Ecology proposes, behaviour disposes: Ecological variability in social organization and male behavioural strategies among wild bonnet macaques*

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The structure and evolution of primate societies are generally shaped by ecological and social forces of natural selection. The habitat and feeding ecology of primate populations, in particular, largely determine the size of the existing social groups and the pattern of interactions between individuals within and across such groups. The bonnet macaque (*Macaca radiata*), an Old World monkey endemic to peninsular India, usually lives in seasonal tropical deciduous forests and occurs in typically large multimale multifemale associations. This species, however, appears to have evolved, in recent years, a fairly high proportion of small, but reasonably stable, unimale troops within one particular population in the Bandipur–Mudumalai wildlife sanctuaries of southern India. Demographic analyses indicate that, as compared to multimale troops, unimale groups are relatively depleted in subadult and juvenile males, exhibit a unique female-biased birth sex ratio and display extensive female dispersal, all of which may have arisen in response to reproductive monopolization by the solitary resident male. Several ecological factors, including food provisioning, may have led to the evolution of this social organization, unique for a seasonally breeding cercopithecine primate. Provisioning of primate groups also leads to a significant increase in intra-troop 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 males were also analysed for one particular troop of bonnet macaques in the Mudumalai Wildlife Sanctuary under two ecological situations – as they foraged on their natural diet and when they gathered provisioned food from tourists visiting the sanctuary. Although feeding competition increased markedly as these individuals alternated between natural foraging and competing for provisioned food, individual macaques were able to adopt appropriate social strategies under such rapidly changing ecological regimes. These studies demonstrate the behavioural and social plasticity of a primate species and the value of demographic studies of multiple groups and populations in different ecological environments.

Keywords: Bonnet macaque, *Macaca radiata*, ecology, demography, social organization, social behaviour.

THE ultimate evolution of social organizations is believed to be usually driven by two kinds of selective forces – natural selection, primarily involving ecological factors, and sexual selection, involving the mating strategies of the individuals constituting that society[1–3]. At the proximate level, however, a social organization emerges from the interactions of its individuals, each of which is selected to maximize its own chances of reproduction and that of its genetic relatives; this together leads to an increase in what has been termed the inclusive fitness of the individual[4].

In non-human primates, ecological and social pressures have together been invoked to explain not only the formation of societies, but also the size of social groups and the pattern of interactions between individuals within and across such groups[5,6]. The actual nature of the relationship between these selective forces in social evolution has, however, often been visualized rather differently. One school[7–11], which gives primary importance to mating strategies as selective agents, thus suggests that social relationships evolve, mainly by sexual selection, within group struc-

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*This paper is dedicated with admiration and gratitude to Dr Roddam Narasimha.

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tures that form and disperse under the influence of certain ecological pressures, particularly feeding competition. A second school, on the other hand, considers ecological factors to be most crucial in determining the spatial distribution and social relationships of females, and then explains the evolution of social structure as emerging from the interactions between female distribution and male mating strategies[3,12–14]. The rationale for such an approach is that, given the levels of female involvement and investment in primate reproduction and the usual lack of paternal investment therein, it is female social relationships and behaviour that are most likely to be determined by ecological factors since female fitness would tend to be limited by environmental pressures; male mating strategies and social behaviour could be subsequently influenced by patterns of female distribution and associations.

Although these schools of thought appear to have different conceptual foundations, they are not mutually exclusive and it is likely that many primate populations may exhibit social dynamics characteristic of both[15]. Most of these hypothesized evolutionary pathways are theoretically elegant and have been used *a posteriori* to explain the remarkable variation in social systems exhibited by many extant primate groups. In contrast, the actual evolution of new stable groups, with unique individual social strategies, driven by changing ecological and social conditions within an existing population, has only very rarely been observed. Long-term studies of natural primate populations that can potentially reveal processes of social evolution are, however, essential if a direct understanding of the selective forces driving such evolution is to be achieved.

The bonnet macaque (*Macaca radiata*, Geoffroy), a cercopithecine primate endemic to but widely distributed in peninsular India, appears to be unusual in exhibiting remarkable social flexibility and a wide variety of behavioural strategies, all of which enable it to adapt successfully to very different ecological habitats[16]. This paper first describes the demographic structure of a particular population of the species and investigates the ecological and social factors that may be driving social evolution within this population, even today. It then examines the behavioural strategies of individual males of one particular troop within this population under different ecological regimes that vary even over the short-term. Taken together, these analyses document the social lability and individual behavioural variability of a species that is able to evolve novel social structures and strategies that promote more effective survival and reproduction under periodically changing, but challenging, ecological situations.

Bonnet macaques: Ecology, demography and behaviour

The most common of the five primate species found in southern India[17] and sometimes referred to as 'the common performing monkey of southern India'[18], bonnet macaques are remarkable for primarily two reasons – first, their inordinate ability to successfully adapt to almost any kind of environment and second, the intense love–hate relationship that they enjoy with the people of southern India[19,20]!

Ecology

A striking feature of bonnet macaques, commented on by various authors, is their inherent tendency to gravitate towards human habitations and the associated habit of becoming relatively more terrestrial rather than remaining truly arboreal[16,17,20,21]. In classical literature, the description of a monkey – most likely a bonnet macaque – 'in the town's commons' in a Tamil poem written about 2000 years ago[16] seems most remarkable! In fact, significant populations of completely wild bonnet macaques in interior forests have rarely been reported. This tendency to move has often naturally led to serious conflict between the monkeys and the people whose crops and homes they raid; such situations continue to remain problematic even today.

The bonnet macaque thus occupies two major ecological niches: a variety of forests and areas of human cultivation and habitation. The different forest types inhabited by this species include the montane evergreen rainforests of the Nilgiri hills (sometimes even up to an altitude of about 2100 m[22]), low-lying semi-evergreen forests of coastal Kerala, moist and dry deciduous forests of Karnataka and Tamil Nadu, bamboo forests, and the arid scrub jungles so typical of the central areas of the Deccan plateau. This species is, nevertheless, much more common in areas of human habitation – whether they be villages bordering agricultural fields and plantations, small towns (where they are most likely to be encountered at temples or railway and bus stations) or even large cities like Chennai and Bangalore[18,19,22].

One of the principal reasons that have made the bonnet macaque ubiquitous in southern India is the wide diversity of food resources that it can successfully use. They are known to feed on vegetative, floral and fruit buds, leaves, petioles, stems, pith, tendrils, roots, flowers, fruits, seeds and even leaf-galls of different herbs, climbers, shrubs, trees and grasses[20–24]. Remarkably, a total of about 86 plant species has been recorded as food for this primate in a dry deciduous forest[23] and about 39 in a tropical evergreen forest[24].

Bonnet monkeys are omnivores and have also been observed feeding on insects including crickets, cicadas, grasshoppers, termites and insect pupae, and on spiders and bird eggs[23,25]. Fruits, however, usually form the most important component of the diet, followed by foliage and invertebrates[20,23,24].

Demography and behaviour

The bonnet macaque usually lives in large multimale multifemale troops of 8 to 60 individuals[16,26]. Although highly variable, group sizes tend to be much smaller in natural forests and significantly larger in or near human habitations; forest troops in the Bandipur–Mudumalai wildlife sanctuaries of southern India, where a long-term study on the behavioural ecology of the species is in progress, thus exhibit a mean (± SE) group size of 10.6 ± 1.2 individuals, while those inhabiting human settlements in areas adjoining these sanctuaries and around Mysore consist of 25.7 ± 3.7 individuals[16].

Female bonnet macaques, like many other cercopithecines, usually remain in their natal group throughout their lives, and during adulthood, form strong, linear, matrilineal dominance hierarchies with daughters occupying dominance ranks just below those of their mothers[16]. Females usually develop close affiliative relationships, with high levels of allogrooming exchanged between genetic relatives as well as between unrelated individuals across the dominance hierarchy[23,27,28].

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[16]. Adult bonnet macaque males, in contrast to females, form unstable dominance hierarchies through direct aggression and coalitions, tending to occupy low ranks when very young or old but relatively high positions when mature and in the prime of their health. Bonnet macaque males are also unique amongst cercopithecine species in demonstrating high levels of allogrooming and other affiliative behaviour towards each other, comparable in quality and levels to that shown by the females[23,29]. The absence of any correlation between individual dominance ranks and the levels of such affiliative behaviour displayed or received indicates that bonnet macaque males may, in general, adopt individual social strategies that are much less constrained by the rank hierarchy than is typical for males of most cercopithecine species living in multimale groups[29].

In terms of sexual behaviour, bonnet macaques are typically promiscuous with ample mating opportunities for both males and females. Adult males appear to follow different sexual strategies, with some males forming consortships of varying periods of time while others simply copulate opportunistically with the available females[16,21,22]. Whatever be the strategy, which varies across individuals and situations, only rarely do bonnet males interrupt the copulation of others or harass them in any way, even if they are subordinate males[16,21,22,30]. Subadult or juvenile males are also not denied access to oestrus females. Finally, although bonnet macaque females appear to be remarkably undiscriminating, mating freely with males of all ages and ranks[21,22], females often actively exercise mate choice by rather subtle manipulative strategies[16]. Bonnet macaque females also clearly prefer to sexually solicit new immigrant males over resident males, even if the latter are much more dominant[16].

The study troops

The present analysis is based on data acquired through demographic monitoring and behavioural observations on three populations of bonnet macaques, which have been studied for different periods of time over the last eleven years, beginning March 1993.

Population I primarily consists of 21 troops (Troops UM1 to UM11, MM12 to MM21) inhabiting the southeastern region of Bandipur National Park, Karnataka state, and a small adjoining section of the contiguous Mudumalai Wildlife Sanctuary, Tamil Nadu state, in southern India (11°57′–11°76′N, 76°55′–76°68′E). Although a range of tropical forest vegetation types – from moist deciduous forest through semi-evergreen forest to dry evergreen forest – occur within these sanctuaries, the study groups largely inhabited areas with predominantly dry and moist deciduous vegetation. The demographic structure of these troops, summarized over an observation period from March 2000 to February 2001, is shown in Table 1A.

A detailed study was specifically conducted on the behavioural ecology of a free-ranging, partially provisioned, troop in Population I – Troop MM19 – which ranged along the Moyar river near the Theppakadu Forest Office of the Mudumalai Wildlife Sanctuary (*c*. 11°58′N, 76°58′E). During the observation period from December 1996 to March 1997, this troop consisted of 34 individuals with 9 adult females, 6 adult males, as well as 3 subadults and 10 juveniles of both sexes. Six infants were born in the group during that particular period of study.

The socioecological analysis of male behavioural strategies is based on approximately 93.8 h of focal animal sampling on the six adult males of this troop with a mean observation time (± SE) of 15.6 (± 0.35) h on each individual. A description of the behaviours observed and the methodology adopted during this study has been described elsewhere[31].

Population II consists of two troops – Troops GK1 and GK2 – inhabiting 1 km^2 of dry deciduous scrubland and mixed forests in the GKVK campus of the University of Agricultural Sciences in Bangalore city (*c*. 12°98′N, 77°58′E), Karnataka state[32]. A long-term observational study was conducted on the behavioural ecology of these two partially provisioned troops, occupying adjacent overlapping home ranges, continuously during the period from March 1993 to September 1996. The demographic structure of these troops during the study period is shown in Table 1B.

Population III also comprises two troops – one multimale (Troop BG1) and the other unimale (Troop BG2) – inhabiting dry deciduous forests of the Bannerghata National Park near Bangalore city. Individual and social behaviour exhibited by these troops were studied for a period of about eight months during April to November 2000; their demographic structure during this period is shown in Table 1B. The observational methodology fol-

Table 1A. Demographic structure of the study populations of bonnet macaques: Population I

Troop	Troop size	Adults Mal	Adults Fem	Subadults Mal	Subadults Fem	Juveniles Mal	Juveniles Fem	Infants Mal	Infants Fem
Population I									
Unimale troops									
UM1	7	1	1	0	0	2	2	1	0
UM2	6	1	2	1	0	2	0	0	0
UM3	9	1	2	0	0	3	2	0	1
UM4	7	1	3	0	0	1	1	1	0
UM5	13	1	3	0	1	4	2	0	2
UM6	12	1	3	1	2	0	2	0	3
UM7	14	1	3	0	2	1	5	0	2
UM8	12	1	3	0	2	Nk	Nk	Nk	Nk
UM9	10	1	4	0	0	0	1	Nk	Nk
UM10	13	1	4	0	1	3	3	Nk	Nk
UM11	16	1	4	0	2	3	2	Nk	Nk
Multimale troops									
MM12	8	2	1	0	0	4	1	0	0
MM13	8	2	1	1	1	2	0	1	0
MM14	16	2	4	0	0	3	4	1	1
MM15	16	3	4	1	3	1	2	1	1
MM16	18	3	5	1	1	3	1	1	3
MM17	17	4	5	0	1	4	1	1	1
MM18	30	5	6	3	3	4	5	Nk	Nk
MM19	26	5	7	0	2	4	4	Nk	Nk
MM20	37	6	5	4	2	12	3	3	2
MM21	26	6	7	1	0	3	4	2	3

The figures represent the number of individuals in different age-sex categories within each troop during the observation period. Mal and Fem refer to males and females respectively, while Nk refers to unavailable data.

Table 1B. Demographic structure of the study populations of bonnet macaques: Populations II and III

Troop	Troop size	Adults Mal	Adults Fem	Subadults Mal	Subadults Fem	Juveniles Mal	Juveniles Fem	Infants Mal	Infants Fem
Population II									
GK1	44–52	8–11	10–11	0–3	0–2	7–10	5–8	0–5	0–4
GK2	30–35	5–7	9–11	0–1	0–2	4–6	6–8	0–4	0–5
Population III									
BG1	18–32	3–4	6	0–8	0	4	4	0–3	1–3
BG2	9–11	1	3	0–1	0	1	3	0	1–2

Each cell represents either an absolute value or a range of values over the respective observation period of each troop; the range has been provided since the troops were continuously monitored over this time. Mal and Fem refer to males and females respectively.

lowed for these troops and the behaviours analysed are exactly as described in an earlier study[31].

The natural diet of the study troops consisted mainly of fruits, flowers, or leaves of *Tamarindus indica*, *Azadirachta indica*, *Ficus benghalensis*, *Ficus retusa*, *Alphonsea sclerocarpa*, *Zizyphus oenoplia*, *Memecylon edule*, *Randia malabarica*, assorted herbs, as well as tender shoots of several grasses, including bamboo (*Bambusa arundinacea*), particularly in the riverine tracts of the Bandipur National Park and the Mudumalai Wildlife Sanctuary. Insects, including crickets and grasshoppers, also formed an important part of their diet. The troops comprising Populations II and III were partially provisioned owing to their home ranges being around human habitations and occasionally fed on human foods discarded by the local people. In addition, some of the troops of Population I occasionally fed on high-calorie human food handed out by tourists passing along the highway running through the sanctuaries. Such food, however, formed only a small fraction of the total dietary intake of these groups. It was also seasonal, unpredictable and directly proportional to the tourist inflow into the sanctuaries.

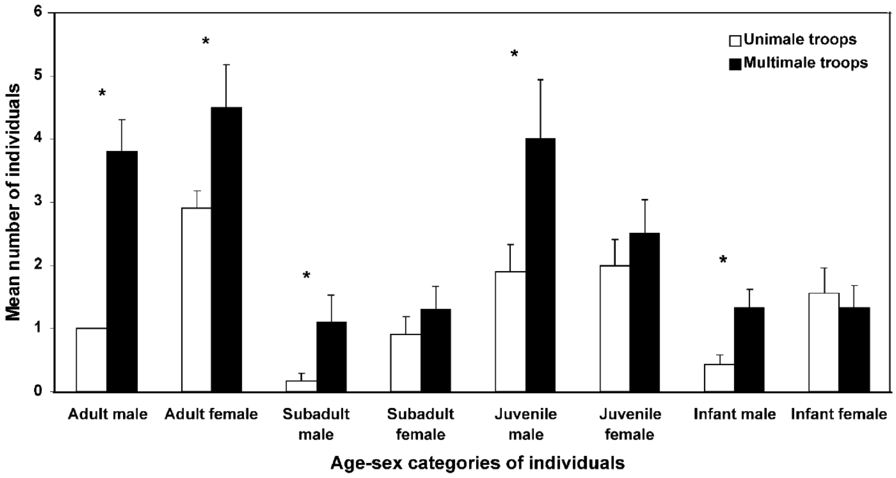

Figure 1. Mean number of individuals of different age-sex categories in unimale and multimale troops in Population I. The bars indicate standard errors of the mean, while the asterisks represent statistically significant differences in those categories.

Social organization in bonnet macaques

An enumeration of the 21 bonnet macaque troops in Population I (listed in Table 1A) revealed the presence of 11 unimale troops, which had a single adult male each during the observation period[32]. This was surprising because bonnet macaques have always been reported to reside in multimale groups, a feature common to most cercopithecine primates[6,18]. What is also noteworthy is that several earlier demographic studies of this species in this particular area have either not explicitly reported the occurrence of unimale troops[33,34], or have provided evidence of only a very small proportion of such groups in the population – 12.5 to 13.8%[22,26], as compared to 52.4% in Population I.

Demography of unimale and multimale troops

The unimale troops, with a mean (± SE) of 10.82 (± 0.98) individuals in each group, were significantly smaller than the multimale troops, each with a mean of 20.20 (± 2.97) individuals (Table 1A; Mann–Whitney U-test; $n = 11$ unimale, 10 multimale troops; $p < 0.02$), and had less number of adult females (Figure 1; $p < 0.05$). In contrast to earlier reports[21,35], the adult male/adult female ratio exhibited striking variation – ranging from 0.25 to 1.0 for the unimale groups and from 0.60 to 2.0 for the multimale troops (data from Table 1A).

In comparison to the multimale troops, the unimale groups were remarkably depleted in all categories of males, including subadults (Figure 1; Mann–Whitney U-test, one-tailed; $n = 11$ unimale, 10 multimale troops; $p < 0.05$), juveniles ($n = 10$, 10; $p < 0.05$) and infants ($n = 7$, 8; $p < 0.05$). There were, however, no significant differences in the number of female subadults (Figure 1; $p > 0.10$), juveniles ($p > 0.10$) and infants ($p > 0.10$) or in the total number of individuals in these categories (Table 1A; subadults: $n = 11$, 10; $p > 0.10$; juveniles: $n = 11$, 10; $p = 0.10$; infants: $n = 11$, 10; $p > 0.05$).

The significant bias toward female infants (1 : 4) displayed by the unimale bonnet macaque troops over that in multimale groups (1 : 1.1) in the Bandipur–Mudumalai population could result either from high rates of male infant mortality, due to infanticide or some other reason, or a genuine skew in birth sex ratios. Since the birth rate (as measured by the ratio of infants to adult females) of the unimale groups (mean ± SE of 0.61 ± 0.08) in this population appeared to be virtually identical to that of the multimale troops (0.60 ± 0.06), it seems unlikely that differential infant mortality could be responsible for the observed patterns.

It is then possible that the birth sex ratio within the unimale population is genuinely skewed in favour of female infants – perhaps the first example of a variation in social organization leading to variable birth sex ratios in any mammalian species. Although specific proximate mechanisms underlying skews in infant sex ratio either in captive bonnet macaques[36] or in other primates[37] remain unknown, female primates may themselves facultatively determine the sex of their infants in response to appropriate environmental or social stimuli[36]. Whatever be the underlying mechanism, however, the observed skew in infant sex ratio in the unimale bonnet macaque troops may have arisen in response to the reproductive monopolization practised by the resident adult male in these groups.

Individual and social behaviour in unimale and multimale troops

Bonnet macaques typically live in multimale troops where adult males are remarkably tolerant of the reproductive efforts and acts of other adult and subadult males[16,21,22]. In unimale troops, however, the resident male enjoys a complete reproductive monopolization of the troop females, and this appears to be related to a strong intolerance of other males, both within and outside the group. As prevails in most unimale harem systems[6], there are several behavioural manifestations of this intolerance, each of which appears to be unique to unimale troops – whether in Population I or the lone such troop in Population III – but virtually never encountered with in multimale social groups in any of the three study populations.

Display of severe aggression towards subadult and juvenile males: The solitary adult male in unimale troops exhibits very high levels of aggression towards subadult and juvenile males in the troop, while such aggression is usually much lower or less unidirectional within multimale troops.

This is exemplified by a comparison between the multimale troop BG1 and the unimale troop BG2 in Population III. In the latter troop, the resident adult male showed high levels of total aggression – consisting of both contact aggression and non-contact aggression – towards the sole juvenile male in his troop (total of 1.14 acts/h), while the alpha male of the multimale troop exhibited much lower levels of total aggression, and that too primarily non-contact aggression, towards the four juveniles in that troop (mean ± SE of 0.64 ± 0.05 acts/h). The absolute nature of dominance exercised by the solitary male in an unimale troop is also evident from the fact that the juvenile male in troop BG2 did not exhibit even a single act of either contact aggression or non-contact aggression towards the resident male, while the juveniles in troop BG1 displayed both kinds of aggression towards the alpha male at a fairly high combined frequency of 1.45 ± 0.25 acts/h.

Herding of females: The resident adult male in all unimale troops often herd group females; such herding usually intensifies in the presence of neighbouring troops, especially when extra-troop males approach the unimale group. Typical of certain other unimale primate social organizations[6], regular herding of this kind was never seen in multimale troops in any of the populations except during periodic consortships when certain dominant males intensely guard particular oestrous females one-on-one for varying periods of time, successfully preventing other intra-troop males any access to them[16].

A comparison again between the multimale troop BG1 and the unimale BG2 in Population III, for example, showed that the resident male in the latter troop exhibited aggressive approach towards the three troop females at a much higher frequency (mean ± SE of 0.96 ± 0.21 acts/h) than did the most dominant male of the multimale troop towards the six females in his troop (0.43 ± 0.11 acts/h; Mann–Whitney U-test, $p < 0.08$). The females in the unimale troop also retreated at higher frequencies from the resident male in the unimale troop (1.06 ± 0.23 acts/h) than did the females from the alpha male in the multimale troop (0.56 ± 0.14 acts/h; Mann–Whitney U-test, $p < 0.13$). Although not statistically significant perhaps due to small sample sizes, these differences in the behaviour of the adult males and females in these two kinds of social organizations are clearly indicative of the variability of behavioural strategies adopted by individuals when confronted with changed socioecological situations.

Involvement in active troop defense: The resident male of unimale troops invariably defends the troop during inter-troop encounters and physically interacts with the male(s) of the other troop, sometimes inflicting grievous injuries on them. In striking contrast, the most dominant (or the alpha) males in the dominance hierarchy of multimale troops never ever participate in inter-troop encounters, but, accompanied by the troop females, observe the interactions between the other group males and the challenging troop from a certain distance.

Thus, of the six physical interactions, involving at least one unimale troop, observed in Population I, the single male of the unimale troop attacked and inflicted an injury on a rival male on four occasions. Again, the resident male of the only unimale troop in Population III drew blood from an interacting male on one out of the four interactions that his troop had with the other (multimale) troop during the observation period; this was in spite of the fact that the unimale troop was chased away on all four occasions. Notably, the alpha male of the interacting multimale troop did not participate in any of these encounters – either in Population I or in Population III.

Prevention of male immigration: Adult males in unimale groups are rather successful in preventing immigration of other males into their troops since the cost that would ensue in terms of their potential future reproductive success is obviously higher than that to resident males in multimale troops with less-skewed adult sex ratios.

There was, thus, a complete absence of any immigration into seven unimale troops in Population I that were monitored during the mating season within the observation period while a total of 10 males had successfully joined six multimale troops during the same period (Mann–Whitney U-test, $p < 0.02$). There was also a strong positive correlation between the number of resident males in a troop and the number of immigrant males joining such a troop (Figure 2; Kendall's rank correlation, $n = 13$ troops, $p < 0.0001$). Resident males in large multimale troops may thus be indifferent to the entry of new males into the group because, with increase in troop size, such immigration would have progressively decreasing effect on the adult sex ratio (and hence, the per capita number of available females) in these troops.

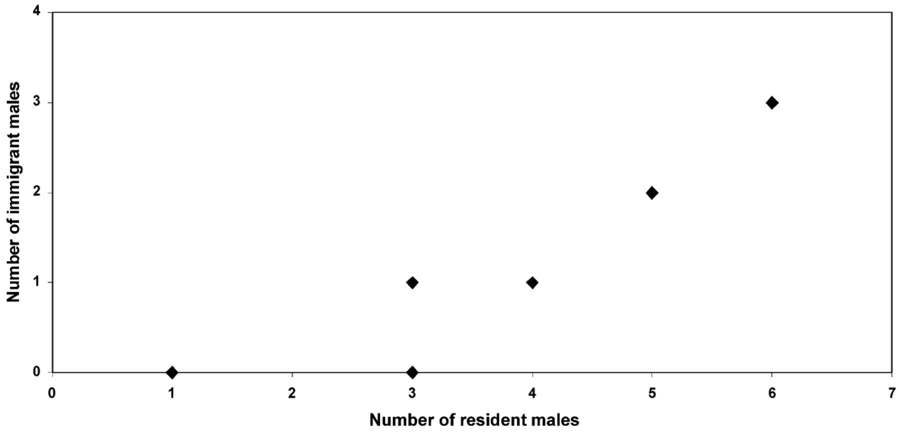

Figure 2. Male immigration in relation to resident males in unimale and multimale troops in Population I. Sample sizes for unimale and multimale troops are 7 and 6, respectively.

Such despotic behaviour of the resident male in unimale troops may, in turn, lead to increased male emigration from such groups and result in the characteristic depletion of subadult males in unimale troops. Since male emigration at a relatively young age could potentially entail heavy costs, females in unimale bonnet macaque troops may have been selected to bear and raise daughters, who would remain in the troop and contribute to the matriline, rather than sons, who would almost invariably be driven away. Notably, the skew in birth sex ratio within the unimale troops of Population I is unlikely to have contributed to the observed depletion of subadult males because the intermediate juvenile sex ratio in these groups appears to be restored to unity, possibly due to high rates of infant female mortality (Sinha, unpubl.; see also ref. 38).

What leads certain bonnet macaque males to solitarily take over small groups of females and enjoy reproductive monopolization over them? Given the great variation in reproductive strategies demonstrated by individual bonnet macaque males even within multimale troops[16,21,23], it is plausible that many bonnet macaque populations may harbour small numbers of males genetically predisposed to be behaviourally aggressive and uncharacteristically intolerant of reproductive competition. Certain ecological situations, as prevails in the Bandipur–Mudumalai wildlife sanctuaries and described below, however, may either provide opportunities or actually select for such males to take over small groups of females and successfully establish a system of unimale 'harem' polygyny, a form of social organization displayed by forest guenons and patas monkeys[39].

There are several unimale troops in Population I (for example, UM3 and UM5; Table 1A) that have subsequently become multimale with one to several individuals joining each of them. Preliminary behavioural observations on these troops have revealed that some of the resident males (of the earlier unimale troops) have, at least partially, adopted the behavioural strategies appropriate to a multimale social organization[32]. Such males may have been able to achieve this through phenotypic flexibility, a mechanism which refers to context-dependent reversible phenotypic transformations in behaviour in response to variations in ecological and social environments, independent of any direct genotypic influence[40]. Such flexibility could conceivably occur even within single individuals, imparting to them an advantage in terms of individual fitness and subsequently becoming an integral part of the life-histories of these individuals. Interestingly, only a small subset of adult males in Population I appear to be capable of displaying such behavioural flexibility and moreover, such differential behavioural strategies – as prevails in unimale and multimale social organizations – have become apparent in the population only over a relatively short time-period of about ten years[32]. It is, therefore, more likely that the observed patterns reflect examples of phenotypic flexibility rather than any underlying genetic change since, in addition, it is difficult to conceive how such unpredictable short-term changes in behavioural strategies within the same individual could be mediated by any kind of direct genetic control. Stronger support for such behavioural flexibility may finally come from long-term observations when the life-history strategies of particular males in unimale and multimale troops would be known more completely and those of their offspring, born and raised in the two kinds of social groups, can be followed more accurately.

An ecological drive in social evolution

What factors, particularly ecological, could have led to the dramatic increase in the proportion of unimale social groups, a rather unusual form of social organization in bonnet macaques, in Population I in recent years?

The adult sex ratio in most primate groups, including macaques, appears to be related to the length of the breeding season and the degree of oestrus synchrony among females[41–43]. Macaque species have the widest ecological distribution among primates with the exception of humans, and occur in a range of seasonal and non-seasonal environments. Species living in seasonal habitats have a relatively shorter breeding season, during which mature females become sexually receptive synchronously. The number of females in oestrus at any given time during the breeding season is thus expected to be larger in a seasonal habitat, compared with a reproductive unit of comparable size in a non-seasonal environment[41]. In fact, females of the latter species could even be expected to stagger their reproduction in order to reduce competition for resources in non-seasonal habitats; only a few females would thus be sexually receptive in such species at any period of time. Macaques with seasonally reproducing females and also those with large numbers of females in their troops[44] may thus tend to have a multimale configuration with a relatively large number of troop males while those species with non-seasonal breeding females have a smaller number of males, culminating in an unimale form of social organization.

Bonnet macaques generally live in seasonal environments, and accordingly, most females within a troop come into oestrus synchronously. As compared to the situation in certain other species such as the pig-tailed macaque[42] or the lion-tailed macaque[45], this seems to have led to a relatively greater proportion of males within natural groups of bonnet macaques, and correspondingly, a promiscuous mating system. Is it, however, possible that adult females within unimale bonnet macaque troops have a lower degree of oestrus synchrony enabling a single adult male to monopolize each female as they independently become sexually receptive? The relatively higher temporal clustering of births over the observation period in unimale troops of Population I as compared to that in multimale troops, however, seems to argue against such a causal mechanism for the evolution of this form of social organization.

An ecological factor that may have significantly affected primate communities in Indian wildlife sanctuaries in the recent past is the increasing tourist traffic within these protected areas. Since bonnet macaques appear to naturally gravitate towards human settlements and food sources[21,22,26,33], many tourists invariably come in contact with such macaque troops and provision them with typically human foods. Such food is often nutritionally rich and provisioning is thus usually marked by intense within-troop scramble competition and between-troop contest competition among neighbouring troops, especially along the highway (see ref. 7). This is accentuated during the dry summer months when natural food resources within the dry deciduous forests are particularly sparse and very patchily distributed, and most of the troops come and space themselves along the highway. The amount of provisioned human food, however, is also rather unpredictable and clumped in distribution, and like the natural food sources available at this time, can support possibly only small groups of macaques. Since, as in most cercopithecines, bonnet macaque females alone are philopatric and form stable core groups in a particular area, this may have led to the evolution of unusually small troops of closely related females in Population I. Such groups could perhaps then be easily reproductively monopolized by a single dominant adult male, as has been postulated earlier for other species from a comparative analysis of cercopithecine mating systems. A model depicting such an evolutionary pathway for unimale social organization among bonnet macaques in Population I is shown in Figure 3.

Support for such an ecological pressure possibly driving the relatively rapid evolution of unimale troops in recent years comes from the observation that in the study area within the Bandipur National Park, the Mudumalai Wildlife Sanctuary and their surrounding areas, bonnet macaque troops that inhabit human habitations are able to amply forage on unlimited sources of human food; such troops are invariably multimale and occupy relatively large home ranges. Thus, of the 21 troops described in this study, seven were observed to live in the vicinity of human settlements and only one of these troops was unimale in composition. In contrast, 10 of the 14 genuinely forest troops were unimale, the selectivity of habitats being significantly different across the two types of troops (G-test of independence; $p < 0.025$). Interestingly, as has been predicted for competition between groups for rich, but patchily distributed, food resources[7,13], troops living near human habitations were also larger than the forest troops (mean group size ± SE of 21.9 ± 3.1 for habitation troops and 10.6 ± 1.3 for forest troops; Mann–Whitney U-test, $p < 0.002$) and the distribution of their troop sizes also significantly different (Kolmogorov–Smirnov two-sample

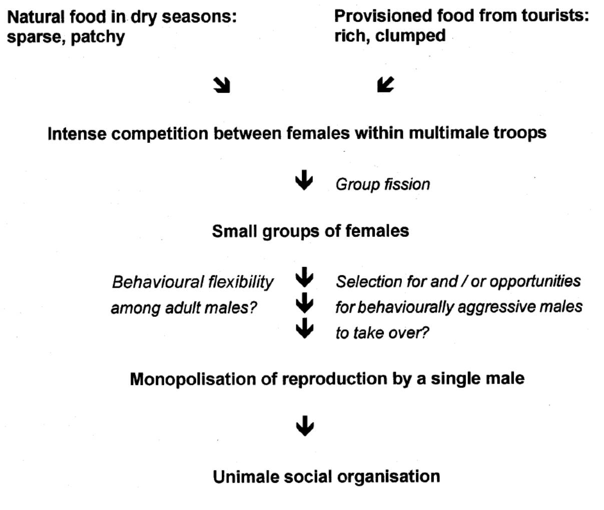

Figure 3. A model depicting the possible evolutionary route for unimale social organization in bonnet macaques.

test, $p < 0.025$). Moreover, only very few or no unimale troops were observed in surveys of bonnet populations along other highways that were not as heavily frequented by tourists within these sanctuaries (Mukhopadhyay and Sinha, unpubl.).

The coexistence of two distinct kinds of societies within the same population of bonnet macaques raises several interesting issues. These concern, in particular, the stability of the unimale troops which must face enormous pressure from potentially immigrant males, resource competition between the smaller unimale and the larger multimale troops, patterns of male emigration and reproductive success across these groups, and the competition for food and mates that females in multimale troops face as well as the lack of mate choice that females in unimale troops must cope with.

An illuminating example of how individual bonnet macaques might be able to respond to newly-emerging socio-ecological problems through the adoption and/or evolution of novel behavioural strategies is that of the extensive dispersal displayed by adult, subadult and juvenile females in Population I of Bandipur–Mudumalai. Thus, a total of 14 females, including six adults, two subadults and six juveniles, emigrated out of their troops, either singly or in small associations, during the observation period. It is possible that this unusual phenomenon may have arisen in response to a lack of mate choice faced by females sometimes confined to an unimale form of social organization. This is suggested by the fact that female dispersal has only been observed in this particular population and never encountered with in either Population II or III in spite of more than 3000 h of casual and structured observation on them over a combined period of almost five years. Female emigration occurred in five unimale and three multimale troops with three of the six adults, both the subadults, and four of the six juveniles dispersing from the former. In terms of the entire population, dispersal was thus displayed by nine of the 62 females in unimale and five of the 83 females in multimale troops (G-test of independence; $0.20 > p > 0.10$) – a trend towards relatively more emigration out of unimale troops, as would be predicted by the above hypothesis.

Behavioural strategies of bonnet macaques

Changes in social structure in response to ecological parameters, as described for the bonnet macaques in Bandipur–Mudumalai, have also been observed in other animal societies[46]. Although most of these species usually have an evolutionarily selected basic pattern of social organization, intraspecific variations, as in the case of the bonnet macaques, 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 troops, in addition to bringing about demographic and social changes at the group-level as outlined above, may also lead to changes in intra-group 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 investigated[47], 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.

As noted above, free-ranging groups of bonnet macaques are often provisioned by tourists visiting wildlife sanctuaries in southern India. 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.

The patterns of resource availability and the nature of food items have a profound effect on the social behaviour of these macaques. Adult female bonnet macaques in one such troop, BM19 in Population I, for example, significantly changed their behavioural strategies as they regularly alternated between bouts of natural foraging and feeding on provisioned foods, often during the course of the same day[31]. Provisioning was marked by a sharp increase in feeding competition, accompanied by severe aggression and feeding supplants, but individual females were also able to adopt appropriate strategies aimed at reducing social tension within the group.

Socioecology of male bonnet macaques

Since the males of most macaque species usually emigrate out of their natal troops on reaching sexual maturity, there is usually very little investment by males in social relationships. Bonnet macaque males, however, do not invariably disperse from their natal troops, some individuals even remaining behind to become the alpha males in their respective troops[16]. The males of this species, therefore, develop strong social bonds with each other, form coalitions with intense affiliative interactions, and involve themselves in territorial defense[16]. But how sensitive are bonnet macaque males to varying socioecological situations? Do they alter their behavioural strategies in response to changes in competition for food as much as the females in their troop do? An investigation was thus made into the patterns of male social behaviour exhibited by Troop BM19 of Population I under different ecological regimes that changed over the short term.

This troop 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 (henceforth referred to as foraging). The other was a more open area in the vicinity of the Theppakadu Forest Office of the Mudumalai Wildlife Sanctuary where they either interacted with tourists or directly obtained human food from them or where they scavenged on remains left behind by the visitors (henceforth referred to as scavenging). Although social interactions of all kinds regularly occurred in both these areas, those 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 troop when provisioned with typically human food.

Although the six adult males of the troop spent relatively longer periods of time in the forested area where they foraged because they invariably rested here during periods of inactivity, they exhibited a much higher frequency of scavenging (mean ± SE of 10.24 ± 0.48 acts/h) than they did of natural foraging (3.07 ± 0.29 acts/h; Wilcoxon's signed-ranks test, $p < 0.03$). Interestingly, there did not appear to be any significant correlation in the frequency of either foraging (Kendall's rank correlation, $p < 0.57$) or scavenging ($p > 0.85$) with the rank position of the adult males in the dominance hierarchy.

Feeding competition on provisioning

There was a marked increase in social tension in the study group during periods of scavenging from that exhibited during natural foraging; this was usually manifested as enhanced aggression among the adult males of the troop. Thus, although there was an increase in the overall rates of total aggression and its two components – non-contact aggression and contact aggression, a statistically significant increase was observed only in aggressive approach and feeding supplant (Figure 4; Wilcoxon's signed-ranks test, $n = 30$ dyads; total aggression: $p < 0.09$, non-contact aggression: $p < 0.16$, contact aggression: $p < 0.10$, aggressive approach: $p < 0.003$, feeding supplant: $p < 0.007$).

A closer examination of the agonistic interactions between the males revealed a marked dependence of aggression on the dominance ranks of both the individuals involved, especially under conditions of provisioning. Contact aggression is possibly the most effective, though costly, form of aggression under extreme situations. There was thus a strong positive correlation between the frequency of this behaviour, which showed a marked increase when individuals were scavenging, and the dominance rank of the actor, while no such relationship existed when low levels of contact aggression was displayed under conditions of natural foraging (Figure 5; Kendall's rank correlation, $n = 30$ dyads, natural foraging: $p > 0.60$, provisioning: $p < 0.03$). The frequencies of aggressive approach and feeding supplant, on the other hand, exhibited contrasting relationships with the dominance rank of the target individuals under the two ecological regimes. While aggressive approach was preferentially directed towards adversaries of lower rank under conditions of natural foraging ($p > 0.10$), this behaviour was relatively more indiscriminately shown towards other individuals when provisioning led to an in-

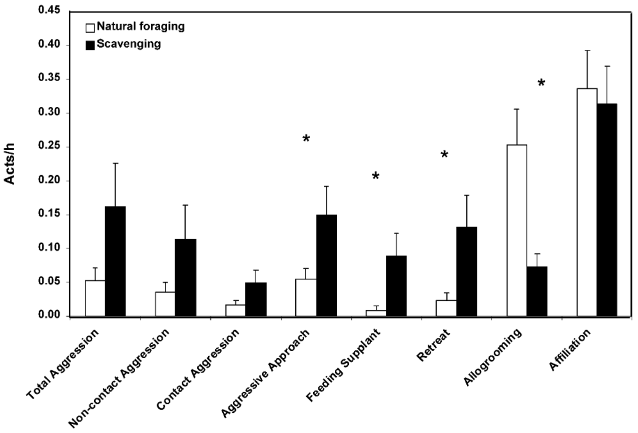

Figure 4. Different aggressive and affiliative behaviours displayed by adult males of Troop BM19 during natural foraging and scavenging. The bars represent the mean frequency of the behaviour under the two conditions, while the error bars indicate the standard error of the mean. The asterisks indicate a statistically significant difference between the means.

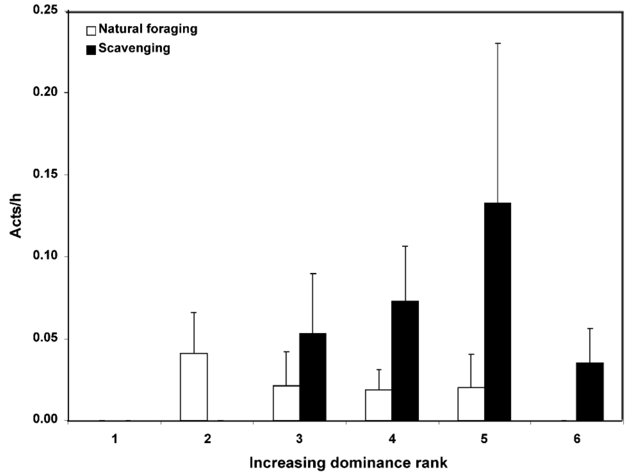

Figure 5. Contact aggression shown by adult males of increasing dominance rank of Troop BM19 during natural foraging and scavenging. The bars represent the mean frequency of the behaviour under the two conditions, while the error bars indicate the standard error of the mean.

Table 2. Frequency of dyadic behavioural acts (mean number of acts per hour ± SE) displayed by dominant and subordinate males under conditions of natural foraging and scavenging

	Natural foraging		Scavenging	
Behaviour	Dominant to subordinate	Subordinate to dominant	Dominant to subordinate	Subordinate to dominant
Total aggression	0.099 ± 0.033	0.006 ± 0.006	0.319 ± 0.117	0.006 ± 0.006
Non-contact aggression	0.072 ± 0.025	0	0.221 ± 0.095	0.006 ± 0.006
Contact aggression	0.027 ± 0.011	0.006 ± 0.006	0.098 ± 0.034	0
Aggressive approach	0.101 ± 0.024	0.010 ± 0.005	0.265 ± 0.073	0.035 ± 0.012
Feeding supplant	0.017 ± 0.011	0	0.176 ± 0.061	0
Retreat	0	0.045 ± 0.022	0	0.265 ± 0.080
Allogrooming	0.175 ± 0.044	0.330 ± 0.090	0.064 ± 0.021	0.082 ± 0.031
Affiliation	0.341 ± 0.092	0.332 ± 0.069	0.390 ± 0.097	0.236 ± 0.054

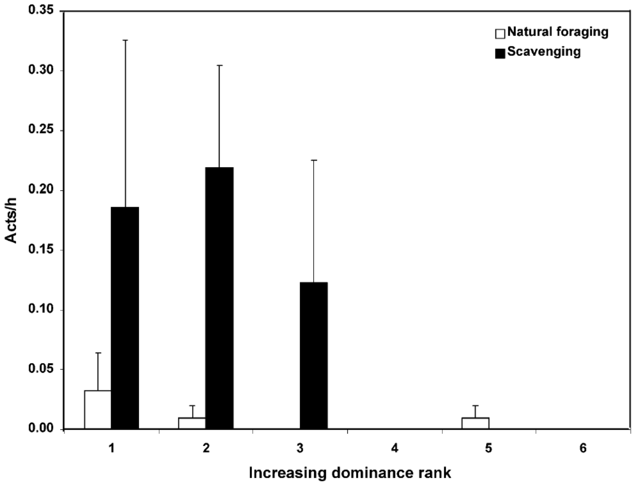

Figure 6. Feeding supplants directed by dominant males of Troop BM19 towards subordinate males of increasing dominance rank during natural foraging and scavenging. The bars represent the mean frequency of the behaviour under the two conditions, while the error bars indicate the standard error of the mean.

crease in feeding competition ($p < 0.03$). In such situations, however, feeding supplants were directed relatively more towards lower ranked individuals, possibly because it was easier to take away food from such individuals (Figure 6; Kendall's rank correlation, $p < 0.0001$); under more relaxed conditions of natural foraging, there was no such obvious pattern ($p > 0.20$).

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 2; Wilcoxon's matched-pairs test, $n = 15$ dyads, $p < 0.06$), contact aggression ($p < 0.04$), aggressive approach ($p < 0.02$) and feeding supplant ($p < 0.007$). Subordinate males, in turn, attempted to avoid such agonistic interactions and retreated at significantly higher frequencies from dominant individuals as the troop moved from the area where they foraged on natural food sources to the one where they were provisioned (Table 2; $p < 0.003$).

An interesting pattern observed under conditions of natural foraging was the strong negative correlation between the dominance rank of an individual and the levels of total aggression (Kendall's rank correlation, $p < 0.006$), non-contact aggression ($p < 0.02$) and contact aggression ($p < 0.003$) directed by him towards subordinates during dyadic interactions. During such interactions, therefore, lower-ranked dominant individuals were more aggressive towards their subordinate counterparts. On being provisioned, however, these correlations were lost (total aggression, $p > 0.07$; non-contact aggression, $p > 0.15$; contact aggression, $p > 0.23$) as individuals became more competitive and aggressive encounters were initiated indiscriminately by individuals across the dominance hierarchy. This is also supported by the observation that while individuals preferentially attacked lower-ranked subordinates during natural foraging (total aggression, $p < 0.02$), they no longer did so when they were provisioned ($p > 0.52$). Feeding supplants, which did not yield a clear correlation with dominance rank during natural foraging ($p > 0.58$), on the other hand, developed a strong negative correlation during periods of scavenging, with middle-ranked individuals becoming more competitive and preferentially supplanting subordinates at feeding sites ($p < 0.03$).

The adult males of Troop BM19 did not typically exhibit any aggressive behaviour towards those higher than them in the dominance hierarchy, particularly under conditions of natural foraging (Table 2). During scavenging, however, when there was an evident rise in overall aggression within the troop, some males in the study troop did display enhanced aggressive approach (Table 2; Wilcoxon's signed-ranks test, $n = 15$ dyads, $p < 0.06$) towards their dominant counterparts during dyadic interactions.

Affiliative strategies during feeding competition

There was a significant decrease in the frequency of allogrooming (Figure 4; Wilcoxon's matched-pairs test, $n = 30$ dyads, $p < 0.0002$), but surprisingly not of affiliation ($p > 0.64$) exhibited by the males as the troop moved to the provisioning site from areas of natural foraging.

Allogrooming displayed was independent of the dominance rank of the actor (Kendall's rank correlation, $p > 0.90$) but preferentially directed towards targets of increasing dominance rank under conditions of natural foraging ($p < 0.04$), while no such correlation was evident for affiliation in this situation (rank of actor: $p > 0.41$, rank of target: $p > 0.09$). These affiliative behaviours were, however, more indiscriminately displayed when the troop was provisioned, with no correlations of their levels with the dominance rank of either actors (allogrooming: $p > 0.19$, affiliation: $p > 0.71$) or their targets (allogrooming: $p > 0.13$, affiliation: $p > 0.98$) during scavenging.

A close examination of the dyadic interaction patterns revealed that individual males significantly decreased the display of allogrooming, but not affiliation, towards their subordinate counterparts during periods of scavenging (Table 2; Wilcoxon's matched-pairs test, $n = 15$ dyads; allogrooming: $p < 0.04$; affiliation: $p > 0.80$). The latter, too, similarly reduced their allogrooming towards their dominant partners while scavenging (Table 2; $p < 0.002$); the levels of affiliation, however, remained comparable across the two ecological situations ($p > 0.15$). Since the males in the study troop 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, these individuals could perhaps devote very little time to such energy- and time-intensive interactions as allogrooming. Such a hypothesis appears to be supported by the observation that virtually all individuals, irrespective of their dominance ranks, significantly decreased the display of allogrooming when they were provisioned.

A significant role for affiliation, a complex behaviour consisting of several short-duration affiliative behaviours[31], in reducing social tension during provisioning regimes became evident when the influence of dominance rank on its performance during dyadic interactions was analysed. Dominant males exhibited this behaviour towards their subordinate partners as a negative function of their rank only during scavenging (Figure 7; Kendall's rank correlation, $n = 15$ dyads, $p = 0.05$), but not during provisioning ($p > 0.73$); relatively lower-ranked dominant individuals thus showed relatively higher levels of the behaviour. No such relationship was, however, evident for allogrooming in either ecological situation (natural foraging: $p > 0.41$, scavenging: $p > 0.85$). Levels of affiliation shown by dominant males also decreased as a function of the rank difference with their subordinate targets, but only during periods of scavenging (Figure 8; $p < 0.03$, natural foraging: $p > 0.54$). Middle-ranked males thus preferentially directed affiliative behaviours towards subordinate individuals closest to them in rank, individuals who are most likely to compete with them for available resources.

Subordinate males involved in dyadic relationships, however, invested significantly in allogrooming their dominant counterparts in all situations; such grooming increased with the increasing rank of the actor, both during foraging (Kendall's rank correlation, $p < 0.02$) and scavenging ($p < 0.05$). There were, however, no significant correlations between allogrooming displayed by subordinate individuals and the absolute rank of the target or rank difference with the target, or between affiliation and any of these parameters under either of the ecological regimes (data not shown).

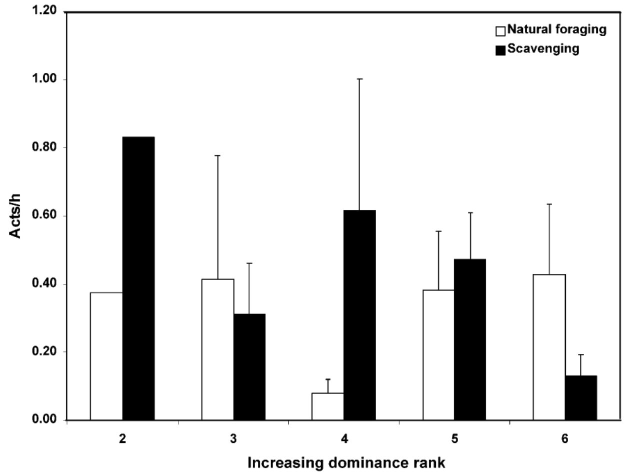

Figure 7. Affiliation exhibited by dominant males of increasing dominance rank towards subordinate males in Troop BM19 during natural foraging and scavenging. The bars represent the mean frequency of the behaviour under the two conditions, while the error bars indicate the standard error of the mean. Note that the male with dominance rank 1 is missing because he was the lowest in the hierarchy, while the male with dominance rank 2 had only a single individual subordinate to him.

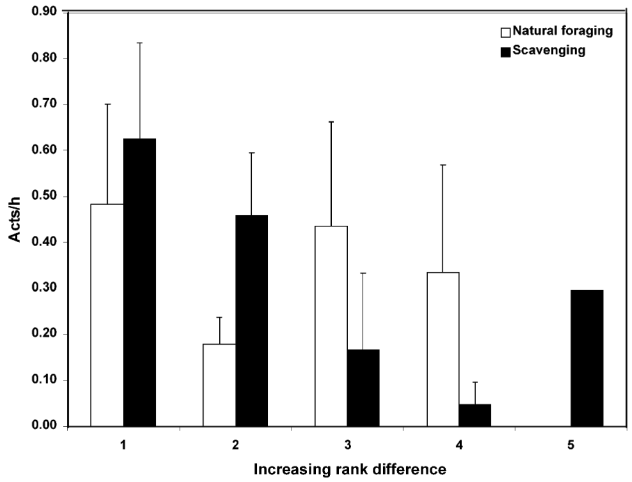

Figure 8. Affiliation displayed by dominant males of Troop BM19 towards subordinate males with increasing rank difference during natural foraging and scavenging. The bars represent the mean frequency of the behaviour under the two conditions, while the error bars indicate the standard error of the mean. Note that there was only a single dyad with a rank difference of 5.

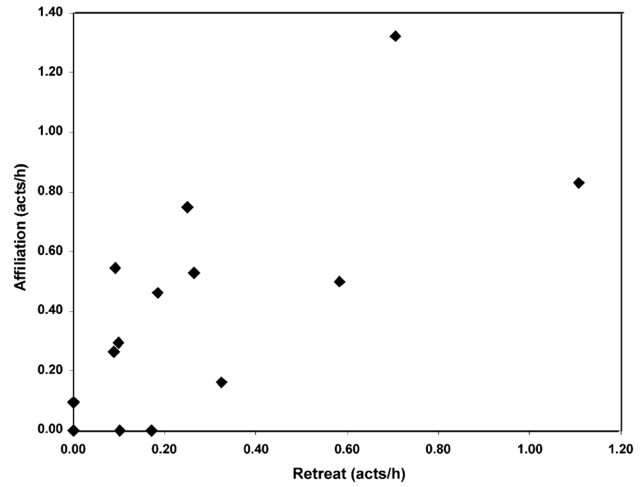

Figure 9. Correlation between the frequency of affiliation directed by dominant males of Troop BM19 towards subordinate individuals during scavenging and the frequency of retreats exhibited by the latter away from them.

Finally, it was possible to examine whether allogrooming and other affiliative behaviours were reciprocated or exchanged by individual males under these situations. It is noteworthy that while affiliation was reciprocally exchanged between the adult males of the study troop during foraging (Kendall's rank correlation, $n = 30$ dyads, $p < 0.03$; allogrooming: $p > 0.11$), only allogrooming was reciprocated during scavenging ($p < 0.02$; affiliation: $p > 0.12$). Allogrooming directed towards subordinate individuals during natural foraging also correlated with that shown during scavenging ($p < 0.05$) – this behaviour, therefore, did not appear to be significantly modulated in response to changing ecological situations.

The importance of affiliation as a behavioural strategy to defuse social tension during provisioning was, however, reiterated by the observation that not only did dominant males preferentially target this behaviour towards those subordinate individuals who retreated from them more (Figure 9) (Kendall's rank correlation, $p < 0.01$), but subordinate males also directed their affiliation towards those dominant individuals who exhibited more aggressive approaches towards them during scavenging ($p < 0.02$). It is perhaps illuminating that neither did such exchanges occur during natural foraging, nor was allogrooming ever exchanged with any of the agonistic behaviours under any condition (data not shown). Furthermore, the ability of individuals to employ appropriate behavioural strategies even across ecological situations was demonstrated by the fact that, during periods of natural foraging, subordinate males preferentially directed affiliation towards those dominant males who had exhibited the highest frequency of feeding supplants towards them during provisioning (Kendall's rank correlation, $p < 0.05$).

In conclusion, the clumped distribution of the provisioned food around their human sources could be most 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[20] 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 unlikely to occur under such 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 thus 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 very easily monopolized. This, in turn, may have led to scramble competition, characterized by intense aggression, within the troop and the subsequent need to adopt suitable behavioural strategies aimed at reducing such intra-troop tension. 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, however, need to be investigated further.

These observations on the behavioural ecology of bonnet macaques faced with significant variation in resource availability and distribution throw light on the potential extent to which a primate species is able to exhibit flexible behavioural patterns, ecological adaptability and a labile social organization, all of which may enable it to evolve along new and often unpredictable routes.

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