

Changing social strategies of wild female bonnet macaques during natural foraging and on provisioning

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Provisioning of free-living primate groups usually leads to a significant increase in competition among individuals for the newly available resources. Do such individuals, however, exhibit altered behavioural strategies to alleviate social tension? Changing patterns of social interactions between adult females was studied in a wild group of bonnet macaques (*Macaca radiata*) in the Mudumalai Wildlife Sanctuary, Tamil Nadu, southern India, under two conditions of foraging. The group spent approximately 66% of the observation time foraging on its natural diet; during the remaining period the group gathered provisioned food from tourists visiting the sanctuary. Provisioning was marked by a sharp increase in aggression and feeding supplants within the group. Dominant females directed contact aggression specifically towards higher-ranked subordinates, while subordinate females increased non-contact aggression towards their dominant counterparts. Allogrooming was, however, much more reciprocated at the group level during provisioning. Subordinate females also initiated relatively more allogrooming towards those dominant individuals who were most aggressive during this period. Social tensions thus increase markedly when bonnet macaques move from natural foraging to competing for provisioned food; individual macaques, however, can adopt appropriate social strategies under such rapidly changing ecological regimes.

PRIMATE societies are generally structured organizations 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 cercopithecine societies, including that of macaques¹. Individual primates, however, are also capable of occasionally altering their usual patterns of interactions, especially when the social or ecological environment makes such behavioural flexibility advantageous²⁻⁴.

Short-term behavioural changes in response to changing conditions of food availability and distribution have been investigated in only a few species of primates, both in captivity⁵⁻¹⁰ and in the wild¹¹⁻¹⁵. Although most 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 focused on the mechanisms by which social tensions are subsequently reduced.

A notable exception to this is the early experimental study by de Waal⁷ 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 repairable. 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 aggression².

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 Muruthi¹⁶, 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 that of individual activity patterns and foraging choices alone.

Free-ranging groups of bonnet macaques (*Macaca radiata radiata* and *M. radiata diluta*, family Cercopithecinae) are typically provisioned by tourists visiting a number of wildlife sanctuaries in southern India. Since the food obtained during such interactions is not only nutritionally rich but also clumped in distribution, provi-

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sioning 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 regularly alternates between bouts of natural foraging and feeding on provisioned foods, often during the course of the same day. It documents the sharp increase in feeding competition during provisioning, and examines the behavioural flexibility of individuals that allows them to adopt strategies aimed at reducing social tension within the group.

Methods

Study species

The bonnet macaque (*M. radiata radiata*, Geoffroy), an endemic cercopithecine primate occurring ubiquitously in peninsular India, commonly lives in multi-male, bisexual troops of about 15 to 60 individuals¹⁷. Females of this species usually 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 mothers¹⁸. 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 troops¹⁸. Adult males form unstable dominance hierarchies through direct aggression and coalition, with individuals in most coalitions demonstrating extensive affiliative interactions with each other^{19,20}.

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 nine adult females, six adult males,

three sub-adults and ten 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 or leaves of *Tamarindus indicus*, *Azadirachta indica*, *Ficus benghalensis*, *Ficus 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 behaviour

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

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. Scavenging, in contrast, has been used here to refer to their feeding on human foods offered by tourists during direct interactions and their scavenging on the remains left behind by these visitors.

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.

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 (Sinha, A., unpublished ethogram).

Total 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. 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 (Sinha, A., unpublished ethogram).

Aggressive approach refers to an approach made by an individual towards another, that 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. Feeding supplant consists of the replacement of a feeding individual by another at a feeding site, which may or may not be accompanied by snatching of the food by the supplanting individual.

The nine adult females in the study group formed a linear transitive dominance hierarchy that could be unambiguously assigned on the basis of the direction and frequency of either contact aggression or aggressive approach 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 animals during the study.

Behavioural data, used for this analysis, are based on approximately 139.2 h of focal animal sampling²¹ on the nine adult females in the group with a mean (\pm SE) of 15.5 (\pm 0.5) 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 inter-individual interactions within every female–female dyad that necessarily involved the focal individual. The number of focal animal samples on each of the females was an outcome of the time that these individuals chose to spend in two adjacent areas within their home range – one in which they foraged on their natural diet and the other where they were provisioned by tourists and also scavenged on food left behind by them.

Such sampling totalled a mean (\pm SE) of 20.4 (\pm 0.2) h per female–female dyad in the former area and a mean of 10.6 (\pm 0.1) h per dyad in the latter area.

Data analysis

Foraging and scavenging by focal individuals 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, total aggression, non-contact aggression, contact aggression, aggressive approach, retreat and feeding supplant has 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 analyses of the data have employed both conventional and derived non-parametric statistical tests^{22,23}. All tests, unless otherwise specified, are one-tailed.

Behavioural differences under the different ecological regimes have been examined by tests that primarily focus on dyadic- and group-level interactions. Two statistical problems need to be addressed while examining such data at both the dyadic and group levels. First, the involvement of an individual in more than one dyad leads to potential non-independence of the data. Secondly, the presence of a few extreme values (or ‘outliers’) may disproportionately influence the results of these tests. Hence, non-parametric statistical methods and randomization tests have been employed to overcome these problems, as explained below.

The distributions of dyadic interactions under different conditions have been compared using two novel statistical procedures – the Pairs Test and the Matched Pairs Test. In the Pairs Test, the two data series (for the two behaviours under comparison) are arranged in one-dimensional arrays. The test statistic is the fraction of comparisons in which one value drawn from one array or distribution is greater than that drawn from the other. Comparisons are made of all possible pairs while evaluating this statistic. For example, the Pairs Test can be used to test whether, during dyadic interactions between female bonnet macaques, the subordinate individual exhibits more grooming towards its dominant partner than does the latter towards the former. The null hypothesis here is that there is no difference in the grooming initiated by the two classes of individuals towards each other. In order to test for this, the frequencies of allogrooming initiated by the subordinate individuals in all the ob-

served dyads can be listed in one data array and those initiated by the dominant individuals in another. The test statistic of the Pairs Test, in this case, is the fraction of comparisons where a datum from the first array is greater than one from the second, after all possible pair-wise comparisons across the two arrays have been made. It may be noted that since the statistic for this test is a 'relative' one, the problem of 'outliers' disproportionately influencing the results does not arise here at all.

One problem that often arises while analysing dyadic interactions within a social matrix is that of potential non-independence of data. In the above case, for example, it may be argued that different interacting dyads that include one common individual may not truly represent independent data points. In order to account for the possible non-independence of such data while performing the Pairs Test, a random permutation procedure was employed to generate a distribution which could then be used to assign P values to the observed test statistic. For this, the two data arrays are pooled together and a random set of values (equal to the number of entries in each array) are selected from the pooled data to generate two randomized arrays (corresponding to the two distributions being compared), and the test statistic again computed as described above. A large number of such permutations (10,000 for each analysis in this article) was performed to generate a random distribution of the test statistic for each test, and the location of the observed test statistic within this distribution noted to determine its P value.

In the Matched Pairs Test, the data series (for the two behaviours under comparison) are again arranged in one-dimensional arrays, as was done for the Pairs Test, the difference being that the test statistic is the fraction of comparisons in which one value drawn from one array is greater than its corresponding matched pair in the other. Thus, only matched pairs of data are compared across the two arrays while evaluating this statistic. For example, the Matched Pairs Test could be used to test whether, during dyadic interactions, subordinate individuals initiate as much allogrooming towards their dominant counterparts under conditions of provisioning as they do when they are naturally foraging. The null hypothesis here is that there is no difference in the frequencies of allogrooming initiated under the two conditions. In the Matched Pairs Test, designed to test for the alternative hypothesis, the frequencies of allogrooming initiated by the subordinate individuals of all interacting dyads under conditions of provisioning constitute one data array, while those initiated by the same individuals within the same dyads under conditions of natural foraging form the other corresponding array. The test statistic is the fraction of cases where the datum in the first array is greater than its corresponding paired datum in the other; unlike the Pairs Test where all possible paired comparisons are made, only matched pairs are considered in this test.

In the case of the Matched Pairs Test too, a random permutation procedure was employed to generate a distribution of the test statistic in order to assign P values to the observed test statistic. In contrast to the Pairs Test, however, only one of the arrays (constituting one distribution) is permuted randomly and only matched pair comparisons carried out to yield the simulated test statistic. Again, 10,000 such simulations were carried out for each test to determine the P value of the observed test statistic. It may be noted that the Pairs Test and the Matched Pairs Test could, in a sense, be considered variants of the conventional non-parametric Mann-Whitney U-test and the Wilcoxon signed-ranks test respectively.

Tests of correlation between interaction matrices have been used to analyse reciprocity and interchange of behaviours between individuals at the group level instead of at the dyadic level. Here again the data are not independent since the same individual recurs leading to cross-matrix dependence of the rows and columns involving that individual. This feature of these matrices precludes the usage of conventional procedures like Pearson's or Kendall's rank correlation which assumes the independence of data. Distribution-free tests for association between matrices^{22,24-26}, which take into account the non-independence of data, therefore, need to be employed.

In this article, more specifically, the Kr -test, developed by Hemelrijk²², has been used to examine the inter-individual variability in behavioural patterns which might exist at the group level. In this test essentially involving the correlation between two social interaction matrices (say, for example, under conditions of natural foraging with that under conditions of provisioning), all pairs of corresponding cells along the rows of the matrices, but not along the columns, are compared. To put it verbally, the Kr -statistic is the sum of the number of pairs of cells in these matrices in which the values change in the same direction (or are 'correlated') minus the number of pairs of cells in which the values increase in one matrix and decrease in the other (values 'uncorrelated'). Since the test can obviously compare between any number of cells and since the calculation of the test statistic involves only addition and subtraction, Kr can take any positive or negative integral value; these indicate a positive or negative correlation between the two matrices respectively. For a detailed mathematical treatment of the test and a computed example, see Hemelrijk²². The Kr -statistic, being a 'relative' one, does not take into consideration the 'absolute' values of the matrix entries, and is again, therefore, not plagued by the problem of 'outliers'.

The significance of the Kr -statistic has been calculated by a special random permutation procedure: the quadratic assignment method^{25,26}. One of the matrices is permuted at random by placing the individuals in all possible orders, while the other matrix is kept unchanged. The order of the individuals in the rows is, however, kept identical to that in the columns in order to preserve the diagonal.

The Kr value is then calculated for each such permutation. A sufficiently large number of permutations (10,000 permutations in each analysis) generated a distribution of Kr values which then allowed for a comparison with the observed Kr value, and, hence, a calculation of the P value in each case. This random permutation procedure once again takes into account the potentially non-independent nature of the data set.

Results

Natural foraging and provisioned feeding

The study group regularly moved between two kinds of habitats 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 scavenged on remains left behind by the visitors. Although social interactions of all kinds regularly occurred in both these areas, the ones displayed in the former area have been considered in this analysis to be associated with natural foraging and those in the latter area with scavenging by the study group when provisioned with typically human food.

The adult females of the troop spent relatively longer periods of time in the foraging area during the observation period (91.5 h) than in the area where they scavenged (47.7 h), because they invariably rested during periods of inactivity in the former area and also because tourists were usually present in the provisioning area only during evenings. In spite of the less time spent in the scavenging area, however, the females exhibited a

much higher frequency of scavenging (mean \pm SE of 13.23 ± 0.90 acts/h) here than that of foraging (3.73 ± 0.51 acts/h; Wilcoxon's signed-ranks test, $T = 4$, $n = 9$ individuals, $P < 0.03$) in the foraging area. Interestingly, there did not appear to be any significant correlation in the frequency of either foraging or scavenging with the ranks of the adult females in the dominance hierarchy (Figure 1).

Feeding competition on provisioning

There was a marked increase in social tension in the study group during periods of scavenging; this was usually manifested as enhanced aggression among the adult females of the troop. Thus, the overall rates of total aggression and its two components – non-contact aggression and contact aggression – as well as aggressive approach and feeding supplant increased significantly during this period from those exhibited during natural foraging (Figure 2; Matched Pairs Test, $n = 36$ dyads; total aggression: $P < 0.0001$, non-contact aggression: $P < 0.0004$, contact aggression: $P < 0.0007$, aggressive approach: $P < 0.008$, feeding supplant: $P < 0.0001$). But did all females in the group become increasingly aggressive when they scavenged competitively? A close examination of the agonistic interactions between the females revealed a marked dependence of aggression on the dominance ranks of both the individuals involved. There was thus a sharp increase in total aggression (natural foraging: mean \pm SE of 0.129 ± 0.048 acts/h, provisioning: 0.349 ± 0.154 acts/h; Matched Pairs Test, $n = 10$ dyads, $P < 0.025$), consisting of both non-contact aggression (natural foraging: 0.086 ± 0.032 acts/h, provisioning: 0.246 ± 0.119 acts/h; $P < 0.05$) and contact aggression

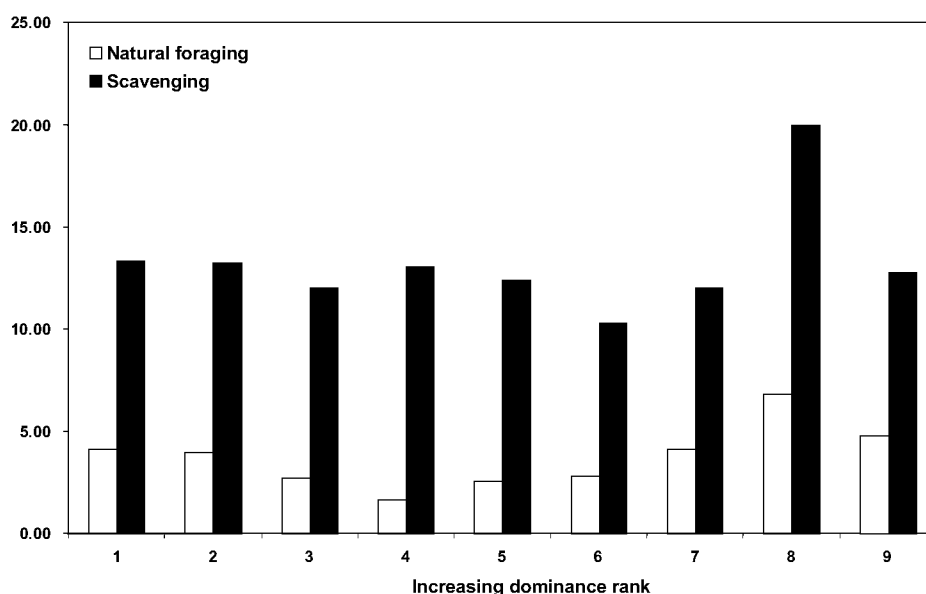


Figure 1. Frequency of foraging and scavenging by adult females of different dominance ranks during natural foraging and on being provisioned.

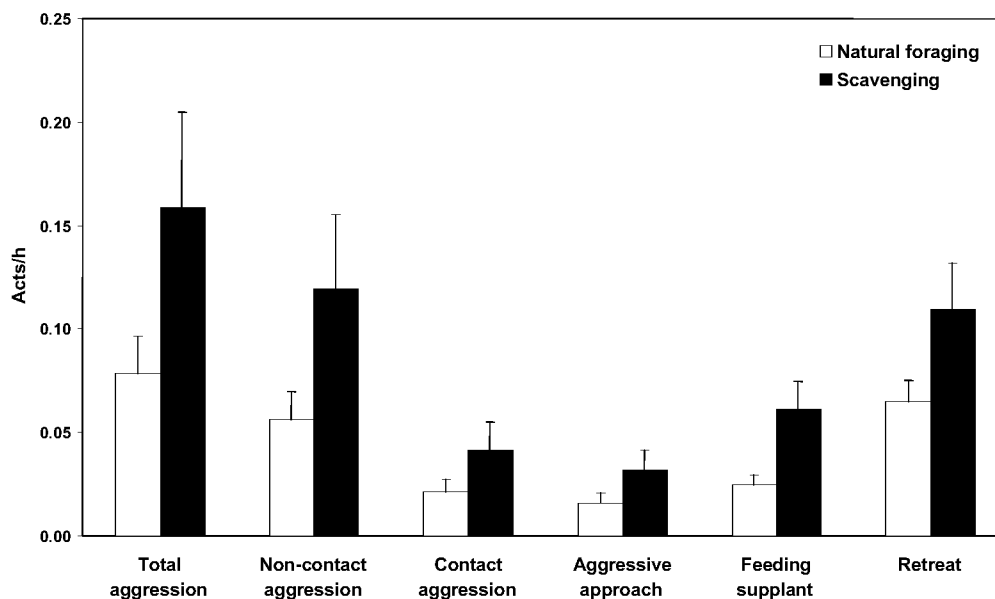


Figure 2. Aggression, aggressive approach, feeding supplant and retreat among adult females during natural foraging and scavenging. Bars represent mean frequency of behaviour under the two conditions, while error bars indicate standard error of the mean.

(natural foraging: 0.044 ± 0.019 acts/h, provisioning: 0.103 ± 0.044 acts/h; $P < 0.04$), directed specifically by individual females in the upper part of the dominance hierarchy (dominance ranks from 9 to 5) towards each other. Females in the lower part of the hierarchy (dominance ranks from 5 to 1), in contrast, did not significantly increase the level of any form of aggression under these conditions.

When dyadic patterns of aggression directed by dominant individuals towards their subordinate counterparts were analysed separately, periods of scavenging were marked by a significant increase in total aggression (Table 1; Matched Pairs Test, $n = 36$ dyads, $P < 0.002$), non-contact aggression ($P < 0.03$), contact aggression ($P < 0.006$), aggressive approach ($P < 0.03$) as well as feeding supplant ($P < 0.009$). Even in dyadic interactions during scavenging, some forms of aggression were selectively displayed by females towards those closest in the dominance hierarchy. Females in the upper part of the dominance hierarchy (dominance ranks from 9 to 5) thus exhibited more contact aggression, possibly the most effective form of aggression during food competition, towards subordinates within this part of the hierarchy (mean \pm SE of 0.207 ± 0.077 acts/h) than they did towards those in the lower section of the hierarchy (dominance ranks from 4 to 1; 0.035 ± 0.009 acts/h; Pairs Test, two-tailed; $n = 10$, 20 dyads; $P < 0.025$). This is also supported by the positive correlation between the frequency of contact aggression shown by individual females and the absolute rank of the subordinate females who receive such aggression, but only during scavenging

(Figure 3, $Kr = 20$, $n = 9$ individuals, $P < 0.04$; natural foraging: $Kr = 28$, $P > 0.05$).

Adult bonnet macaque females typically do not exhibit aggression towards those higher than them in the dominance hierarchy (Sinha, A., unpublished data). During scavenging, however, when there is an evident rise in overall aggression within the troop, do individuals now direct aggression towards their dominant adversaries? Indeed, females in the study troop did display significantly enhanced total aggression (Table 1; Matched Pairs Test, $n = 36$ dyads, $P < 0.006$) and non-contact aggression ($P < 0.002$) towards their dominant counterparts in dyadic interactions when they were scavenging on human food. Remarkably, no acts of contact aggression were ever observed under these conditions.

Moreover, when analyses of reciprocity or exchange of aggressive behaviours between dominant and subordinate individuals were carried out, total aggression directed towards subordinates was observed to be negatively correlated with the total aggression that dominant individuals received under conditions of natural foraging ($Kr = -13$, $n = 9$ individuals, $P < 0.05$). In other words, aggression was primarily directed by dominant individuals towards those subordinates from whom retaliation was least likely. The situation was, however, strikingly reversed during scavenging when total aggression shown was positively correlated with that received ($Kr = 17$, $P < 0.002$)—subordinate individuals were now likely to retaliate against the aggression that they received. Notably, of the two forms of aggression, non-contact aggression alone was significantly exchanged under these

Table 1. Frequency of dyadic behavioural acts (mean number of acts per hour \pm SE) displayed by dominant and subordinate individuals under conditions of natural foraging and scavenging

Behaviour	Natural foraging		Scavenging	
	Dominant to subordinate	Subordinate to dominant	Dominant to subordinate	Subordinate to dominant
Total aggression (116; 124*)	0.140 \pm 0.032	0.017 \pm 0.009	0.281 \pm 0.086	0.035 \pm 0.018
Non-contact aggression (84; 93)	0.096 \pm 0.024	0.016 \pm 0.009	0.204 \pm 0.067	0.035 \pm 0.018
Contact aggression (32; 31)	0.041 \pm 0.011	0.001 \pm 0.001	0.083 \pm 0.025	0
Aggressive approach (24; 24)	0.030 \pm 0.008	0.003 \pm 0.002	0.060 \pm 0.018	0.002 \pm 0.002
Feeding-supplant (35; 48)	0.047 \pm 0.009	0.001 \pm 0.001	0.117 \pm 0.023	0.005 \pm 0.004
Retreat (96; 85)	0.008 \pm 0.004	0.122 \pm 0.014	0.010 \pm 0.005	0.208 \pm 0.038
Allogrooming (610; 100)	0.322 \pm 0.049	0.478 \pm 0.076	0.093 \pm 0.029	0.170 \pm 0.038
Affiliation (1073; 255)	0.745 \pm 0.111	0.671 \pm 0.087	0.419 \pm 0.144	0.264 \pm 0.064

*The two numbers in brackets represent the total number of acts displayed by all individuals during periods of natural foraging and scavenging respectively.

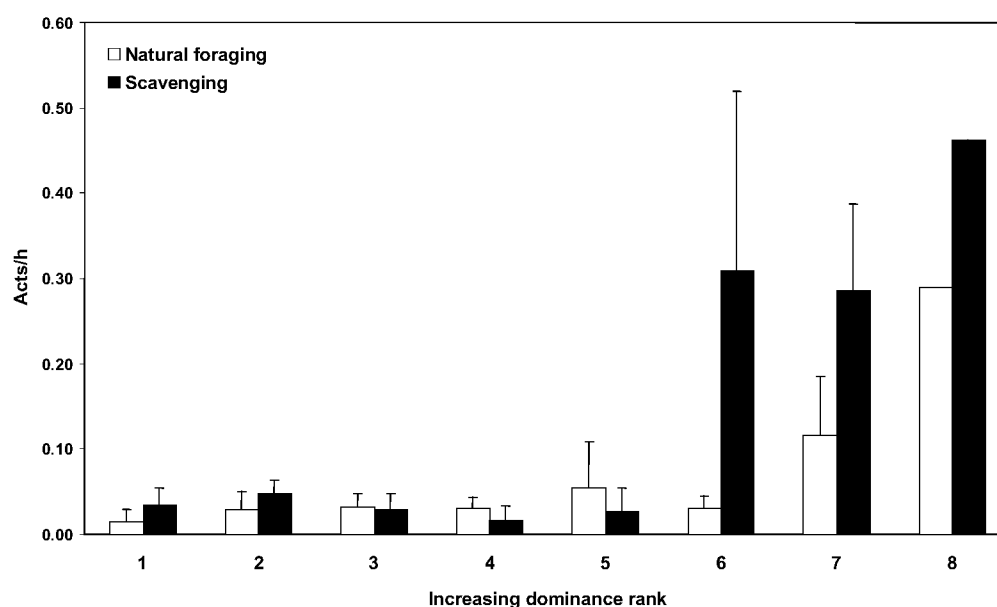


Figure 3. Contact aggression directed by dominant females towards subordinate females of increasing dominance rank during natural foraging and scavenging. Bars represent the mean frequency of behaviour under the two conditions, while error bars indicate standard error of the mean. Note that the female with dominance rank 8 received aggression from only a single female above her in the hierarchy.

conditions ($Kr = 13$, $P < 0.02$; natural foraging: $Kr = -6$, $P > 0.80$); the costly acts of contact aggression continued to be unidirectional.

A point to note here is that since a large number of simultaneous comparisons were performed during the above analyses, the Bonferroni correction could have been applied to these tests. But, since the focus of this article has been on the elucidation of some basic patterns that characterize the behavioural interactions of a small group of individuals and given the controversy surrounding its application, the correction was not employed. It will, however, be more appropriate to apply the Bonferroni correction or other standard corrections when more rigorous analysis is subsequently carried out.

Changes in affiliative interactions

There was a significant decrease in the frequency of allogrooming and affiliation across all dyadic interactions as the females moved to the provisioning site from areas of natural foraging (Figure 4; Matched Pairs Test, two-tailed; $n = 36$ dyads; allogrooming: $P < 0.02$; affiliation: $P < 0.003$). A closer examination of these patterns revealed that individual females significantly decreased the display of both allogrooming and affiliation towards their subordinate counterparts during periods of scavenging (Table 1; Matched Pairs Test, two-tailed; $n = 36$ dyads; allogrooming: $P < 0.003$; affiliation: $P < 0.001$). The latter, however, did not reduce the display of either of

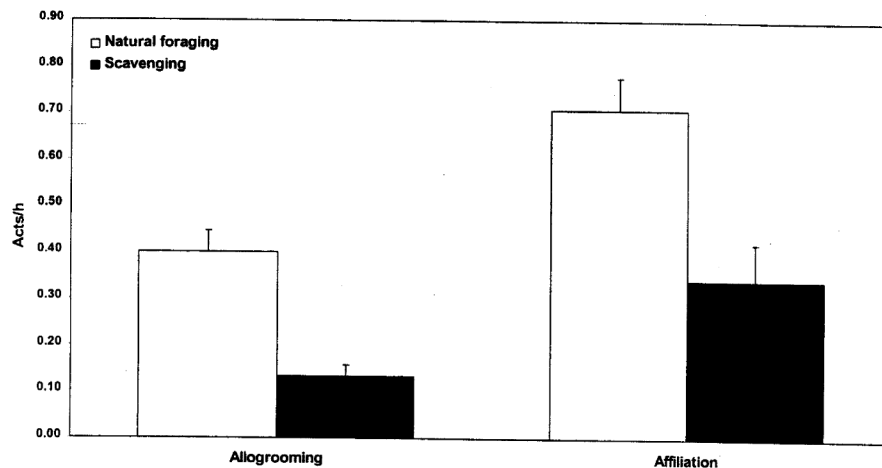


Figure 4. Allogrooming and affiliation among adult females during natural foraging and scavenging. Bars represent mean frequency of behaviour under the two conditions, while error bars indicate standard error of the mean.

these affiliative behaviours towards their dominant partners and their levels remained comparable across the two ecological situations (allogrooming: $P > 0.30$; affiliation: $P > 0.15$).

It was also possible to examine whether allogrooming and other affiliative behaviours were reciprocated or exchanged by individual females under these situations. It is noteworthy that while only affiliation, but not allogrooming, was reciprocally exchanged between the adult females of the study troop during foraging (allogrooming: $Kr = 44$, $n = 9$ individuals, $P > 0.05$; affiliation: $Kr = 99$, $P < 0.0002$), both were reciprocated during scavenging (allogrooming: $Kr = 41$, $P < 0.04$; affiliation: $Kr = 74$, $P < 0.009$). When the behavioural strategies of females were examined in relation to their relative dominance ranks, however, only subordinate females reciprocated all affiliative behaviour that they received from their dominant counterparts under both ecological regimes (natural foraging – allogrooming: $Kr = 31$, $n = 9$ individuals, $P < 0.009$; affiliation: $Kr = 36$, $P < 0.002$; scavenging – allogrooming: $Kr = 20$, $P < 0.03$; affiliation: $Kr = 25$, $P < 0.02$). Dominant females, in contrast, only reciprocated affiliation (natural foraging: $Kr = 25$, $P < 0.03$; scavenging: $Kr = 23$, $P < 0.02$), but not allogrooming (natural foraging: $Kr = -9$, $P > 0.75$; scavenging: $Kr = 13$, $P > 0.06$), under these conditions.

Behavioural strategies to reduce social tension

There appeared to be a marked tendency for the adult females in the study troop to avoid each other as they moved from a regime of natural foraging to that in which they scavenged aggressively for provisioned food. This was evident from the sharp increase in the frequency of retreat displayed by these individuals during dyadic in-

teractions while scavenging (Figure 1; Matched Pairs Test, $n = 36$ dyads, $P < 0.0004$). There was also a significant positive correlation between the group-level frequency of retreat shown by individuals from their dominant adversaries and the absolute dominance rank of the retreating individuals ($Kr = 23$, $n = 9$ individuals, $P < 0.04$) – higher-ranked individuals thus tended to retreat more under conditions of scavenging. No such pattern was evident, however, during natural foraging ($Kr = -11$, $P > 0.79$). Interestingly, there was no correlation between the frequency of aggressive approach made by individual females towards their subordinates and the dominance ranks of the latter during periods of scavenging ($Kr = 13$, $P > 0.11$) – high-ranked individuals may not have thus necessarily retreated in response to the aggressive approaches that they received.

Amongst the affiliative behaviours, allogrooming was clearly exchanged between females in the group as a general strategy only under conditions of scavenging, as noted above. In addition, when individual strategies were examined during direct dyadic interactions, subordinate females exhibited relatively more allogrooming towards their dominant partners, than did the latter towards the former, during scavenging (Table 1; Pairs Test, two-tailed; $n = 36$ dyads; $P < 0.02$); grooming was much more comparable within dyads during natural foraging ($P > 0.10$). Levels of affiliation displayed by the dominant and subordinate partners were, however, comparable across all dyads under both conditions (Table 1; natural foraging: $P > 0.44$; scavenging: $P > 0.20$).

Finally, when the exchange of different behavioural acts between the females in the group was analysed, individuals were observed to display significantly more allogrooming and affiliation towards those dominant adversaries who exhibited relatively higher levels of non-contact and contact aggression towards them during

scavenging regimes (allogrooming – non-contact aggression: $Kr = 32$, $n = 9$ individuals, $P < 0.003$; allogrooming – contact aggression: $Kr = 19$, $P < 0.04$; affiliation – non-contact aggression: $Kr = 25$, $P < 0.02$; affiliation – contact aggression: $Kr = 27$, $P < 0.008$). Such behavioural interchange was, however, strikingly absent during social interactions associated with natural foraging (allogrooming – non-contact aggression: $Kr = 4$, $P > 0.35$; allogrooming – contact aggression: $Kr = 2$, $P > 0.41$; affiliation – non-contact aggression: $Kr = 6$, $P > 0.30$; affiliation – contact aggression: $Kr = 10$, $P > 0.17$). It is also noteworthy that subordinate females exhibited increased allogrooming, but not affiliation, towards those dominant individuals from whom they had received high levels of aggressive approach during scavenging (allogrooming – aggressive approach: $Kr = 18$, $P < 0.05$; affiliation – aggressive approach: $Kr = 8$, $P > 0.21$). These examples of behavioural exchange clearly seem to suggest a strategic role for certain kinds of affiliative behaviour, particularly allogrooming, in reducing social tensions that prevail during periods of scavenging. More direct evidence for a temporally phased cause–effect relationship between such behavioural acts and their counter-strategies must, however, await further detailed observations and analyses.

Discussion

Changes in social structure in response to ecological parameters have often been observed in different animal societies²⁷. Although most of these species usually have an evolutionarily selected basic pattern of social organization, 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.

Provisioning of wild primate groups usually leads 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 naturally foraging and provisioned groups have been investigated¹⁶, observations on the nature of changing social relationships within such groups have remained surprisingly neglected. Such studies are, however, essential for a basic understanding of the behavioural strategies that individuals display 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.

The free-ranging group of bonnet macaques investigated here, regularly alternated between bouts of natural foraging and visits to a site where they were provisioned with human food. Although the adult females of this

group 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 they obtained food from 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 exhibited at this site relative to that during bouts of foraging on their natural food during the greater part of the day.

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 aggression, aggressive approaches and feeding supplants during these periods over that during natural foraging. Bonnet macaques are generalist feeders^{28,29} and usually space themselves out as they forage on widely dispersed, abundant leaves, flowers and fruits of several commonly available plant species. Opportunities for monopolization of food are, therefore, rare during natural foraging and strong competition may not occur under these circumstances.

The provisioned food, in contrast, was markedly clumped in distribution, not only in time, as noted above, but also in space – within a small area habituated by large numbers of tourists. Although concentrated within this particular area, the most important feature of such food, nevertheless, was its exact spatial unpredictability; individual macaques could not predict where food items would precisely be thrown. This, coupled with the wide, and again unpredictable, range of size and nutritional value of particular food items, did not allow such provisioned food to be easily monopolized. Thus, access to both the tourists and the food items themselves, appeared to be largely indefensible under these conditions; limited contest competition could, however, occur once an individual was able to gain access to a particular item. The exact extent to which the elevated levels of feeding competition, observed during scavenging regimes, depend on the temporal and spatial availability, size and nutritional quality of the food provided, nevertheless, needs to be investigated further.

Potentially expensive acts of aggression over provisioned food appeared to be demonstrated more by high-ranked females, who could obviously afford such encounters, and were preferentially directed towards high-ranked subordinates who, by virtue of their position in the hierarchy, would be the most threatening adversaries during such feeding competition. Thus, challenges during contest competition would most likely come not only from individuals of higher rank, but from those most closely ranked in the dominance hierarchy as well.

Another mechanism that may yield a similar pattern of interactions is that low-ranking, subordinate females may avoid costly conflicts by physically occupying positions away from high-ranking individuals, thus giving rise to specific group spatial structures during feeding competi-

tion¹⁴. The spatial unpredictability of the provisioned food, discussed above, however, led to a situation when all the adult females in the group scavenged together, in close proximity, and no distinct group spatial organization could be discerned. Moreover, females across the rank hierarchy enjoyed comparable scavenging success when provisioned, in contrast to what has earlier been observed in female Japanese macaques³⁰ and olive baboons¹⁴. Finally, the hypothesis that aggression may be preferentially directed towards certain individuals during enhanced feeding competition and may not simply be an emergent property of individual positional choices comes from the observation that, when provisioned, subordinate females displayed enhanced aggression towards their dominant adversaries and significantly reciprocated the aggression that they received.

Feeding competition during provisioning was marked by a significant increase in contact aggression directed by high-ranked females towards each other. Although potentially very costly, contact aggression becomes necessary when individuals physically compete for choice food items. The intensity of competition over provisioned food was manifest also in the appearance of agonistic acts directed by subordinate females towards their dominant counterparts – a feature rather unusual for adult female bonnet macaques in most troops. Such females, however, could obviously not afford costly aggressive encounters; enhanced aggression up the dominance hierarchy, therefore, principally consisted of non-contact aggressive acts.

It has been suggested that stable linear hierarchies in female primates are a result of conflict competition for food^{10,31–34}. Interestingly, however, the dominance hierarchy in this particular troop of bonnet macaques became comparatively unstable under conditions of provisioning. While, during natural foraging, there existed a significant negative correlation between aggression received by individual females from their dominant adversaries and the aggression that they showed towards them, this completely changed when the same individuals were provisioned. Subordinate females now reciprocated the aggression that they received – a striking change of behavioural strategy.

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. Although, overall, there were no significant differences in feeding rates across the dominance hierarchy, there could be other behavioural measures reflecting the advantage of being a high-ranked female, which have not been considered in this study. These could include, amongst others, differences in total feeding time, daily food intake or even dietary diversity^{15,35} – such parameters need to be investigated further.

A considerable decrease in the display of allogrooming and other affiliative behaviour marked the movement of

the troop from a regime of natural foraging to that of provisioning. Individuals were able to opportunistically spend only short periods of time at the provisioning site and even this was marked by high rates of scavenging as well as intense conflict over food. Individuals could now perhaps devote little time to such energy- and time-intensive interactions as allogrooming. This seems particularly true of high-ranking individuals who significantly decreased the display of all affiliative behaviours towards their subordinate counterparts when they were provisioned.

An alternative hypothesis for the observed patterns of affiliative interactions could again 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 is, however, belied by the observation that, during dyadic interactions, subordinate females did not significantly decrease allogrooming and the display of other affiliative behaviour, while at the group level, they reciprocated all affiliative behaviour that they received from their dominant partners at frequencies comparable to those during natural foraging.

The adult females in the study group appeared to exhibit two distinctive kinds of behavioural strategies, apparently to reduce social tension brought about by enhanced feeding competition. First, individuals of high-dominance rank actively avoided interacting with more dominant females, retreating from them at much higher rates than they did under the less-stressful conditions of natural foraging. Avoidance of this kind may be the only strategy that can be utilized 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 interacting with each other.

The second kind of behavioural strategy 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 Waal³⁶ who emphasised that primates, being highly adaptable, would, when confronted with a stressful situation, modify their behaviour to reduce the risk of aggression. Thus, when the Mudumalai troop was provisioned, subordinate females not only displayed more allogrooming towards dominant individuals than they received from them, but they also exhibited significantly more grooming and affiliation towards those adversaries from whom they received relatively higher levels of aggression. Finally, the energy-intensive activity of allogrooming was significantly reciprocated during provisioning; grooming was only asymmetrically exchanged during natural foraging.

How successful were these behavioural strategies in actually reducing social tension? The fact that there continued to be high levels of aggression during provisioning suggests that these strategies may not have had enough power to completely reduce the adverse effects of feeding competition on intra-group social relationships. Individuals may nevertheless be capable of exhibiting conditional social strategies that reduce the risk they face from their more powerful adversaries. The question of whether the ability to adopt altered strategies is genetically determined or is based on individual-specific cognitive abilities clearly demands attention.

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