = 0.472, n = 28 \text{ dyads}, p = 0.001) \), allogrooming frequency \( (\tau = 0.490, p = 0.001) \), allogrooming time \( (\tau = 0.284, p = 0.05) \) and affiliative approach \( (\tau = 0.330, p = 0.03) \). Subordinate females, thus, preferentially directed more affiliative behaviour towards dominants relatively closely ranked to them.

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Fig. 4.2c  Affiliative approach initiated towards dominant (negative abscissa values) and subordinate (positive abscissa values) females of increasing rank difference.

Fig. 4.2d  Hinde’s Index of affiliative interest exhibited towards dominant (negative abscissa values) and subordinate (positive abscissa values) females of increasing rank difference.
4.4.2.3 Dyadic affiliative interactions between dominant and subordinate females

When all pairwise dyadic interactions amongst the females were analysed, there were no differences observed in affiliation frequency, allogrooming frequency or allogrooming time that the dominant and subordinate member of each dyad directed towards one another (Table 4.3). The only difference that could be detected was in the Hinde's Index of affiliative interest, wherein dominant females showing more significantly more interest in their subordinate counterparts than was reciprocated (Table 4.3).

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Affiliation frequency</th>
<th>Allogrooming frequency</th>
<th>Allogrooming time</th>
<th>Hinde's Index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wilcoxon's Z</td>
<td>-1.441</td>
<td>-0.029</td>
<td>-1.070</td>
<td>-2.476</td>
</tr>
<tr>
<td>Statistical significance</td>
<td>0.15</td>
<td>0.98</td>
<td>0.29</td>
<td>0.01</td>
</tr>
</tbody>
</table>

aWilcoxon's matched-pairs signed-ranks test, two-tailed
Statistically significant difference at p = 0.05 (bold letters)

4.4.3 Relationship between agonistic behaviours and dominance rank

The frequencies of agonistic behaviours, including total aggression, non-contact aggression, contact aggression, aggressive approach or retreat, initiated (data now shown) and received by the study females did not show any significant patterns and were not related to rank of the actor or that of the target (data not shown). Total aggression exhibited a non-significant trend of increasing aggression received with decreasing dominance rank of the target individual but its constituent behaviours did not show any such pattern (data not shown).

4.4.3.1 Agonistic behaviour of dominant and subordinate females

When the distribution of agonistic behaviours shown by adult females towards their dominant or subordinate counterparts were analysed separately, the only
significant pattern observed was that of retreats received by females, which were
negatively correlated to the rank of the dominant female from which the actors
retreated ($\tau = -0.344$, $n = 28$ dyads, $p = 0.05$). Relatively lower-ranked dominants
were thus retreated more from than were those of higher ranks, possibly because
very high-ranked individuals were typically avoided from a distance; competition
was, in general, more intense between closely-ranked females.

4.4.3.2 Relationship between rank difference and agonistic behaviours

Agonistic behaviours were exclusively directed by females towards subordinate
individuals in the study troop. It was also significant that individuals directed their
total aggression only towards subordinates one or two dominance ranks below
them; likewise, virtually all aggression was also received only from females one or
two ranks above the target individuals (Fig. 4.3a). Only rarely was aggression
targeted towards subordinates of much lower rank; aggressive approach, however
was directed to all the lower-ranked females (Fig. 4.3d).

Amongst the different agonistic behaviours, aggressive approach directed towards
subordinates tended to decrease with increasing rank difference (Fig. 4.3d); contact
and non-contact aggression, however, did not show any such clear trend (Fig. 4.3b
and c).

4.4.3.3 Dyadic agonistic interactions between dominant and subordinate
females

During dyadic interactions, all agonistic behaviours were principally directed by the
dominant individual towards her subordinate partner and hence, these differences
were all statistically significant (Table 4.8). Note that retreat was exclusively shown
by subordinate females from their dominant counterparts.
Table 4.4  Comparison of agonistic behaviours displayed by dominant and subordinate individuals during dyadic interactions

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Total aggression</th>
<th>Contact aggression</th>
<th>Non-contact aggression</th>
<th>Aggressive approach</th>
<th>Retreat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wilcoxon’s Z&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-2.803</td>
<td>-2.666</td>
<td>-2.023</td>
<td>-3.783</td>
<td>-3.827</td>
</tr>
<tr>
<td>Statistical significance</td>
<td><strong>0.005</strong></td>
<td><strong>0.008</strong></td>
<td><strong>0.04</strong></td>
<td><strong>0.000</strong></td>
<td><strong>0.000</strong></td>
</tr>
</tbody>
</table>

<sup>a</sup>Wilcoxon’s matched-pairs signed-ranks test, two-tailed
Statistically significant difference at p = 0.05 (bold letters)

![Graph](image1)

**Fig. 4.3a**  Total aggression initiated towards dominant (negative abscissa values) and subordinate (positive abscissa values) females of increasing rank difference

![Graph](image2)

**Fig. 4.3b**  Contact aggression initiated towards dominant (negative abscissa values) and subordinate (positive abscissa values) females of increasing rank difference
4.4.4 Relationship between affiliative and agonistic behaviours

It is possible that some affiliative and agonistic behaviours may correlate to one another, usually due to certain troop characteristics including inter-individual proximity, kinship and reconciliation. The presence of such relationships was thus
tested for amongst the females in the study troop. The only significant result that could be obtained was a negative correlation between the frequency of initiated non-contact aggression and frequency of initiated affiliation (Kendall’s rank correlation, $\tau = -0.800$, $n = 56$, $p = 0.05$) and a positive one between received non-contact aggression and received affiliation ($\tau = 0.800$, $p = 0.05$). Individual females thus initiated and received more non-contact aggression towards and from individuals with whom they had weak affiliative interactions, including individuals towards whom they directed relatively low frequencies of affiliation or those from whom they received less affiliation.

4.4.5 Behavioural correlations across dominant and subordinate females

The occurrence of similar correlations was independently tested for using behaviours directed only towards dominant or towards subordinate individuals. The frequency of affiliation initiated by individuals towards dominant females was correlated to their retreat from them ($\tau = 0.368$, $n = 28$ dyads, $p = 0.02$) as was also their affiliative approach towards these dominant individuals ($\tau = 0.358$, $p = 0.03$). Subordinate females, thus, retreated more from individuals towards whom they showed increasing frequencies of affiliation and affiliative approach.

4.4.6 Idiosyncratic behaviours

Most of the analyses of female social relationships have so far assessed general patterns but there were individual-level differences that appeared to be independent of group-level parameters like dominance rank.

A striking example of this in the study troop was the relatively high levels of affiliative behaviours, including affiliation frequency, allogrooming frequency, allogrooming time and affiliative approach, exhibited by the second- and third-highest ranked females CF and FN (dominance ranks 7 and 6, respectively; Fig. 4.1a, c, e and g). Hinde’s Index of initiated affiliative interest was also relatively high for these two females (Fig. 4.1i) but their values for the Index of received affiliative interest was the lowest amongst all the troop females (Fig. 4.1j). These two females
thus displayed high levels of affiliative interest in the other troop females but, on the contrary, received very less affiliative interest from the others.

The more dominant of the two females, CF, was a young adult while FN was middle-aged; age-related behavioural profiles could not, thus, explain these patterns. Given their physical resemblance, relative age, adjacent positions in the dominance hierarchy and characteristic behavioural profiles, FN was possibly an older maternal aunt of CF. This close kinship between the two females and perhaps their personality (A. Sinha, pers. comm.) could possibly explain the unusual affiliative behavioural patterns exhibited by them but more investigations are clearly required.

4.5 Discussion

4.5.1 Behavioural patterns among adult females

The adult females in the study troop initiated affiliation and allogrooming towards virtually all the other females in the troop. Such a large allogrooming clique or network is typical of small- to medium-sized troops of cercopithecine primates, including bonnet macaques, in which the maintenance of affiliative associations and allogrooming diversity is relatively easier than in larger troops (Henzi and Barrett 1999; Silk 1999). In larger troops, the distribution of affiliative behaviours like allogrooming may often become restricted by rank, age, kinship and other parameters to a small subset of females (Henzi and Barrett 1999; Silk 1999). In such troops, dominance rank could be correlated to the total number of grooming partners indicating a relatively larger network for dominant than for subordinate females.

While allogrooming has a physical function of cleansing the fur and removing ectoparasites (Tanaka and Takefushi 1993; Zamma 2002), its primary function appears to be the establishment and maintenance of social relationships and alliances (Sade 1965; Oki and Maeda 1973; Seyfarth 1977; Dunbar and Sharman 1984; Dunbar 1991, 1996). Affiliation and allogrooming thus play extremely important roles in female social relationships, often working as stress relievers in
highly competitive primate societies (Gust et al. 1993), where they apparently relieve stress by having a relaxing effect both on the groomer (Shutt 2007) and on the groomee (Boccia et al. 1989; Keverne et al. 1989; Aureli et al. 1999). Given its importance in releasing stress and facilitating the development and maintenance of social relationships, allogrooming can serve as a long-term tradable commodity in biological markets (Barrett et al. 1999; Leinfelder et al. 2001).

4.5.2 Dominance rank and affiliative behaviour

In this study, subordinate females tended to receive relatively higher levels of affiliation, allogrooming and affiliative approach; these behaviours were thus preferentially directed down the dominance hierarchy (see also Sinha 1996). Higher-ranked females, in contrast, received very little affiliation and allogrooming. An examination of the effect of rank difference also revealed that while dominant females did not generally discriminate between their subordinates with varying rank difference in terms of affiliation directed towards them, subordinate females significantly reduced the frequency of affiliative behaviour towards their dominant counterparts with increasing rank difference. The one exception to this was in the Hinde’s Index of affiliative interest, which showed that dominant females were markedly interested in maintaining affiliative relationships with subordinate females that were increasingly subordinate to them.

Associating with a higher-ranked female is thought to be beneficial to lower-ranked females, as the former may provide various benefits in terms of access to food and other resources or agonistic support in return for the affiliation and allogrooming that she receives in the biological market (Barrett et al. 1999; Henzi and Barrett 1999; Leinfelder et al. 2001; Schino et al. 2007, 2008). Therefore, in most primate societies, higher-ranking females not only receive more frequent allogrooming than do lower-ranking females (Sade 1972; Seyfarth 1977) but allogrooming also tends to be preferentially directed up the hierarchy (in despotic species: Sade 1972; Oki and Maeda 1973; Fairbanks 1980; Silk 1982; Sambrook et al. 1995; Matheson and Bernstein 2000; in captive egalitarian species: Silk 2001).
The patterns observed in this study are similar to those seen in other egalitarian species, wherein affiliation and allogrooming show a relaxed relationship with dominance rank, with the distribution of these behaviours either not being influenced by dominance rank or being markedly directed down the dominance hierarchy (Defler 1978; de Waal and Luttrell 1989; Thierry et al. 1990; Sinha 1996; Cooper and Bernstein 2000).

Allogrooming is a costly exercise and thus, the high amount of grooming directed by dominant females towards lower-ranked individuals in the absence of any agonistic support (Seyfarth 1977), as is prevalent in bonnet macaques, or any exchange of other affiliative behaviour in the biological market is perplexing and striking. In this study, lower-ranked females reciprocated affiliation frequency while allogrooming time was exchanged for affiliation received; affiliation thus appeared to be a commodity for bartering in biological market, not only for itself but also for allogrooming time (see Barrett et al. 1999; Henzi and Barrett 1999). This could be made possible as increasing allogrooming time ensures that two individuals spend significant time together, thus facilitating the distribution of short-duration affiliative behaviours. Allogrooming time, however, was not reciprocated for either itself or for allogrooming frequency.

4.5.3 Dominance rank and agonistic behaviour

In many species of primates, agonistic interactions may occur frequently but usually in the form of ritualised threat (Southwick et al. 1967); overt acts of aggression, like contact aggression, are low in frequency. Dominant individuals, by virtue of their rank, can initiate higher levels of aggression, which may increase their probability of survival (Pulliam and Caraco 1984). Aggression, however, has costs associated with it and the benefits of dominance could decline with frequent aggressive interactions (Jarvi and Bakken 1984). Due to these trade-offs, but given the benefits of dominance, a higher-ranking individual may show variable levels of aggression and the relationship between dominance rank and aggression could take on complex forms; not surprisingly, therefore, this has remained a widely debated issue (Francis 1988). The female bonnet macaques that I studied did not reveal any significant relationship between agonistic interactions and dominance rank. In general, lower-
ranked females received more aggression while dominant females initiated more agonistic acts.

4.5.4 **Relationship between affiliation and aggression**

Relationships between affiliative and aggressive behavioural interactions may form due to proximity factors or reconciliation after agonistic interactions (McKenna 1978), also termed as ‘redirected affection’ (de Waal and Roosmalen 1979; de Waal and Yoshihara 1983; de Waal 1989). The females in the study troop did not show any significant positive association between affiliation and aggressive behaviours; individual females, however, initiated and received more non-contact aggression towards and from individuals with whom they had weak affiliative interactions, respectively. Subordinate individuals that exhibited high levels of affiliation and affiliative approach towards higher-ranked females also showed more retreats, possibly due to apprehension of impending aggression (see Maslow 1937). Thus, even in a so-called egalitarian society as that of bonnet macaques (Thierry et al. 2000), the dominance hierarchy can still play an important role in female affiliative relationships though it contributes more directly to agonistic behavioural interactions.

4.5.5 **Individual behavioural profiles**

An important observation in the study troop was the strong individual differences in affiliative behaviours displayed by two dominant individuals, CF and FN. The affiliative interactions initiated by them did not follow the general pattern expressed by the other females in the troop. Their apparently idiosyncratic behavioural profiles could neither be explained by dominance ranks as other dominant females did not show such behavioural deviations nor by age as these two females belonged to different age categories. What is, however, important to note is that individual-level differences in behavioural profiles do exist in bonnet macaques and these patterns may require explanations beyond the usually accepted troop-level parameters such as dominance ranks, age or kinship. One possible explanatory mechanism is that of temperament and personality, which could vary significantly across individuals. Time is perhaps ripe for the exploration of the extent to which
such individual-specific properties could explain behavioural strategies and complex decision-making processes in primates, hitherto referred to as idiosyncratic behaviours.

In the next chapter, I examine the nature of social relationships and the influence of the dominance hierarchy on such relationships in female rhesus macaques; the understanding of social relationships and behavioural interactions in these two macaque species would serve as baselines for a later comparative study of the behavioural patterns exhibited by mixed-species troops of these two species.