

REPORT  
REPORT  
REPORT  
REPORT



# Behavioural Strategies of Wild Bonnet Macaques during Natural Foraging and Provisioning

SUNITA RAM  
ANINDYA SINHA



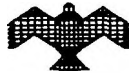
**NATIONAL INSTITUTE OF ADVANCED STUDIES**  
Indian Institute of Science Campus  
Bangalore 560 012 India

**Behavioural Strategies of  
Wild Bonnet Macaques  
during Natural Foraging and  
Provisioning**

**Sunita Ram\* & Anindya Sinha**

**\*Salim Ali School of Ecology and  
Environmental Sciences,  
Pondicherry University, Pondicherry**

**NIAS REPORT R1 - 99**



**National Institute of Advanced Studies**

Indian Institute of Science Campus

Bangalore 560 012 India

© National Institute of Advanced Studies  
1999

**Published by**  
National Institute of Advanced Studies  
Indian Institute of Science Campus  
Bangalore 560 012

Price : Rs. 50/-

**Copies of this report can be ordered from:**

The Controller  
National Institute of Advanced Studies  
Indian Institute of Science Campus  
Bangalore 560 012  
Phone : 080-3344351  
Email : [mgp@hamsadvani.serc.iisc.ernet.in](mailto:mgp@hamsadvani.serc.iisc.ernet.in)

**Typeset & Printed by**  
Verba Network Services  
139, Cozy Apts., 8th Main, 12th Cross  
Malleswaram, Bangalore 560 003  
Tel.: 334 6692



## Abstract

---

**A**rtificial provisioning of free-living primate groups usually leads to a significant increase in competition for these newly available resources. Are individuals, however, capable of adopting suitable behavioural strategies to alleviate such tension? We studied the changing patterns of social interactions between adult females of a wild group of bonnet macaques (*Macaca radiata radiata*) in the Mudumalai Wildlife Sanctuary, Tamil Nadu, under two conditions of foraging. The group spent approximately 66 % of the observation time foraging on their natural diet; during the remaining period they gathered provisioned food from tourists visiting the sanctuary. Behavioural observations primarily consisted of about 139 hours of focal animal sampling on the 9 adult females in the group. Statistical analyses employed non-parametric tests including Kendall's rank correlation, Mann-Whitney *U*-test and Wilcoxon's signed-ranks test. Provisioning was marked by a sharp 2-fold increase in Aggression, particularly Non-contact Aggression, and in Feeding-supplants (2.5-fold) directed down the dominance

hierarchy. Dominant females directed Contact Aggression specifically towards higher-ranked subordinates. Subordinate females too increased Non-contact Aggression towards dominant individuals but Retreated more from them than they did under conditions of natural foraging. Frequency of Allogrooming and other affiliative behaviour, in contrast, decreased significantly by 50 - 65 % during provisioning when most of the time was spent in active feeding or scavenging. Subordinate females, nevertheless, initiated relatively more Allogrooming towards dominant individuals during this period; grooming was much more reciprocal under conditions of natural foraging. Finally, dominant females showed less Aggressive Approaches towards those females who had groomed them more during these provisioning episodes. Social tensions thus increase significantly among bonnet macaques when they interact with tourists; such stress, however, appears to be reduced, though only partially, through social strategies adopted by individuals under these conditions. These findings may have implications for the management of endangered primates in our country.

### **Key words**

---

Social behaviour, foraging, provisioning, bonnet macaque, *Macaca radiata radiata*, Mudumalai Wildlife Sanctuary

## **Introduction**

---

Primate societies are generally structured organisations with fairly clear social rules that determine patterns of interactions between different classes of individuals comprising these societies. Kinship and dominance rank, for example, are important factors regulating within-group cooperation and competition among individuals in typical cercopithecline societies including that of macaques (Smuts *et al.* 1986). Individual primates, however, also have fairly sophisticated social cognitive abilities that allow them to occasionally alter their usual patterns of interactions especially when the social or ecological environment makes such behavioural flexibility advantageous (de Waal 1989a, Cheney and Seyfarth 1990, Sinha 1998a).

Short-term behavioural changes in response to changing conditions of food availability and distribution have been investigated in only a few species of primates (in captivity: Erwin *et al.* 1976, de Waal 1984, Belzung and Anderson 1986, Boccia *et al.* 1988, Gore 1993; in the wild: Post 1978, Whitten 1983, Barton and Whiten 1993). Although most of these studies have documented the nature of feeding competition and aggression that develops within groups faced with either low availability or clumped distribution of food, they have not typically focussed on the mechanisms by which social tensions are subsequently reduced.

A notable exception to this is the early experimental study by de Waal (1984) on behavioural interactions in small captive isosexual groups of rhesus macaques provided with different amounts of food. He observed that individuals were willing to exhibit a particular adaptive behavioural response, such as aggression, if the situation so demanded, but only if the negative consequences of such behaviour were reparable. Allogrooming turned out to be a successful social mechanism by which individuals were able to restore peace amongst themselves. Reconciliation through such affiliative interactions is now known to be the most effective way individual primates re-establish the harmony of social relationships temporarily disrupted by uncharacteristic aggression (reviewed in de Waal 1989a).

Very little is known about the nature of such behavioural interactions in free-ranging primates faced with variability in food distribution and abundance. A particularly interesting situation is that of a number of Asian and African cercopithecine groups that are occasionally provisioned or have adapted to scavenging from neighbouring human habitations. Altmann and Muruthi (1989), in one such study, compared feeding patterns and energy intake of naturally foraging and scavenging troops of savanna baboons in Amboseli, Kenya, but their behavioural analyses were restricted to only that of individual activity patterns and foraging choices.

Free-ranging groups of bonnet macaques (*Macaca radiata*) are typically provisioned by tourists visiting a number of wildlife sanctuaries in southern India (Sinha, unpublished observations). Since the food obtained during such interactions is not only nutritionally rich but also clumped in distribution, provisioning is usually marked by a significant increase in feeding competition among individual troop members. The amount of such food available is, however, unpredictable and directly proportional to the tourist inflow into the area. These macaque groups, therefore, regularly forage on their natural food sources, and only resort to provisioned food during particular seasons and during certain times of the day when tourist traffic peaks within the sanctuary.

This study investigates the changing patterns of social interactions among adult female bonnet macaques in one such group that alternates between bouts of natural foraging and feeding on provisioned foods, often during the course of the same day. It documents the dramatic increase in feeding competition during provisioning, and examines the behavioural flexibility of individuals in adopting strategies to reduce social tension within the group. Finally, implications of these findings for the management of wild primate populations in sanctuaries and other protected areas are discussed.



## Methods

---

### *Study Species*

The bonnet macaque (*Macaca radiata radiata*, Geoffroy), an endemic cercopithecine primate occurring ubiquitously in peninsular India, commonly lives in multi-male, bisexual troops of about 15 to 60 individuals (Prater 1971). Females of this species, like those of many other cercopithecines, remain in their natal group throughout their lives, and during adulthood, form strong, linear dominance hierarchies with daughters occupying dominance ranks just below those of their mothers. Juvenile and adult males usually emigrate from their natal troops, another typical cercopithecine feature, but bonnet macaque males appear to be unique in being rather unpredictable in this regard, some individuals even staying back to become the most dominant males in their respective natal troops (Sinha, unpublished). Adult males form unstable dominance hierarchies through direct aggression and coalitions, with individuals in most coalitions demonstrating extensive affiliative interactions with each other (Silk 1994, Sinha 1998b).

### *Study Group*

The study was conducted in the Mudumalai Wildlife Sanctuary, Tamil Nadu, southern India on a free-ranging partially provisioned group of bonnet macaques that ranged along the Moyar river near the Theppakadu Forest Office of the sanctuary (c. 11°30'N, 76°33'E). Although a range of vegetation types,

from moist deciduous forest through semi-evergreen forest to dry evergreen forest, can be seen within the sanctuary, the study troop inhabited an area with predominantly dry mixed deciduous vegetation.

During the observation period, the troop consisted of 34 individuals with 9 adult females, 6 adult males, and 3 subadults and 10 juveniles of both sexes. Six infants were born in the group during the course of the study.

The natural diet of the study troop consisted predominantly of fruits, flowers, and leaves of *Tamarindus indicus*, *Azadirachta indica*, *Ficus bengalensis*, *F. retusa*, *Alphonsea sclerocarpa*, *Zizyphus oenoplia*, *Memecylon edule*, *Randia malabarica*, assorted herbs and several grasses. Insects also formed an important part of their diet; these included crickets, grasshoppers, and caterpillars. In addition, the group occasionally fed and scavenged on high-calorie human food handed out or left behind by tourists visiting the sanctuary. The amount of such food accessible to the troop was, however, seasonal, unpredictable and directly proportional to the tourist inflow into the sanctuary.

### ***Observed Behaviours***

The behaviours that have been considered in the present analysis include Foraging, Provisioning, Allogrooming, Affiliation, Aggression (including Contact Aggression and

Non-contact Aggression), Aggressive Approaches, Retreats and Feeding-supplants (Sinha, unpublished ethogram).

**Foraging** has been defined as the feeding by the study individuals on any component of their natural diet; this includes leaves, flowers, and fruits of different food plants and insects.

**Provisioning**, in contrast, refers to their feeding on human foods offered by tourists during direct interactions and their scavenging on the remains left behind by these visitors.

**Allogrooming** (here 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.

**Affiliation** 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.

**Aggression** is also a composite behaviour, 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. **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 that is followed by the former displaying any of the acts of Contact and Non-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 Contact and Non-contact Aggression shown by the latter.

**Feeding-supplants** consists of the replacement of a feeding individual by another at a feeding site, which may or may not be accompanied by a snatching of the food by the supplanting individual.

The 9 adult females in the study group formed a linear dominance hierarchy that could be unambiguously assigned on the basis of the direction and frequency of Contact and Non-contact Aggression between each pair of females.

### ***Data Collection***

Data were collected from the study troop during a continuous period of four months – from December 1996 to March 1997.

Initial qualitative observations *ad libitum* for two months (May - June 1996) allowed the observers and the troop to habituate to each other and led to the identification and naming of all the adult individuals in the troop on the bases of their physiognomy as well as other facial and body marks. The study troop was found to be active approximately between 0700 h in the morning and 1800 h in the evening. Observations were, therefore, conducted during three sessions – Morning (0800-1100 h), Midday (1100-1400 h) and Afternoon (1400-1700 h) – with data being collected only during any two sessions on each day in order to avoid observer fatigue.

The study troop, being accustomed to the presence of humans, allowed detailed observations at close range, although binoculars were used whenever the individuals were in areas that were physically unapproachable. No attempt was made to feed or interfere otherwise with the study animals during the study.

Behavioural data, used for this analysis, are based on approximately 139.2 h of focal animal sampling (Altmann 1974) on the 9 adult females in the group with a mean ( $\pm$  SD) of 15.5 ( $\pm$  1.4) h of sampling per female. Each focal sample of an individual, chosen randomly without replacement, had a duration of 10 min. Observations were primarily directed towards every occurrence of Foraging and Provisioning for the focal individual, and all inter-individual interactions for

each female-female dyad that necessarily involved the focal individual. Such effectively focal dyad sampling was distributed according to the time spent by these females in periods of foraging (on their natural diet) and on being provisioned (when they fed or scavenged on human foods), and totaled a mean ( $\pm$  SD) of 20.4 ( $\pm$  1.4) h per dyad during foraging and a mean of 10.6 ( $\pm$  1.2) h per dyad during provisioning.

### ***Data Analyses***

Foraging by focal individuals and their Provisioning have been measured in terms of the frequency of their feeding on the respective food sources during the observation period. The initiation of an Allogrooming event by an individual has been considered as basic data for the analysis of grooming relationships in this study. Accordingly, Allogrooming frequency has been expressed as the number of grooming events initiated by an individual towards another per hour. The display of Affiliation, Contact and Non-contact Aggression, Aggressive Approach, Retreat and Feeding-supplants have similarly been measured in terms of their demonstrated frequency per unit time. For all these behaviours that occasionally involved more than two individuals, only dyadic interactions between pairs of females have been considered in the final analysis.

The statistical analyses of the data employed primarily non-parametric tests including the Mann-Whitney *U*-test, Wilcoxon's signed-ranks test, and Kendall's rank correlation, whenever appropriate. These were performed as described by Sokal and Rohlf (1995). All tests, unless otherwise specified, were two-tailed.

## **Results**

---

### ***Foraging and Provisioning***

The study group regularly moved between two kinds of habitats, roughly comparable in area, within their home-range. One was a relatively more forested area where they foraged on their natural diet of leaves, flowers, fruits, and insects. The other was a more open area in the vicinity of the Forest Office where they either interacted with tourists and directly obtained human food from them, or where they scavenged on remains left behind by the visitors. All social interactions in the former area have been considered to be associated with natural foraging, and those in the latter area with the artificial provisioning of the study individuals.

The adult females in the study group spent a significantly greater length of time in the foraging area during the observation period (91.5 h) than in the area where they were provisioned (47.7 h) than would be expected by chance alone (chi-square test,  $X^2 = 13.78$ ,  $df = 1$ ,  $p < 0.001$ ). In spite of the

less time spent in the provisioning area, however, the females exhibited a much higher frequency of Provisioning (mean  $\pm$  SD of  $13.23 \pm 2.70$  acts/h) than they did of Foraging ( $3.73 \pm 1.53$  acts/h; Wilcoxon's signed-ranks test,  $T = 4$ ,  $n = 9$  individuals,  $p < 0.03$ ).

### ***Feeding competition during provisioning***

There was a marked increase in social tension in the study group during periods of provisioning; this was usually manifested as enhanced aggression among members of the troop. The overall rates of Aggression, Non-contact Aggression and Feeding-suppliants between the adult females, for example, increased significantly during this period from that exhibited during foraging (Figure 1; Wilcoxon's signed-ranks test,  $n = 72$  dyads; Aggression:  $T = 204.5$ ,  $p < 0.01$ ; Non-contact Aggression:  $T = 171.5$ ,  $p < 0.02$ ; Feeding-suppliants:  $T = 103$ ,  $p < 0.003$ ). Interestingly, however, there was no marked change in the levels of Contact Aggression under the two conditions (Figure 1;  $T = 84$ ,  $p > 0.1$ ).

A closer examination of the patterns of Contact Aggression, nevertheless, revealed that dominant females exhibited increasing rates of Contact Aggression towards subordinates of increasing rank only during foraging (Figure 2, panel A;  $t = 0.2811$ ,  $n = 36$  dyads,  $p < 0.02$ ). During provisioning, such aggression was almost exclusively displayed by the highest-ranked females in the group and preferentially only towards



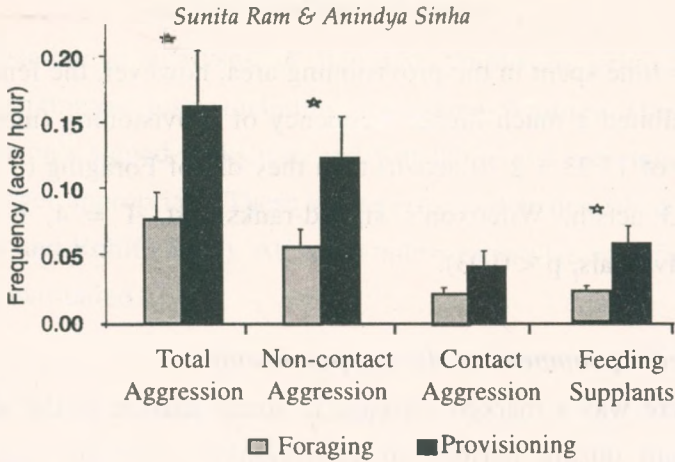


FIGURE 1. Aggression and Feeding-supplants among adult females during foraging and provisioning. Error bars represent standard deviation. The asterisk denotes a statistically significant difference between the displayed frequencies of that particular behaviour across the two conditions (Wilcoxon's signed ranks test,  $n = 72$  dyads,  $p < 0.05$ )

subordinates closest to them in the dominance hierarchy (Figure 2, panel B;  $\tau = 0.1822$ ,  $p > 0.10$ ). In fact, Contact Aggression was significantly more often directed towards subordinate females in the upper half of the rank hierarchy (mean  $\pm$  SD of  $0.21 \pm 0.24$  acts/h,  $n = 10$  dyads) than those in the lower half ( $0.04 \pm 0.05$  acts/h,  $n = 26$  dyads) during provisioning (Mann-Whitney  $U$ -test,  $U = 186$ ,  $p < 0.05$ ); no such discrimination was evident during foraging (towards subordinates in the upper half of the hierarchy:  $0.08 \pm 0.11$  acts/h; towards those in the lower half:  $0.02 \pm 0.04$  acts/h;  $U = 164$ ,  $p > 0.10$ ).

Agonistic attacks in the form of Contact Aggression, although not very frequent, was also increasingly directed by dominant individuals towards those subordinate females who exhibited

more Aggression during provisioning (Kendall's rank correlation,  $\tau = 0.2570$ ,  $n = 36$  dyads,  $p < 0.05$ ). In contrast, foraging dominant females preferentially directed milder forms of agonism, such as Non-contact Aggression, towards subordinates who showed relatively less Aggression ( $\tau = -0.2591$ ,  $p < 0.05$ ).

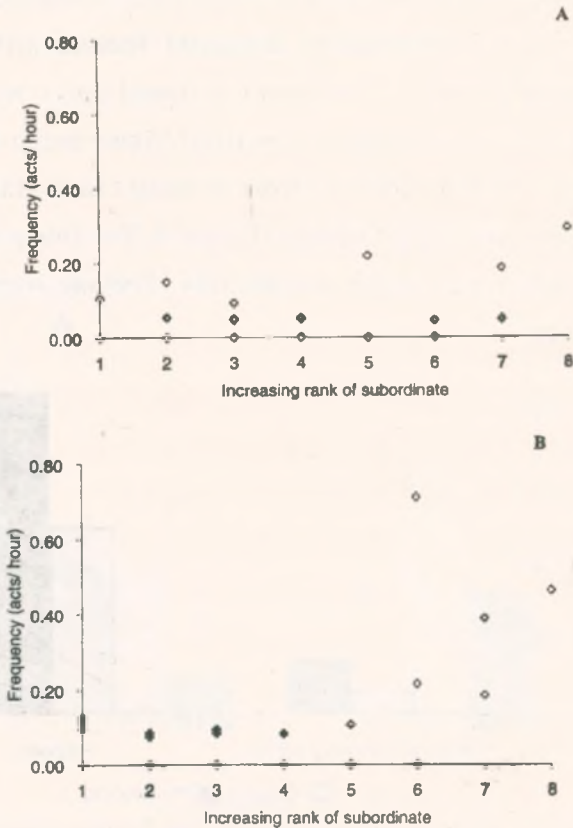


FIGURE 2. Contact Aggression directed by dominant females towards subordinate individuals of increasing dominance rank. Panel A: during foraging (Kendall's rank correlation,  $\tau = 0.2811$ ,  $n = 36$  dyads,  $p < 0.02$ ). Panel B: during provisioning ( $\tau = 0.1822$ ,  $p > 0.10$ )

Adult bonnet macaque females typically do not exhibit aggression towards those higher than them in the dominance hierarchy (Sinha, unpublished observations). During provisioning, however, when there is an evident rise in overall aggression within the troop, do subordinate individuals now direct aggression towards their dominant adversaries? Indeed, subordinate females did display significantly enhanced Non-contact Aggression towards dominant individuals during provisioning (Figure 3; Wilcoxon's signed-ranks test, one-tailed,  $T = 3$ ,  $n = 36$  dyads,  $p = 0.05$ ). Subordinate females also Retreated at higher rates from dominant individuals than they did during natural foraging (Figure 3;  $T = 196$ ,  $p < 0.05$ ). Finally, dominant females successfully (Feeding-)supplanted

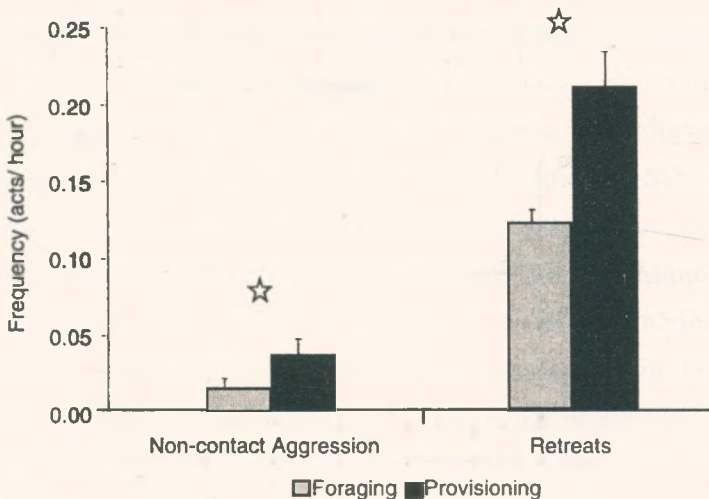


FIGURE 3. Non-contact Aggression towards and Retreats from dominant individuals displayed by subordinate females during foraging and provisioning. Error bars represent standard deviation. The asterisk denotes a statistically significant difference between the displayed frequencies of that particular behaviour across the two conditions (Wilcoxon's signed ranks test, one-tailed,  $n = 36$  dyads,  $p < 0.05$ )

subordinate individuals much more during provisioning (mean  $\pm$  SD of  $0.12 \pm 0.14$  acts/h) than during foraging ( $0.05 \pm 0.05$  acts/h;  $T = 122.5$ ,  $p < 0.01$ ). As expected, no such difference in the supplanting of dominant individuals by subordinates were observed under the two conditions (provisioning:  $0.005 \pm 0.022$  acts/h, foraging:  $0.001 \pm 0.009$  acts/h;  $T = 1$ ,  $p > 0.10$ ).

### *Affiliative interactions during provisioning*

There was a significant decrease in the frequency of Allogrooming and Affiliation as the females moved to the provisioning site from areas of natural foraging (Figure 4; Wilcoxon's signed-ranks test,  $n = 72$  dyads; Allogrooming:  $T = 190$ ,  $p < 0.0005$ ; Affiliation:  $T = 303$ ,  $p < 0.0005$ ). An

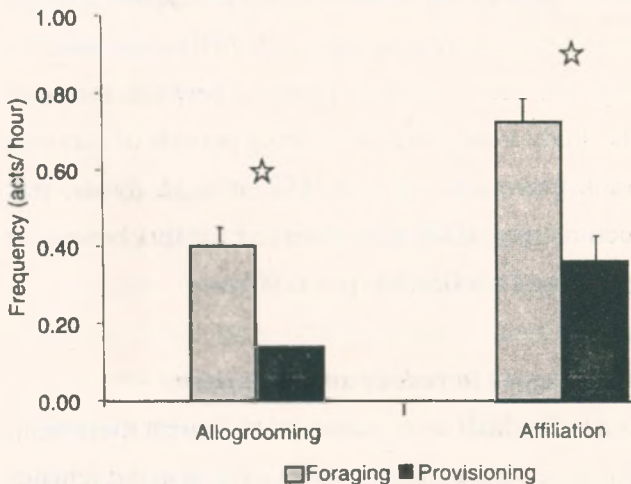


FIGURE 4. Allogrooming and Affiliation among adult females during foraging and provisioning. Error bars represent standard deviation. The asterisk denotes a statistically significant difference between the displayed frequencies of that particular behaviour across the two conditions (Wilcoxon's signed ranks test,  $n = 72$  dyads,  $p < 0.0005$ )

examination of individual patterns of these affiliative behaviours, however, revealed that while subordinate females decreased the display of both Allogrooming and Affiliation towards dominant individuals (Allogrooming: foraging – mean  $\pm$  SD of  $0.48 \pm 0.45$  acts/h, provisioning –  $0.17 \pm 0.23$  acts/h, Wilcoxon's signed-ranks test,  $n = 36$  dyads,  $T = 71$ ,  $p < 0.0005$ ; Affiliation: foraging –  $0.67 \pm 0.52$  acts/h, provisioning –  $0.26 \pm 0.38$  acts/h,  $T = 94$ ,  $p < 0.0005$ ), the latter only reduced Allogrooming of their subordinate partners (foraging:  $0.32 \pm 0.30$  acts/h, provisioning:  $0.09 \pm 0.17$  acts/h,  $T = 115$ ,  $p < 0.0005$ ).

Was reciprocation of affiliative behaviours, a typical feature of social relationships among female bonnet macaques, affected by provisioning? It is interesting that only Affiliation, and not Allogrooming, was reciprocally exchanged between the adult females of the study troop, and only during periods of foraging (Kendall's rank correlation,  $\tau = 0.2452$ ,  $n = 36$  dyads,  $p < 0.05$ ). No such reciprocation was observed for this behaviour during provisioning ( $\tau = 0.0143$ ,  $p > 0.90$ ).

### ***Behavioural strategies to reduce social tension***

Higher-ranked individuals were observed to Retreat more from their dominant adversaries during provisioning than did females of relatively low rank (Kendall's rank correlation,  $\tau = 0.3005$ ,  $n = 36$  dyads,  $p < 0.01$ ) – a pattern not evident during foraging ( $\tau = -0.0362$ ,  $p > 0.70$ ). Surprisingly, with the rise of aggression

during provisioning, dominant females Retreated from subordinate individuals as well; the frequency of Retreat increasing significantly with increasing dominance rank of the subordinate (provisioning:  $\tau = 0.2412$ ,  $p < 0.05$ ; foraging:  $\tau = 0.1837$ ,  $p > 0.10$ ).

Patterns of affiliative interactions changed dramatically as the study troop alternated between periods of foraging and provisioning. For example, there was a prominent decrease in Allogrooming displayed by dominant individuals towards their subordinates during provisioning (discussed above). What is remarkable, however, is that levels of Affiliation did not change significantly, frequencies of this behaviour remaining comparable across the two situations (foraging: mean  $\pm$  SD of  $0.75 \pm 0.67$  acts/h, provisioning:  $0.42 \pm 0.87$  acts/h, Wilcoxon's signed-ranks test,  $n = 36$  dyads,  $T = 327$ ,  $p > 0.80$ ).

Affiliative behaviours, which are of a reciprocal nature, can also be analysed at the level of dyadic interactions. Such an examination revealed that subordinate individuals exhibited relatively more Allogrooming towards their dominant partners, than did the latter, during provisioning (Figure 5; Mann-Whitney  $U$ -test;  $n = 36$  dyads;  $U = 823$ ;  $p < 0.05$ ). Grooming was much more reciprocal during natural foraging ( $U = 760$ ,  $p > 0.20$ ). No such change in dyadic patterns was, however, evident for Affiliation under the two conditions (data given above; foraging:  $U = 664.5$ ,  $p > 0.80$ ; provisioning:  $U = 748.5$ ,  $p > 0.20$ ).

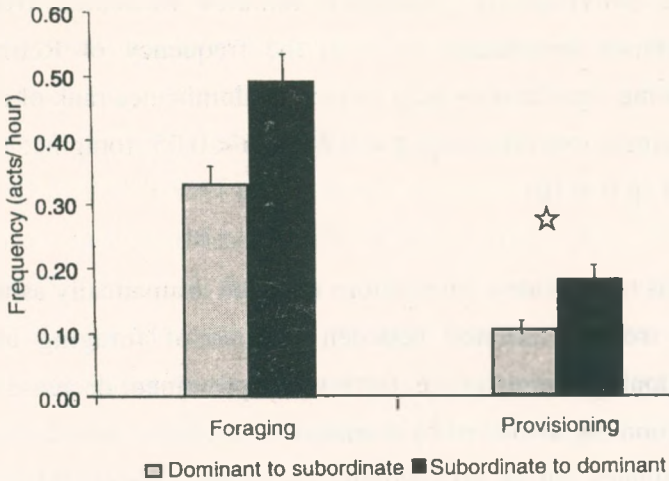


FIGURE 5. Allogrooming between dominant and subordinate members of adult female dyads during foraging and provisioning. Error bars represent standard deviation. The asterisk denotes a statistically significant difference between grooming frequencies in the two directions (Mann-Whitney *U*-test,  $n = 36$  dyads,  $p < 0.05$ )

Finally, during provisioning, dominant females displayed significantly less Aggressive Approaches towards those subordinate individuals who had Allogroomed them more under these conditions (Figure 6, panel A; Kendall's rank correlation,  $\tau = -0.3152$ ,  $n = 36$ ,  $p < 0.01$ ). This particular behavioural interchange was, however, absent during periods of foraging (Figure 6, panel B;  $\tau = -0.0140$ ,  $p > 0.90$ ).

Provisioning in wild bonnet macaques

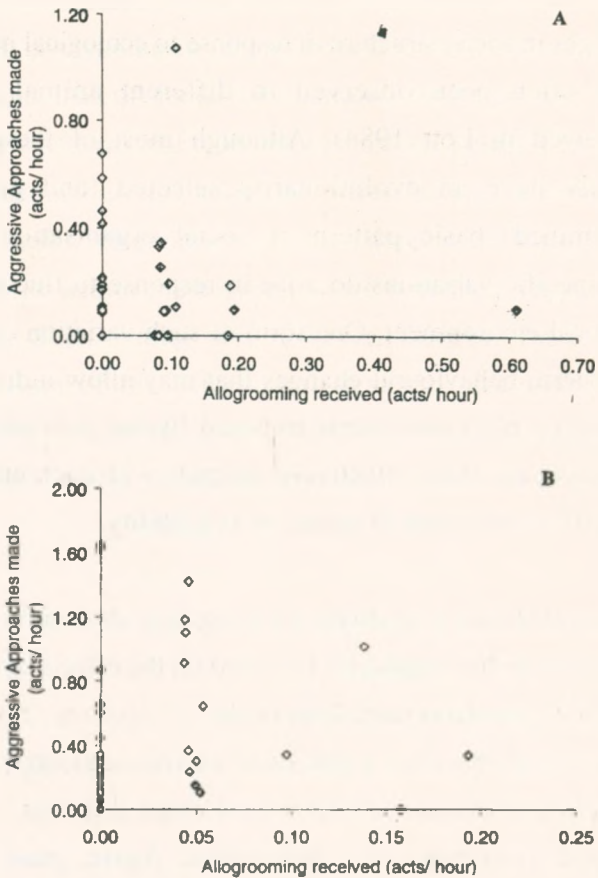


FIGURE 6. Aggressive Approaches displayed by dominant females towards subordinate individuals as a function of Allogrooming received. Panel A: during provisioning (Kendall's rank correlation,  $\tau = -0.3152$ ,  $n = 36$  dyads,  $p < 0.01$ ). Panel B: during foraging ( $\tau = -0.0140$ ,  $p > 0.90$ ). Note that the scaling of the ordinates in the two figures are different



## **Discussion**

---

Changes in social structure in response to ecological parameters have often been observed in different animal societies (reviewed in Lott 1984). Although most of these species usually have an evolutionarily selected (and genetically determined) basic pattern of social organisation, limited intraspecific variations do arise in response to fluctuations in the local environment. One form of such variation consists of short-term behavioural changes that may allow individuals to overcome rigid constraints imposed by the prevailing social structure, and thus, effectively compete with each other under changing conditions of resource availability.

Classical studies in primates investigating short-term variation in behaviour have typically focussed on the effects of crowding and high population densities on social structure (reviewed in de Waal 1989b). Only a few studies have considered changing patterns of behavioural interactions under different conditions of food availability and distribution. Again, most of these studies have examined the influence of food competition on social behaviour in only captive groups of different species (Erwin *et al.* 1976, de Waal 1984, Belzung and Anderson 1986, Boccia *et al.* 1988, Gore 1993). In contrast, investigations into the social dynamics of free-ranging groups faced with ecological variation in food distribution and abundance are few (Post 1978, Whitten 1983, Barton and Whiten 1993).

### ***Foraging and Provisioning***

Artificial provisioning of wild primate groups usually lead to changes in behavioural strategies, both at the level of individual activity and that of social interactions. Although individual behavioural patterns and food choices in such naturally foraging and provisioned groups have been investigated (Altmann and Muruthi 1988), observations on the nature of changing social relationships within these groups have remained surprisingly neglected. Such studies are, however, essential for a basic understanding of the behavioural strategies that individuals adopt when faced with rapidly changing food regimes and the mechanisms that facilitate the promotion of social harmony in the midst of rising intra-group competition for food.

This study examines the changing nature of social relationships among the adult females of a free-ranging group of bonnet macaques that regularly alternated between bouts of natural foraging and visits to a site where they were provisioned with human food. Although these females spent a significantly smaller period of time feeding or scavenging on provisioned food, this was more a reflection of the short periods of the day (usually in the evenings alone) when food was provided by tourists visiting the sanctuary. That this food was nevertheless greatly attractive to the monkeys is borne out by the much higher rates of feeding or scavenging (Provisioning) exhibited at this site relative to that during bouts of foraging on their natural food during the greater part of the day (Foraging). It

would be worthwhile to compare the nutritional values of these two kinds of food in order to investigate the possibility that the provisioned diet was so much more attractive also because it was relatively richer in its energy content (see Altmann and Muruthi 1989).

***Feeding competition during provisioning***

The clumped distribution of the provisioned food around their human sources was likely to be directly responsible for the observed significant increase in intra-group feeding competition that accompanied provisioning over that during natural foraging. It is also possible that the nutritional quality of the human food (if indeed higher than that of the natural diet) could have contributed to such elevated levels of aggression and feeding supplants exhibited by the females. It is noteworthy, however, that it was Non-contact Aggression that greatly contributed to this overall rise in total aggression. Contact Aggression, which imposes higher energetic demands and obviously carries much greater potential costs for the adversaries, did not increase significantly during provisioning.

The patterns of Contact Aggression that characterised provisioning, nevertheless, were different from that during foraging and revealed some interesting features. While foraging dominant females directed physical aggression increasingly towards subordinates of progressively higher rank, such aggression was preferentially directed only towards the highest-

ranked subordinates during provisioning. Contact Aggression was also exhibited significantly more towards those subordinates who had, in turn, shown more aggression during the stressful periods of provisioning. In contrast, under the relatively more peaceful conditions of foraging, aggression was selectively directed towards weaker subordinates who were comparatively less agonistic. In essence, potentially expensive acts of aggression over provisioned food appeared to be demonstrated only by high ranked individuals, who could afford such encounters, and were directed towards high ranked subordinates who, by virtue of their position in the hierarchy, would be the most threatening adversaries during such feeding competition.

The dominance hierarchy among free-ranging adult female bonnet macaques is extremely rigid; subordinate females almost never exhibit either Contact or Non-contact Aggression towards their dominant counterparts (Sinha, unpublished observations). As overall agonism rose during provisioning, however, subordinate females in this particular troop began to display significantly elevated levels of Non-contact Aggression towards dominant individuals. Yet another manifestation of such heightened social tension within the group was the remarkably high frequency with which subordinates Retreated from their dominant counterparts during competition over provisioned food. This, in turn, contributed to the ability of high ranked females to (Feeding-)supplant lower ranked individuals much

more during such encounters. As expected, there was no difference in the supplanting of the former by the latter under the two conditions.

It has been suggested that stable linear hierarchies in female primates are a result of conflict competition for food (Janson 1985, van Noordwijk and van Schaik 1987, Janson and van Schaik 1988, Mitchell *et al.* 1991, Gore 1993). The intensity of competition over provisioned food was manifest not only in the sharp rise of intra-group aggression during this period but also in the appearance of agonistic acts directed by subordinate females towards their dominant counterparts only during provisioning. A strong competitive advantage due to positions of high rank in the dominance hierarchy, nevertheless, did reveal itself as greater success enjoyed by dominant females during Feeding supplants. In addition, there could be other behavioural measures reflecting the advantage of being a high ranked female that have not been considered in this study. These could include, amongst others, differences in feeding rates, total feeding time, daily food intake, dietary diversity, or even dietary composition (Post *et al.* 1980, Barton and Whiten 1993).

### ***Affiliative interactions during provisioning***

The troop's movement from a regime of natural foraging to that of provisioning was accompanied by a significant decrease in the frequency of both Allogrooming and other affiliative

behaviours. The group was able to opportunistically spend only short periods of time at the provisioning site and even this was marked by high rates of feeding and scavenging, as well as intense conflict over food. It is thus possible that there was very little time that individuals could devote to such energy- and time-intensive interactions as Allogrooming during these periods. Support for this comes from the observation that dominant individuals who reduced their frequency of grooming of subordinate females during provisioning did not similarly lower the display of other affiliative behaviours (Affiliation); these consist of simple behavioural actions that are not time-consuming.

An alternative hypothesis for the observed patterns of affiliative interactions could be that the dramatic increase of feeding competition and intra-group social tension brought about by provisioning may have led individuals to avoid each other and thus decrease their rates of affiliative interactions. This would most likely be the situation for the low ranked females in the group who invariably face the brunt of the increasing aggression over food. In addition, if this hypothesis also applies to the dominant individuals, it is perhaps significant that they reduced only the display of Allogrooming, but not Affiliation, towards their subordinate counterparts. Interestingly enough, Affiliation alone was reciprocated symmetrically between each pair of adult females during the more peaceful periods of natural foraging. Allogrooming was also exchanged between these

pairs of individuals; it was, however, not symmetrical in distribution.

***Behavioural strategies to reduce social tension***

The adult females in the study group appeared to adopt two distinctive kinds of behavioural strategies to reduce tension brought about by feeding competition within the group. First, individuals of high rank actively avoided interacting with more dominant females, Retreating from them at much higher rates than they did under less stressful conditions of natural foraging. What was even more remarkable is that dominant individuals too Retreated from their high-ranked subordinates during provisioning – a feature almost never encountered in free-ranging bonnet macaque societies (Sinha, unpublished observations; Rauf Ali, personal communication). Mutual avoidance of this kind may be the only strategy that can be utilised by individuals of high dominance rank to alleviate intra-group aggression. Given the tension that individuals seem to be under during provisioning, attempts to bring about peace through more active affiliative interactions could carry the threat of potentially high costs of physical conflict, a cost that would be maximum for individuals of high dominance rank.

The second kind of behavioural strategies consists of active affiliative interactions directed towards those individuals from whom the threat of aggression is the most, or towards those who are victims of conflict competition. This was originally

suggested by de Waal (1989b) who emphasised that primates, being highly adaptable, would, when confronted with a stressful situation, modify their behaviour to reduce the risk of aggression. Thus, in the Mudumalai troop, subordinate females displayed relatively more initiated Allogrooming towards dominant individuals than they received from them under conditions of provisioning. In contrast, exchange of grooming was much more reciprocal during episodes of natural foraging. Dominant individuals, in turn, did not effectively reduce the frequency of Affiliation directed towards their subordinates as the troop began episodes of provisioning. Levels of Allogrooming, however, did come down significantly. It is perhaps noteworthy that subordinate individuals had to take recourse to the more energetically demanding activity of grooming, while dominant females could afford simpler, shorter, behavioural interactions in order to reduce intra-group social tension.

How successful were these behavioural strategies in actually reducing social tension? The fact that there continued to be high levels of intra-group aggression during provisioning suggested that these strategies may not have had enough power to completely reduce the effects of feeding competition on the nature of social interactions under such stressful conditions. Nevertheless, it is also true that, during provisioning, dominant individuals were less aggressive, as manifest in the reduced display of Aggressive Approaches,



towards those subordinate females who had Allogroomed them more during these periods. Thus, although such interactions may appear to be only partially successful in reducing aggression when overall competition within the troop is considered, individuals may be adept at reducing the risk they themselves face from certain more powerful adversaries through the adoption of flexible social strategies.

A final point concerns the relationship between intra-group conflict competition and reproductive success in wild primates. Although much literature exists on rank-related differences in foraging success as related to differences in reproductive status (reviewed in Harcourt 1987), not much is known about the direct influence of social status and aggressive behaviour on reproductive fitness. High levels of aggression have earlier been shown to decrease reproductive success in free-ranging savanna baboons in at least two African national parks (Gombe, Tanzania: Packer *et al.* 1995; Mikumi, Tanzania: Wasser 1995; but see Altmann *et al.* 1995 for a dissenting view on the baboons in Amboseli, Kenya). These studies clearly indicate that stress brought about by the pressures of maintaining high dominance status through aggression can lead to increased rates of conception failure and abortion in adult female baboons.

Active interactions of wild primates with human beings, particularly tourists, are unavoidable in most sanctuaries and

other protected areas in India. Such interactions would obviously lead to provisioning of these otherwise free-ranging groups. It is imperative that the long-term impacts of increased feeding competition and social tension, brought about by provisioning and scavenging, on the life history parameters of primates be explored urgently. The management implications of such findings for the conservation of the endangered or threatened primate populations of our country can hardly be overstated.

### **Acknowledgements**

---

We sincerely thank the Tamil Nadu Forest Department for permission to work in the Mudumalai Wildlife Sanctuary. We are also grateful to the Centre for Ecological Sciences, Indian Institute of Science, for granting a visitorship to Sunita Ram, the CES Field Station in Masinagudi for extending all its facilities, and Harish Bhat for providing information about vegetation patterns in Mudumalai. This study formed a part of a dissertation submitted by Sunita Ram for a Master's degree at the Salim Ali School of Ecology and Environmental Sciences, Pondicherry University. A part of this work has also been presented at the National Seminar on Wildlife Conservation, Research and Management, held at the Wildlife Institute of India, Dehradun, in August 1998, and will be published in the proceedings of that meeting.

## References

---

- Altmann, J. 1974. Observational study of social behaviour: sampling methods. *Behaviour* **49**: 227-265.
- Altmann, J. and Muruthi, P. 1988. Differences in daily life between semi-provisioned and wild-feeding baboons. *American Journal of Primatology* **15**: 213-221.
- Altmann, J., Sapolsky, R. and Licht, P. 1995. Baboon fertility and social status. *Nature* **377**: 688-690.
- Barton, R.A. and Whiten, A. 1993. Feeding competition among female olive baboons, *Papio anubis*. *Animal Behaviour* **46**: 777-789.
- Belzung, C. and Anderson, J.R. 1986. Social rank and response to feeding competition in rhesus monkeys. *Behavioural Processes* **12**: 307-316.
- Boccia, M.L., Laudenslager, M. and Rete, M. 1988. Food distribution, dominance, and aggressive behaviour in bonnet macaques. *American Journal of Primatology* **16**: 123-130.
- Cheney, D.L. and Seyfarth, R.M. 1990. *How monkeys see the world*. University of Chicago Press, Chicago.
- Erwin, J., Anderson, B., Erwin, N., Lewis, L. and Flynn, D. 1976. Aggression in captive groups of pigtail monkeys: effects of provision and cover. *Perceptual and Motivational Skills* **42**: 319-324.
- Gore, M.A. 1993. Effects of food distribution on foraging competition in rhesus monkeys, *Macaca mulatta* and *Papio hamadryas*. *Animal Behaviour* **45**: 773-786.
- Harcourt, A.H. 1987. Dominance and fertility among female primates. *Journal of Zoology* **213**: 471-497.
- Janson, C.H. 1985. Aggressive competition and food consumption in the brown capuchin monkey (*Cebus apella*). *Behavioural Ecology and Sociobiology* **18**: 125-138.
- Janson, C.H. and van Schaik, C.P. 1988. Recognizing the many faces of primate food competition: methods. *Behaviour* **105**: 165-186.
- Judge, P.G. & de Waal, F.B.M. 1997. Rhesus monkey behaviour under diverse population densities: coping with long-term crowding. *Animal Behaviour* **54**: 643-662.

*Provisioning in wild bonnet macaques*

- Lott, D. 1984. Intraspecific variation in the social systems of wild vertebrates. *Behaviour* **88**: 266-325.
- Mitchell, C.L., Boinski, S. and van Schaik, C.P. 1991. Competitive regimes and female bonding in two species of squirrel monkeys (*Saimiri oerstedii* and *S. sciureus*). *Behavioural Ecology and Sociobiology* **28**: 55-60.
- van Noordwijk, M.A. and van Schaik, C.P. 1987. Competition among adult female long-tailed macaques. *Animal Behaviour* **36**: 577-589.
- Packer, C., Collins, D.A., Sindimwo, A. And Goodall, J. 1995. Reproductive constraints on aggressive competition in female baboons. *Nature* **373**: 60-63.
- Post, D.G. 1978. *Feeding and ranging behaviour of the yellow baboon (Papio cynocephalus)*. PhD thesis. Yale University.
- Post, D.G., Hausfater, G. And McCuskey, S.A. 1980. Feeding behaviour of yellow baboons (*Papio cynocephalus*): relationship to age, gender and dominance rank. *Folia Primatologia* **34**: 170-195.
- Prater, S.H. 1971. *The book of Indian animals*. Bombay Natural History Society, Mumbai.
- Silk, J.B. 1994. Social relationships of male bonnet macaques: male bonding in a matrilineal society. *Behaviour* **130**: 271-291.
- Sinha, A. 1998a. Knowledge acquired and decisions made: triadic interactions during allogrooming in wild bonnet macaques, *Macaca radiata*. *Philosophical Transactions of the Royal Society, London: Biological Sciences* **353**: 619-631.
- Sinha, A. 1998b. Affiliative relationships and coalition formation among wild male bonnet macaques. Abstract at the 17th Congress of the International Primatological Society, Antananarivo, Madagascar, August 1998
- Smuts, B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. and Struhsaker, T.T. 1987. *Primate societies*. University of Chicago Press, Chicago.
- Sokal, R.R. and Rohlf, F.J. 1996. *Biometry* (third edition). Freeman, San Francisco.
- de Waal, F.B.M. 1984. Coping with social tension: sex differences in the effect of food provision to small rhesus monkey groups. *Animal Behaviour* **32**: 765-773.
- de Waal, F.B.M. 1989a. *Peacemaking among primates*. Harvard University Press, Cambridge, Massachusetts.

*Sunita Ram & Anindya Sinha*

- de Waal, F.B.M. 1989b. The myth of a simple relation between space and aggression in captive primates. *Zoo Biology Supplement* 1: 141-148.
- Wasser, S.K. 1995. Costs of conception in baboons. *Nature* 376: 219-220.
- Whitten, P.L. 1983. Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *American Journal of Primatology* 5: 139-159.

**Biographical sketches**

*Sunita Ram has a Master's degree in Ecology from the Salim Ali School of Ecology and Environmental Sciences, Pondicherry University. Her research interests include behavioural ecology and wildlife conservation; this paper forms a part of her Master's dissertation investigating the behavioural ecology of wild bonnet macaques in Mundanthurai Wildlife Sanctuary, Tamil Nadu. She is currently involved in a biodiversity conservation programme at the Centre for Sustainable Agriculture and Rural Development, Chennai.*

*Anindya Sinha is a Research Fellow at the National Institute of Advanced Studies. He has a PhD in molecular biology from the Tata Institute of Fundamental Research, Mumbai, but subsequently became more involved in organismic biology. His current research interests are in the areas of primate behavioural ecology, evolutionary biology, cognitive ethology and conservation biology.*

