The Monkey in the Town's Commons:
A Natural History of the Indian Bonnet Macaque

Anindya Sinha

NIAS REPORT R2 – 2001

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

Contents

1. Introduction

When the monkey
on the bough
of the jackfruit tree
in the town’s commons

mistakes for fruit
the eye
on the thronged drumheads
hung up there by mendicant bards,

he taps on it,

and the sound rouses
the male swans below
to answering song…

Mutamōciyār
Puranānūru
(Classical Tamil War Poems, c 100 BC – 250 AD,
translated by A K Ramanujan)

Of the five primate species found in southern India, the bonnet macaque is the most common, extensively distributed from the wet montane rainforests of the Western Ghats through the dry scrublands of central southern India to most of the hot, dusty temple towns and bustling cities of the peninsula (Krishnan 1972). Referred to as “the common performing monkey of southern India” (Roonwal and Mohnot 1977), 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 (Schlotterhausen 1992, 1999)! Given these attributes and the fact that they are extremely widespread over the peninsula, it is truly surprising that our knowledge of the comparative ecology of these macaques in different habitats and their individual and social behavioural patterns remains rather fragmentary. This review will focus primarily on our knowledge of the ecology, demography and behaviour of the bonnet macaque in the wild, but will also refer to studies in captivity. It will not, however, attempt to review anatomical, physiological and developmental studies on the species. For earlier reviews, the reader is directed to Simonds (1965), Roonwal and Mohnot (1977) and Fooden (1981, 1986).

2. Taxonomy and Nomenclature

Originally termed *Cercocebus radiatus* (Geoffroy 1812, reported in Roonwal and Mohnot 1977), the bonnet macaque of south India (*Macaca radiata*, Pocock 1931) and the toque macaque of Sri Lanka (*M. sinica*) had been erroneously considered synonymous by Anderson (1878, reported in Pocock 1939) and by Blanford (who termed it *Macacus sinicus*, 1888-91). This confused synonymy was, however, subsequently clarified by Hinton and Wroughton (1921) and re-confirmed by Miller (1933). Hinton and Wroughton were able to clearly distinguish between the two species by differences in the radiating nature of the hairs on the crown; this also served to give these two derived sister taxa within the *sinica*-group of the genus *Macaca* their distinctive common names.

2.1 Vernacular names

The bonnet macaque has often been referred to in the classical texts of peninsular India. The *Ramayana*'s description of the *vānara sena*, or the monkey-army of Rama, which helps him to build the bridge to Lanka, for example, closely matches that of the bonnet monkey. In fact, Krishnan (1955), having studied the depiction of the *Ramayana* in various sculpture and paintings, believes that even Hanuman may have been modelled after a bonnet macaque! The species *per se* has also been portrayed vividly in the arts and sculpture of peninsular India. A notable example of this is the famous sculpture of a bonnet `family', closely huddled together, in Mahabalipuram dating back to the Pallava period of the 7th century AD.

The bonnet is known by a variety of local names, including *bandar* (Hindi), *manga*, *kodaga*, *kothi*, *kapi*, *maungya*, *kemp manga* (Kannada), *mucha*, *kapi*, *korda* (Kodava), *mānkad* (Konkani), *kurangan*, *markadan* (Malayalam), *mākad*, *lal manga*, *wānar*, *kerda* (Marathi), *sengurangu*, *vella kurangu* (Tamil), *kothi* (Telugu), and *kodan* (Toda).

3. Origins and Evolution

Comparative morphological, anatomical, biogeographic and palæontological studies suggest that the earliest discernible ancestral stock of the *sinica* group of the genus *Macaca*, which includes the bonnet macaque, the toque macaque (*M. sinica*), the Assamese macaque (*M. assamensis*) and the Tibetan macaque (*M. thibetana*), may have arisen in or west of Burma during the late Early Pleistocene period, approximately 1 million years ago (MYA). These groups may have then moved west and south into peninsular India to perhaps compete strongly with the indigenous *M. silenus*, ancestors of the present-day lion-tailed macaque (Delson 1980). Later, during the mid Middle Pleistocene period, about 0.5 MYA, *M. silenus* may have become restricted to its present south-west Indian relict distribution, while the northern and southern *sinica*-group members could have become genetically isolated and subsequently could have speciated into the south Indian *M. radiata* and the Sri Lankan *M. sinica*, respectively. Fooden (1989), however, is of the opinion that the sinica group may have originated in peninsular India or Sri Lanka after the origin and dispersal of the silenus group and may have then dispersed northeastward, ultimately as far as east-central China. What is noteworthy, in any case, is that although fossilised skeletal remains have been found of *M. anderssoni*, believed to be the ancestor of the modern-day *M. assamensis* and *M. thibetana*, no such fossils of the ancestral stock of *M. radiata* and *M. sinica* have ever been discovered.

4. Appearance and Morphometrics

The bonnet macaque is a medium-sized, long-tailed monkey typically characterised by a whorl of long hairs on the crown radiating outward and backward to form a small cap with a distinct centre-parting in front (Pocock 1931; McCann 1933). The long radiating hairs of the bonnet and the shorter hairs on the forehead are greyish brown at the base and blackish distally. The dorsal parts of the body, limbs and the tail are olive brown to grayish-brown in colour, while the ventral parts of the body and the inner side of the limbs are clothed with whitish grey hairs that show up conspicuously on the darkly and often patchily pigmented skin of the chest and abdomen. Pocock (1931) reports marked differences in tint across individuals from different regions of the peninsula, but concludes that they are possibly due to seasonal change. The face is bare, pale pink to flesh-coloured. Sexually cycling and lactating females have a dark red face; this colour is apparently acquired after parturition in the latter and gradually fades as lactation comes to an end. A typically broad forehead patch, lighter in colour than its surroundings, bifurcates the forehead longitudinally; variations in the shape and colour of this patch allows for the easy identification of individuals (Sinha *pers. obs.*).

Adult individuals of the two sexes do not always differ greatly in actual length, although males are always more heavily built and have relatively larger heads and canines. Interestingly, amongst all macaques, the bonnet displays the least degree of sexual dimorphism in body weight and morphometrics. The range of reported size measurements include: Head and body length: males, 50-60 cm, females, 34-52 cm; tail length: males, 50-70 cm, females, 48-64 cm; weight: males, 5.5-11.5 kg, females, 3-5.5 kg (Pocock 1931), infants, 0.33-0.37 kg (Hartman 1938).

It is interesting that forest-dwelling bonnets appear to be generally smaller in size than those inhabiting rural and urban areas (Krishnan 1972; Sinha *pers. obs.*) and they seem to reach a larger size in the eastern regions of their distribution than in their western range (Krishnan 1972). The difference in adult size between troops in different areas may not be dependent on the ecology of the troops alone, but on a complex interplay of genetic and environmental factors (Krishnan 1972).

5. Subspecies

Two subspecies of bonnet macaques have been morphologically distinguished: the northern, more common, *Macaca radiata radiata* (henceforth referred to as the northern subspecies), and the southern *Macaca radiata diluta* (henceforth referred to as the southern subspecies), believed to be restricted to the Agastyamalai range of the Western Ghats in the southern districts of Thiruvananthapuram in Kerala and Tirunelveli in Tamil Nadu (Pocock 1931; Fooden 1981) (Figure 1). The southern subspecies, on an average, is smaller in size and has a coat colour that appears to be paler. The hairs on the forehead are buff with darker tips, while the characteristic whorl of hairs on the crown of the head seems much longer and yellowish in colour (Pocock, 1939; Sinha *pers. obs.*). The hairs on the neck and shoulders are also rather long in this subspecies and, like those of the rest of the back, have long buff tips.

Inspite of a detailed study by Ali (1981) on *M. r. diluta*, however, the legitimacy of the two subspecies continues to remain an open question. There have been, unfortunately, no studies that have examined whether they can hybridise with each other, or, for that matter, any aspect of their comparative distribution, ecology or biology.

What has also remained unconfirmed is an interesting report of Krishnan (1972) from the Wynaad district of Tamil Nadu: “a miniature bonnet monkey was noticed, hardly half the size of the commoner specimens…so fugitive in its response to humanity that it was not possible to observe it closely for any length of time…An adult female was seen carrying an infant only the size of a loris…”

6. Distribution and Status

6.1 Distribution

Ubiquitously distributed throughout peninsular India (8°N-21°N; Figure 1), the bonnet macaque was traditionally believed to occur only upto the rivers Godavari and Tapti in the east and west, respectively (Pocock 1939, reviewed in Saha 1984). Extensive surveys now reveal that the northward distribution of the species seems to be limited by an imaginary line running from the north of the Velikonda range of the Eastern Ghats in the east to the Manjra plateau at the northern end of the Western Ghats in the west (Fooden *et al.* 1981; Saha 1984). More specifically, the distribution limit of the species seems to be marked by the town of Surat in Gujarat (ca 21°N) in the northwest and by the town of Guntur in Andhra Pradesh (ca 16°N) in the northeast. A small isolated population of the bonnet macaque also inhabits the Vijayawada Hills area, about 150 km north of the main range of the species (Fooden 1989). The further northward spread of the species seems to be constrained by the equally ubiquitous, but much more geographically successful, rhesus macaque (*Macaca mulatta*) of northern India, whose distribution now seems to extend even south of the river Krishna (Fooden *et al.* 1981; Koyama and Shekar 1981; Kurup 1981). Although sympatric populations of rhesus and bonnet macaques have been reported in certain areas at the northern end of the Velikonda range and central Telengana plateau and even mixed troops including adult bonnet males have been sighted (Saha 1984), it is possible that the better adaptability of the rhesus to secondary habitats and their more aggressive nature may, in fact, be responsible for the displacement of bonnet populations in areas traditionally inhabited by the latter.

Further south in peninsular India, however, bonnet macaques are found in close non-aggressive association and also occasionally in mixed foraging groups with the liontailed macaque, the common langur and the Nilgiri langur in their respective ecological habitats (Sugiyama 1971; Singh *et al.* 1997; Sinha *pers. obs.*). Thus, bonnets occur with liontailed macaques in the wet rainforests of the Anaimalai and Agastyamalai hills, with common langurs in dry deciduous and mixed scrub forests of the central Deccan plateau, and with Nilgiri langurs in middle altitude moist deciduous forests of the Anaimalai and Agastyamalai ranges.

6.2 Status

It has been estimated that the total population of bonnet macaques in the four south Indian states would be of the order of 1,70,000, with about 81,000 monkeys in Karnataka, 64,000 in Andhra Pradesh, 16,000 in Tamil Nadu and 11,000 in Kerala (Kurup 1981). The bonnet macaque populations in

Maharashtra have never been monitored. What also remains unknown is the rate of decline of many of these populations that seems inevitable given the intensification of agriculture in rural areas and the increasing intolerance towards the species in urban localities. Yet another problem plaguing bonnet monkey populations today and one that is likely to become even more serious in the future is the capture of free-ranging monkeys by professional trappers to meet the increasing demand of laboratories involved in biomedical and other research (Sinha *pers. obs.*). Care must be taken that this situation does not burgeon into a problem of the kind faced by the rhesus macaque of northern India, Pakistan and Bangladesh about two decades ago when increasing demand for the species in the developed countries and our export policy to meet this demand severely threatened most of its natural populations.

Long-term monitoring of certain bonnet populations around Mysore in Karnataka have, in fact, revealed that during the last two decades several groups of monkeys have been completely eliminated and that some areas that had abundant populations earlier are now completely devoid of them (M. Singh, *pers. comm.*). It is entirely possible that in such a scenario the common bonnet macaque of today may well become an endangered species of tomorrow.

7. Ecology

7.1 Habitat and habitat preferences

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 (Nolte 1955; Simonds 1965; Sugiyama 1971; Krishnan 1972; Kurup 1981; Pirta *et al.* 1981; D'Souza and Singh 1992; Schlotterhausen 1999). 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 (see above) 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 bonnets include the montane evergreen rainforests of the Nilgiri hills (sometimes even upto an altitude of about 2100 m; Simonds 1965), 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. What is more illuminating, however, is that bonnet troops are relatively rare in very wet montane forests at higher altitudes, and the few troops found here often move down to lower elevation drier deciduous forests (H.S. Sushma *pers. comm.*). They are also extremely rare in the *shola* forests and in the adjoining grasslands of the Nilgiri hills.

Bonnets are, however, much more common in areas of human habitation – whether they be villages bordering agricultural fields (including those of rice, maize, *jowar*, *ragi*, pulses, peanut, and gram) and plantations (areca, tea, coffee, cardamom), 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 (Simonds 1965; Rahaman 1975; Roonwal and Mohnot 1977; Kurup 1981; Schlotterhausen 1992). Kurup's (1981) survey of populations in human habitations indicated that, on an average, 60.1 % of the observed troops were in villages and adjoining cultivated areas, 25 % along roadsides, 8.6 % in towns (with 4 % in temples), and 6.3 % in fallow lands and hillocks.

In rural and urban habitats, bonnets seem to prefer large flowering and fruiting trees such as banyan (*Ficus benghalensis* and *F. benjamina*), mango (*Mangifera indica*), tamarind (*Tamarindus indica*), *neem* (*Azadirachta indica*), pongamia (*Pongamia pinnata*), *jamun* (*Szygium cumini*), and exotics of more recent origin like cashew (*Anacardium occidentale*), *gulmohar* (*Delonix regia*), and copperpod (*Peltophorum ferrugineum*). The banyan seems to be a particular favourite – to the extent that Simonds (1965) comments "if there are no banyan trees, there will probably be no macaques"! Kurup (1981), however, observed that 41 % of his surveyed troops were on tamarind trees, 29 % on *Ficus* species, and the remaining on other trees.

Our knowledge of urban and rural bonnet populations could also owe partly to the fact that true forest bonnets are extremely shy of observers while those around settlements are remarkably habituated to human presence, and hence, much more visible. The former spend much more time in the forest canopy and in the higher branches, rarely descending to the ground (less than 10 % of the diurnal activity of montane evergreen forest troops in the Anaimalai hills, Sugiyama 1971). Rural and roadside populations, in contrast, are much more terrestrial and may even spend more than 30 % of their daytime activity on the ground (Simonds 1965; Sugiyama 1971).

Forest troops prefer to roost overnight near large water bodies such as rivers and lakes, often on trees overhanging them (Krishnan 1972; Ali 1981; Sinha *pers. obs.*), or in dense bamboo thickets in deciduous forests. Even in human environments, elevated objects like temple towers are usually chosen as roosting sites (Kuruvilla 1980). The height use may vary across age-sex classes with adult males tending to use the lowest heights (Ali 1981).

7.2 Food habits and foraging ecology

Dietary diversity

One of the principal reasons that have made the bonnet monkey ubiquitous in southern India is the wide diversity of food resources that it can successfully use. Bonnet macaques 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 (Rahaman and Parthasarathy 1968, 1969a; Sugiyama 1971; Kuruvilla 1980; Makwana 1980; Ali 1981; Krishnamani 1994; Schlotterhausen 1999). Remarkably, a total of about 86 food plant species have been recorded in a dry deciduous forest (Ali 1986) and about 39 in a tropical evergreen forest (Krishnamani 1994).

Bonnet monkeys are omnivores and have also been observed feeding on insects (about 13 % of their diet, Ali 1986) including crickets, cicadas, grasshoppers, termites and insect pupae, and on spiders and bird eggs (Rahaman and Parthasarathy 1979; Kuruvilla 1980). Fruits, however, usually form the most important component of the diet, followed by foliage and invertebrates (Kuruvilla 1980; Ali 1986; Krishnamani 1994; Schlotterhausen 1999). A substantial fraction of their food can also derive from herbs, grasses (including young bamboos shoots) and mushrooms. It must be noted, however, that although most populations are fairly adaptable and exploit a wide variety of plant species, individuals of particular groups tend to monopolise certain species more than others. Thus, only ten species constituted about 72 % of the diet of a troop in the dry evergreen forest (Krishnamani 1994), while eight plant species, different grasses and a host of insects accounted for about 76 % in the dry deciduous forest (Ali 1986); only two plant species were common between these segments of the diet of the two groups. There may also be seasonal changes in plant foods taken by bonnet macaques, as has been carefully documented by Kuruvilla (1980).

Foraging ecology

Free-ranging bonnet troops may display significant variation in the amount of time spent feeding, both between age-sex classes, and between months and the time of the day (Kuruvilla 1980; Ali 1986; Schlotterhausen 1999). Adult males, in general, spent the least amount of time feeding, while subadult males spent the most, followed closely by subadult females and juveniles, respectively (Ali 1986). Krishnamani (1994), however, could not detect any diet variation across age-sex categories in his study troop. Feeding is also more prevalent during mornings and evenings as compared to the midday. Interestingly, although Ali (1986) observed a proportional decrease in insect-eating with an increase in fruit-eating, fruits were preferentially consumed in the morning (and bamboos in the evening) but insects were taken constantly over the entire day.

In a laboratory study, Plimpton *et al.* (1981) observed three basic foraging patterns along a temporal dimension. One group of very dominant adult males and females completed 50 % of their total foraging by the end of the first quarter of the observation session, while another group of very subordinate females completed 50 % of their foraging only during the last half of the session. Interestingly, a third group, consisting of individuals of intermediate dominance ranks, foraged steadily throughout the feeding session.

Bonnet macaques living around human habitations are often provisioned by the local people; such troops occasionally resort to scavenging from garbage dumps as well (~70 % of the diet, Schlotterhausen 1999). Tourists visiting a number of wildlife sanctuaries in southern India also feed bonnets with typically human foods (Ram and Sinha 1999). Since the food obtained during such interactions is not only nutritionally rich but also clumped in distribution, provisioning is often marked by a significant increase in feeding competition among individual troop members. The amount of such food available is, however, usually unpredictable. 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 food from human sources become predictably high and ample for the entire troop. Thus, one particular troop spent only about 34 % of its time begging for food from visiting tourists or scavenging on the remains left behind by them (Ram and Sinha 1999).

Two behavioural features of feeding bonnet macaques are particularly interesting. When feeding on the ground, typically on foods of human origin, bonnets tend to stuff their cheek pouches hurriedly (Krishnan 1972). They later move to a quieter area or climb to some height and leisurely feed on their cheek pouch contents, sometimes even pushing out the food with their palms and fingers. Cheek pouches are, however, filled up much more methodically, or sometimes not at all, when individuals forage on vegetation on trees or in bamboo clumps (Krishnan 1972). Second, when feeding on solid foods picked up from the ground, all bonnet macaques rub the food between the palms (Roonwal and Mohnot 1977) or sometimes on the ground (Sinha *pers. obs.*) before ingestion. Although this may have originally evolved to serve a cleaning function, it may not always serve the purpose especially when the food is rubbed on the ground. It is also interesting to speculate why and how this behavioural feature has evolved to become an inherent feature of all individuals across ecological habitats.

8. Population Biology

8.1 Population density

Kurup (1981), in his survey of rural and urban populations of bonnet macaques (consisting of 1451 troops), estimated a density of 0.34 individual per km^2, or one individual every 2.94 km^2 in southern India. The equivalent figures for the different states were estimated to be 0.30 and 3.31 in Andhra Pradesh, 0.51 and 1.97 in Karnataka, 0.40 and 2.52 in Kerala, and 0.15 and 6.55 in Tamil Nadu.

Density estimates from roadside troops in different ecological habitats of southern Karnataka ranged from 0.33 individuals per km^2 in areas with irrigated cultivation through 1.41 individuals in dry cultivation zones to 11.05 individuals in scrub forests (D'Souza and Singh 1992).

8.2 Demography

Population structure

Like most macaque species, the bonnet macaque usually lives in multimale multifemale troops, with group sizes ranging from 5 to 75 individuals (Roonwal and Mohnot 1977; Kurup 1981). Although group size may be highly variable in a particular ecological area, it tends to be much smaller in natural forests and significantly larger in or near human habitations (Simonds 1965; Krishnan 1972; Pirta *et al.* 1981; Singh *et al.* 1984; Fooden 1986; Sinha and Datta Roy 2001a). Thus, forest troops in the Bandipur-Mudumalai wildlife sanctuaries have been estimated to have a mean group size of 14.6 ± 4.9 (Singh *et al.* 1984) and 10.6 ± 4.4 individuals (Sinha and Datta Roy 2001a), while those inhabiting human settlements in adjoining areas have 22.7 ± 9.6 and 25.7 ± 12.2 individuals, respectively. Kurup's (1981) study of 316 troops of urban and rural macaques reveals a mean group size of 17.7 ± 1.4 individuals, with troops consisting of 11 to 15 members being most frequent. The largest troops reported are those in temples, sometimes with as many as 100 individuals (Fooden 1986).

Each troop typically consists of one to several adult males and females, and a variable number of subadults, juveniles and infants of both sexes. The overall percentage of these age categories may vary from 40 to 56 % for adults, 6 to 17 % for subadults, 16 to 35 % for juveniles and 15 to 20 % for infants (Simonds 1965; Kurup 1981; Singh *et al.* 1984; Sinha and Datta Roy 2001a). The ratios of different age-sex classes within troops usually exhibit some variation across ecological habitats (Pirta *et al.* 1981; Singh *et al.* 1984; D'Souza and Singh 1992, Sinha and Datta Roy 2001a).

Changes in population structure over time, in contrast, have not been investigated much. D'Souza and Singh (1992) documented a marked increase in the number of groups of small size (1 to 10 individuals) and those that were very large (31 to 40 individuals) with a concomitant decrease of medium-sized groups (11 to 20 individuals) in several populations of southern Karnataka over a period of 22 years. There were no significant changes, however, in the demographic structure of the troops.

Adult sex ratio

The adult sex ratio in primate groups appears to be related to the length of the breeding season and the degree of oestrus synchrony among the females. 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 macaques, this seems to have led to a relatively greater proportion of males within natural groups of this species, and correspondingly, a promiscuous mating system. Interestingly, the adult male-female ratio in bonnets is perhaps the most variable amongst the macaques, ranging from 0.12 to 5; values greater than 1 represent an unique situation with adult males outnumbering adult females in the troop (Kurup 1981; Fooden 1986).

What is most remarkable, however, is that bonnets may be unique amongst seasonally breeding macaques in also exhibiting a fairly high proportion of stable unimale troops within certain populations (52 % in the Bandipur-Mudumalai wildlife sanctuaries, Sinha and Datta Roy 2001a). The adult male-female sex ratios in such troops can range from 0.17 to 1 (Kurup 1981; Sinha and Datta Roy 2001a). Preliminary observations indicate that, in comparison to the usual multimale troops, unimale groups may be relatively depleted in subadult and juvenile males, a clear indication of reproductive monopolisation by a single dominant male (Sinha and Datta Roy 2001a). This is more a characteristic feature of liontailed macaques (Kumar and Kurup 1985) and pigtailed macaques (Oi 1996), which breed throughout the year, and extremely unusual for a seasonal breeder such as the bonnet macaque.

8.3 Breeding patterns and reproductive success

Breeding biology

Sexual maturity is attained in females at about two-and-a-half to four years of age (Simonds 1965; Rahaman and Parthasarathy 1969a); in captivity, menarche occurs at an age of 36 ± 4 months (Rao *et al.* 1998). Males become sexually mature at about three to four years of age but socially mature only two to three years later (Simonds 1965; Roonwal and Mohnot 1977). In captivity, however, males less than six years of age are generally incapable of impregnating receptive females (Rao *et al.* 1998).

Bonnet females usually have a series of oestrus cycles every year, with the average cycle length being 28 ± 4.3 days (Rao *et al.* 1998). It has been estimated that in natural troops, females may be receptive for only four to five days during each cycle (Rahaman and Parthasarathy 1971a). Females stop cycling when they conceive, and usually resume two to three months after weaning (Rao *et al.* 1998), which usually occurs when the infant is about six months of age (Rahaman and Parthasarathy 1969b). Oestrus females do not usually exhibit any sexual swelling, although occasionally a redness may appear in the genital region and last the entire cycle (Roonwal and Mohnot 1977; Ali 1981), especially in primiparous females (Rahaman and Parthasarathy 1969a). It is, therefore, usually difficult to visually distinguish between oestrus and anoestrus females (Roonwal and Mohnot 1977; Sinha *pers. obs.*). In captivity, receptivity generally peaks on day 9 or 10 (Rao *et al.* 1998).

Females usually bear their first infant within a year of reaching sexual maturity. In one captive population, most females produced their first infant between 47 and 50 months of age, with a range of 39 to 61 months (Silk *et al.* 1981a); in another, the first conception occurred at an age of 54 ± 4 months (Rao *et al.* 1998).

The gestation period has been reported to be six months (Prater 1980) or about 150 days (Rahaman and Parthasarathy 1969a) in the wild. In captivity, it ranges from 153 to 169 days (Hartman 1938) or from 161 to 171 days, or has a mean of 166 ± 5 days (Rao *et al.* 1998). Parturition occurs during the night – in the wild (Sinha *pers. obs.*) and in captivity (Rosenblum and Kaufman 1967; Rao *et al.* 1998). Only a single offspring is produced (Krishnan 1972); rare cases of twinning have been noticed (Rahaman and Parthasarathy 1969a; Krishnan 1972) but seem to be followed by the death of one of the infants (Sinha *pers. obs.*). The majority of females do not exhibit regular cycles until the infant is weaned, which typically occurs six months after birth in captivity (Rao *et al.* 1998) and about six to 12 months in the wild (Rahaman and Parthasarathy 1969a). Females produce a number of offspring sequentially over their reproductive lives (upto five offspring in captivity, Rao *et al.* 1998), and may continue to be productive until they are 15 or 16 years of age (in captivity, Silk *et al.* 1981a, Rao *et al.* 1998).

In one captive population, female fertility was highest in years when there were relatively few adult females in the group and relatively few adult females per adult male (Silk 1988a). During years when there were many adult females, many infants were born, but relatively few survived. Endogenous social mechanisms, such as reproductive suppression among breeding females, could thus influence levels of female fertility and infant survival in captive bonnet populations. Whether such factors are also operative in the wild, however, remain to be investigated.

Longevity records in captivity indicate a maximum survival age of about 30 years for bonnet macaques (Prater 1980), although the estimated average life expectancy at birth is only about 15 % of the maximum potential life span – approximately 5 years (Fooden 1981). In a natural population, however, an old male has been recorded to be between 20 to 25 years of age (Sinha *pers. obs.*).

Breeding seasonality

Copulations occur throughout the year in both wild and captive populations, and conceptions have been reported across all months. While the peak months for copulation in wild groups are August to November (Parthasarathy 1977; Rahaman and Parthasarathy 1979; Kuruvilla 1980; Makwana 1980), in captivity, 96 % of the conceptions occurred between September and February (Silk 1989).

Most bonnet macaque populations exhibit a peak birth season – approximately 93 % of the births occurred during January to April in one study (Rahaman and Parthasarathy 1979) and during February to April in another (Sinha and Datta Roy 2001a). The peak birth season may vary across populations in different geographical areas due to climatic differences. Kurup (1981), for example, observed a much earlier season – January to March – in the cooler areas of the Western Ghats in Karnataka and Kerala, but a later season well into the monsoons – May to July – in the drier hotter areas of Andhra Pradesh and Tamil Nadu. Krishnan (1972), Roonwal and Mohnot (1977) and Ali (1981) are, however, of the opinion that wild bonnets do not appear to exhibit any pronounced breeding season.

In a captive temperate population, 85 % of all births occurred between March and June (Silk *et al.* 1981a) and 94 % between March and August (Silk 1989). In this population, however, primiparous females produced their first infant later in the first season than did older females (Silk *et al.* 1981a).

Breeding seasonality has been considered advantageous because it serves to concentrate reproductive activity during periods when environmental conditions are most favourable. This may also apply to wild bonnet populations that seem to favour a birth season just prior to or coinciding with the arrival of the north-east monsoons over peninsular India with its flush of new plant growth (Rahaman and Parthasarathy 1969a).

In a captive group, however, Silk (1989) observed marked infant mortality among females who conceived at the peak of the mating season compared with females whose conceptions were more isolated in time. Particularly true for primiparous and low-ranking females, this could be due to increased harassment of conceiving and pregnant females by higher-ranking females during months when conceptions were most common. Social factors could thus conceivably constrain the extent of reproductive synchrony among bonnet females, at least in captive populations.

Reproductive success

The overall reproductive success of wild bonnet populations, expressed as the ratio of births to adult females, varies from 0.45 to 0.84 (Simonds 1965; Kurup 1981; Singh *et al.* 1984; D'Souza and Singh 1992; Sinha and Datta Roy 2001a). There may, however, be significant variation across geographical areas (Kurup 1981), habitats (0.58 in urban areas to 0.78 in scrub forests, Singh *et al.* 1984) and across years (D'Souza and Singh 1992).

In a captive socially housed group, reproductive success ranged from 0.51 to 1.00 across years (Silk 1988)). In a captive individually housed population, however, the average reproductive success during random breeding was 0.60 to 0.65; a value of 0.80 was reached under controlled conditions during peak receptivity (Rao *et al.* 1998). Three exposures to a proven fertile male were required to achieve this peak success – 60 % of the females, nevertheless, conceived after the first exposure (Rao *et al.* 1998).

Infant mortality, from birth to age one year, apparently averages about 50 % in natural populations of bonnet macaques (Fooden 1981). Singh *et al.* (1984) report that the mortality of female infants exceeds that of male infants in non-urban habitats, while it is just the opposite in urban areas.

Variance in reproductive success among captive socially housed females appears to be primarily due to differences in infant survival, with infants of low-ranking females exhibiting lower survival probabilities (Silk *et al.* 1981a). Juvenile daughters of low-ranking females are also more vulnerable to behaviourally induced mortality as a direct result of aggression by unrelated high-ranking adult females (Silk *et al.* 1981a).

Inter-birth interval

There do not appear to be any estimates for inter-birth intervals in wild bonnet troops. In a large captive population, however, it varied between 11 months for non-surviving births to 13 months for that with surviving infants (Silk *et al.* 1981a). Younger females with surviving infants were, however, found to have a prolonged inter-birth interval of about 21 months; this could either be due to their age or parity (Silk *et al.* 1981a). In this population, the inter-birth interval between surviving infants was generally dependent on various factors including maternal parity, age, experience, family size and recent reproductive history (Silk 1988b, 1990). Infant sex and maternal rank, however, did not seem to influence the inter-birth interval. Interestingly, females who conceived early in the mating season generally tended to have shorter inter-birth intervals, although experienced multiparous females who had recently raised infants exhibited shorter inter-birth intervals even if they conceived late in the season (Silk 1990).

Infant sex ratio

The sex ratio at birth in three small local populations of bonnet macaques indicated a 1:1 ratio in these natural groups (17 males - 15 females, Fooden 1981). Interestingly, however, a study of the unimale and multimale troops of bonnet macaques in the Bandipur-Mudumalai wildlife sanctuaries seems to indicate that the unimale groups may exhibit a highly skewed female-biased (1:4) infant sex ratio at birth as compared to a more even (1:1.25) ratio in multimale troops (Sinha and Datta Roy 2001a). It is conceivable that such a skew is in response to the reproductive monopolisation practised by the single adult male in each of these unimale groups – often to the extent that subadult and juvenile males are not easily tolerated in the troop.

Infant sex ratios in a captive population seemed to be significantly influenced by the sex ratio of offspring produced the previous year. Thus, years in which the highest proportion of male infants survived were followed by years in which the largest proportions of the birth cohorts were composed of males; this was also true for female infants (Silk *et al.* 1981a). In another study with solitary captive individuals, however, the infant sex ratio was male-biased (2:1) over the years (Rao *et al.* 1998).

No specific proximate mechanisms have yet been unravelled to explain the observed skews in infant sex ratio either in the wild or in captivity. Although it is possible that specific external environmental factors could consistently skew the sex ratio of conceptions in particular directions in different situations, another plausible hypothesis is that females (or even males?) may themselves facultatively determine the sex of their infants in response to appropriate environmental or social stimuli (Silk *et al.* 1981a; Sinha and Datta Roy 2001a).

9. Behaviour and Social Organisation

9.1 Ranging behaviour

Most bonnet macaque troops have fairly well delimited home ranges, varying in size from 26 ha to 5 km^2 (Nolte 1955; Rajagopal 1965; Simonds 1965; Rahaman and Parthasarathy 1967, 1969a; Sugiyama 1971; Kuruvilla 1980; Ali 1981; Fooden 1986; Schlotterhausen 1999). Although not confirmed, home range area may be positively correlated with troop size

(Fooden 1986). Neighbouring home ranges may overlap to a certain extent (Rahaman and Parthasarathy 1969b; Ali 1981), with the resident troops not being strongly territorial but co-existing peacefully, often foraging close-by (Rahaman and Parthasarathy 1969b) or together (Nolte 1955). Such troops may also regularly schedule their movement to avoid agonistic inter-group encounters (Sinha *pers. obs.*). Anderson (1998) observed a case of home range squatting in which a subordinate troop took over the food-rich core area of a dominant neighbouring troop, but vacated it peacefully when the original troop returned after about two weeks. In general, Ali (1981) suggests that overlapping home ranges are possible in bonnets because groups of different sizes tend to use different resources. Certain urban troops, particularly those with access to rich food sources, are, however, strongly territorial and both the sexes aggressively defend their feeding areas (Rahaman and Parthasarathy 1969b; Sinha *pers. obs.*). Troop home ranges, in general, may be relatively stable over many years (16 years: Makwana 1980), but may also change drastically over a short period of time, especially for troops moving into human habitations from natural forests (six months: Sinha *pers. obs.*).

Movement within and out of the often loosely defined home range appears to be influenced by seasonal diurnal temperature and, perhaps more importantly, availability of food (Rahaman and Parthasarathy 1969b) and drinking water (Koyama 1973). During seasons of insufficient food and water, therefore, the troop movement may extend well beyond the limit of the home range, but usually into known, earlier explored areas. This may also lead, over the years, to an expansion or gradual shifting of the home range to incorporate areas with reliable food sources (Rahaman and Parthasarathy 1969b; Sinha *pers. obs.*).

Unexpected atypical movement of the group out of its usual home range may be followed by high rates of mortality and abnormal behaviour patterns, different from that displayed within its range (Singh and Pirta 1978). The latter could involve a dramatic increase in bipedal movement, quadripedal running, time spent on trees, inter-individual distances and visual exploration of the area. Several individual activities like day resting and sleeping and social interactions, including allogrooming and play, however, may decrease drastically during such periods.

The bonnet macaque is a good swimmer and readily takes to water, entering the water smoothly and often swimming submerged for short distances (Simonds 1965; Krishnan 1972; Agoramoorthy *et al.* 2000). Even females with infants are not averse to water; the infant may either shift from the abdomen to climb onto the back (Krishnan1972) or remain submerged even as the mother crosses a fairly turbulent river (Datta Roy and Sinha *pers. obs.*). Juveniles readily play in pools of water, often pushing each other into the water and preventing them from climbing out (Simonds 1965; Sinha *pers. obs.*); Agoramoorthy *et al.* (2000), however, report a case of juveniles refusing to enter the water even as the adults swam across a river.

9.2 Time-activity budgets

The daily activity pattern of bonnet macaques, like that of most diurnal cercopithecine primates, can be divided into the morning feeding period, midday resting, afternoon and evening periods of activity, and sleeping activity (Nolte 1955; Narain 1965; Simonds 1965; Sugiyama 1971; Rahaman and Parthasarathy 1969a, 1969b, 1978; Krishnan 1972; Roonwal and Mohnot 1977; Makwana 1980; Schlotterhausen 1999). The actual time and energy budgets apportioned to these activities are rather variable and depend on several environmental factors including habitat characteristics, home range size, availability of food and water, and seasonal and daily temperatures, as well as demographic factors such as the size and composition of the group, and the presence of neighbouring troops.

In a comparative study on forest, rural and urban troops, Singh and Vinathe (1990) observed that the average time-activity budget for a troop may not only vary across the three habitats (with urban monkeys, for example, moving significantly more than did those in the other habitats), but also across age-sex classes (with adult males spending significantly more time on sitting, adult females on foraging, and juveniles and infants on social behaviour). It is, however, imperative that individual variation on time-activity budgets within and across groups also be documented – natural selection on activity budgets would best be revealed through individual life-history strategies.

9.3 Emigration

Bonnet macaque females, like those of many other cercopithecines, usually remain in their natal group throughout their lives. Rahaman and Parthasarathy (1969a), Ali (1981) and Moore and Ali (1984), however, provide some evidence that bonnet females may emigrate from their natal troops, a rare feature in most cercopithecine primates, which include the macaques, baboons, mangabeys and guenons.

Juvenile and adult bonnet macaque males often emigrate from their natal troops to join other troops, a typical cercopithecine feature (Sugiyama 1971; Simonds 1974; Makwana 1980; Pirta et al. 1981; Small 1982; Ali 1984). Males may leave either singly or in groups, consisting of brothers or close “friends” – individuals who associate significantly with each other during allogrooming and other affiliative interactions, and participate in coalitions (Sinha *pers. obs.*). Isolation of bonnet males during transfer is, however, rare; males move easily from one troop to another, spending little or no time in isolation (Sugiyama 1971; Simonds 1974, 1992). Males, who have left, may also later return to their original troops – another feature apparently unique to bonnets (Sugiyama 1971; Sinha *pers. obs*.). Bonnet males, however, also seem to rather unusual in being rather unpredictable in their emigration, some individuals even staying back to become the most dominant males in their respective natal troops (Ali 1981; Sinha *pers. obs*.).

Bonnet macaque males prefer to emigrate and join new troops only during the mating season. This may have been selected for since females prefer new immigrant males to resident males as sexual partners (Sinha *unpubl.*) and the costs of moving into new unfamiliar territories could perhaps be offset by this reproductive advantage (Datta Roy and Sinha 2001). The number of males joining a particular troop is also positively correlated to the number of resident males and females in the troop (Datta Roy and Sinha *unpubl.*). Whether such a choice is determined more by the absolute number of females in the group or by the relative reduction in cost to the resident males when the number of males is already high remains to be investigated.

Simonds (1973, 1974) suggests that certain young males may be prevented from being integrated into the network of social relationships prevalent within a troop; some of these males may then become outcast males and leave the troop to form temporary all-male groups within the troop's home range. A few such males may also return later and become reintegrated into the troop (Sugiyama 1971). Male isolation of this kind, a regular feature in rhesus and Japanese macaques (Simonds 1973), however, appears to be very rare among bonnets (Rahaman and Parthasarathy 1969a, Sinha *pers. obs*.). It is also not clear whether the formation of such groups of adolescent males can instead be explained by their motivation to leave their natal troop in search of new troops into which they can potentially emigrate.

9.4 Adult social relationships

Within a typical bonnet macaque troop, adult social relationships are typically characterised by extensive affiliative and agonistic interactions between virtually all individuals of different sex, dominance rank, age, and kinship groups.

Social relationships among females

During adulthood, bonnet females form strong, linear dominance hierarchies with daughters occupying dominance ranks just below those of their mothers, a typical cercopithecine feature (Sinha 1996; but see Silk *et al.* 1981b for matrilineal rank reversals in a captive troop). The linear nature of the hierarchy is very apparent during approach-retreat interactions (Sinha 1996), but not so distinct when other criteria such as competition for food, water, or mating partners are considered (Rahaman and Parthasarathy 1969a; Sugiyama 1971; Koyama 1973).

Aggression is usually directed down the dominance hierarchy, although rarely, subordinate females, and occasionally juvenile females rising in the hierarchy, may display non-contact aggression towards more dominant individuals (Sinha 1986, *unpubl. ethogram*). It is interesting that coalitions between two adult females against a higher-ranking female are almost non-existent among wild bonnet macaques; this could again reflect the rigidity of the dominance hierarchy and its acceptance among adult bonnet females. Such coalitions may, however, form in captive troops, a reflection perhaps of alternative social strategies under more stressful conditions (Silk 1981).

Affiliative relationships between females are usually strong, with high levels of allogrooming exchanged between genetic relatives as well as unrelated individuals (Koyama 1973; Ali 1981; Silk 1981; Small 1982; Kurup 1988; Sinha 1996). Bonnet females appear to distinguish between the frequency of initiated grooming and the duration of time spent grooming thereafter; initiated grooming is generally higher towards unrelated females, but more grooming time is spent with genetic relatives (Sinha 1986). In general, however, mothers with newly born infants attract relatively much more allogrooming than do those without infants (Koyama 1973; Ali 1981).

The exact pattern of allogrooming and other affiliative behaviour displayed by individuals relative to their positions in the dominance hierarchy is, however, extremely variable across different troops (Sinha *unpubl.*). In fact, amongst all primates, extensive unreciprocated grooming of subordinate individuals by dominant females has only been observed in bonnet macaques (Sinha 1996). Although it is still not clear why such unusual grooming patterns have evolved in this species, they could be determined by ecological conditions, genetic factors, or by idiosyncratic individual choice coupled with cultural transmission of such traits (Sinha, *unpubl.*).

In captivity, although adult females appear to allogroom genetic relatives and non-relatives at comparable rates (Defler 1978), they groom their relatives more reciprocally than they groom unrelated females of similar rank (Silk 1981). In addition, females are more likely to support their relatives in aggressive interactions than support non-relatives.

Provisioning of wild groups is usually marked by a sharp temporary increase in aggression and feeding supplants amongst the adult females (Ram *et al.* submitted). Dominant females direct contact aggression specifically towards higher-ranked subordinates, while subordinate females now increase non-contact aggression towards their dominant counterparts. Although the frequency of allogrooming and other affiliative behaviour decrease significantly during provisioning, grooming is much more reciprocated at the group level. Subordinate females also initiate relatively more allogrooming towards those dominant individuals who are most aggressive during this period. Social tensions thus increase markedly when bonnet macaques move from natural foraging to competing for provisioned food; individual females, however, can adopt altered behavioural patterns and modified social strategies under such rapidly changing ecological regimes.

Social relationships among males

Adult bonnet males form dominance hierarchies (linear amongst the more highly ranked individuals) that are apparently much more distinct than those amongst adult females (Simonds 1965; Sugiyama 1971). Male dominance hierarchies, however, appear to be much more unstable over time; this could be because they are usually reinforced through direct aggression and, therefore, dependent on the individuals' age and body condition (Sinha 1998a, *pers. obs.*). Occasional presenting to a dominant male followed by the mounting of the subordinate male is an important ritual that serves to display and reinforce the rank of a dominant male. Bonnets are, however, unusual in that dominant individuals too may solicit mounts from their subordinate counterparts (Simonds 1965; 33 % of the total mounts, Sugiyama 1971; Sinha *unpubl. ethogram*). Such mounts, especially amongst closely ranked adult males, are often accompanied by affiliative grappling, grunts and genital fondling, behaviours which possibly reduce tension and help to establish social relationships (Sugiyama 1971; Sinha *unpubl. ethogram*).

Aggression among male bonnet macaques is typically related to status striving, but much less constrained by the dominance hierarchy and by kinship relations than is aggression among females (Simonds 1965; Sugiyama 1971; Sinha *unpubl.*). In captivity as in the wild, unrelated males frequently form coalitions against other males; members of these coalitions support each other during aggressive encounters (Silk 1994; Sinha *unpubl.*). Although such coalitions could conceivably aid individuals to rise in the rank hierarchy, this was not apparently achieved in a captive troop (Silk 1993). Interestingly, male members of this captive group often held and carried male infants either as they approached, or when they were approached or threatened by dominant males (Silk and Samuels 1984). Since such males were less likely to be threatened, infants perhaps provide an effective buffer against aggression from other males. Ali (1981) also observed several cases of similar interaction involving adult and infant males in the wild, but could not confirm whether they were indeed true examples of agonistic buffering.

Bonnet males are unique amongst cercopithecine species in demonstrating extensive allogrooming and other affiliative behaviour towards each other, comparable in quality and levels to that shown by the females (Rajagopal 1965; Simonds 1965, 1977; Sugiyama 1971; Ali 1981; in captivity, Silk 1994). Individuals in most coalitions demonstrate extensive allogrooming and other affiliative interactions with each other (Simonds 1974; Ali 1981; Sinha 1998a; in captivity, Silk 1992, 1994). The absence of any correlation between individual dominance ranks and the levels of such affiliative behaviour displayed or received, however, indicates that bonnet 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 (Sugiyama 1971; Sinha 1998a).

Strong affiliative relationships rarely develop amongst cercopithecine primate males. The short overlap in residence time that average adult males share with each other, within the natal group or in the new groups that they subsequently join, might make investment in such relationships rather costly. But since bonnet males often tend to persist in their natal groups well past sexual maturity, strong social bonds may serve to increase inter-individual cohesion between them. A related interesting observation is that bonnet males actively defend group territories (Sinha, *unpubl.*); it is, however, the females that take over the mantle of territorial defence in other macaque species in which males invariably emigrate from their natal troops.

9.5 Sexual behaviour

Adult bonnet macaque males appear to follow different sexual strategies, with some males (dominant in the hierarchy, Sugiyama 1971) forming consortships of varying periods of time while others (subordinate or younger males, Sugiyama 1971) simply copulate opportunistically with the available females (Simonds 1965; Sinha *unpubl.*). In the southern subspecies (Ali 1981) and in some troops of the northern subspecies (Rahaman and Parthasarathy 1969a), however, consortships are apparently not formed. In captivity, Glick (1980) reports the formation of regular consortships that followed the age-graded pattern suggested by Sugiyama (1971).

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 – either in the wild (Rajagopal 1965; Simonds 1965; 0.01 % of the observed copulations, Rahaman and Parthasarathy 1969a; Sugiyama 1971; Ali 1984; Sinha *pers. obs.*) or in captivity (Glick 1980). Subadult or juvenile males are also not denied access to oestrus females.

Ali (1981), however, reports a positive correlation between male dominance rank and copulation frequency, a possible indicator of reproductive success, in *M. r. diluta*. Such a pattern may also hold for the unimale troops of the northern subspecies, where the single adult male apparently enjoys reproductive monopoly over the females and actively herds them away from other males in the vicinity (Datta Roy and Sinha 2001).

Most acts of copulation within the troop appear to be solicited by males (93 %, Simonds 1965; 78 %, Rahaman and Parthasarathy 1969a; Ali 1981). The copulatory act usually begins with a visual, olfactory or gustatory inspection of the female's genitalia by the male, often associated with specific behaviours like copulatory bobbing or copulatory lipsmacking (Simonds 1965; Kaufman and Rosenblum 1966; Sinha *unpubl. ethogram*). Since sexual swellings are not very apparent in females, the males actively examine most of the females every day during the mating season; receptivity is thus believed to be communicated to males primarily through olfactory signals (Rahaman and Parthasarathy 1971a).

Although bonnet macaque females are believed to be remarkably undiscriminating, mating freely with males of all ages and ranks (Simonds 1965; Rahaman and Parthasarathy 1969a; Sugiyama 1971), only rarely does a oestrus female walk up to a male, present to him and openly seek mating (Simonds 1965). It is, however, possible that females may often actively exercise mate choice by rather subtle manipulative strategies. These may include copulating with multiple males in rapid succession (Rahaman and Parthasarathy 1969a), refusing a copulatory solicitation (Simonds 1992), gazing at and leading a particular male away from the troop and secretly soliciting copulations from him behind rocks or trees (Sinha 2001), or breaking off a copulatory act and escaping from the male just prior to ejaculation (Rahaman and Parthasarathy 1969a; Sinha *unpubl.*).

Bonnet females clearly prefer to sexually solicit new immigrant males over resident males, even if the latter are much more dominant (Sinha *unpubl.*) Oestrus females from a troop have also been observed to sequentially leave the natal troop (one female on a particular day) and consort with a solitary adult male from a neighbouring troop – copulating several times with him to ejaculation – and then returning to the troop at the end of the day (Sinha *unpubl.*). It is conceivable that such strategies, in addition to providing genetic variability, could also serve as inbreeding avoidance mechanisms for a species where males may not invariably emigrate from the natal troop (see also Simonds 1992).

In experiments with paired captive bonnet macaques, familiarity between the sexual partners reduced aggression, enhanced allogrooming interactions, and led to successful copulation (Nadler and Rosenblum 1969). The age and dominance status of the sexual partners also appear to be important factors. Two-year-old bonnet males, for example, were capable of displaying adult copulatory patterns with young or relatively small receptive females, but not with mature adult females (Rosenblum and Nadler 1971).

Bonnet macaques represent one of the cercopithecine species that usually practice single mounts to copulation (Simonds 1965, 1992; Rahaman and Parthasarathy 1969a). Approximately 91-100 % of the observed copulations are of this kind; each mount consists of about five to 30 pelvic thrusts (Simonds 1965; five to 21 in captivity, Glick 1980) and lasts six to 16 seconds (Simonds 1992). Since single-mount ejaculations may be a strategy to ensure successful reproduction in competitive multimale situations, it would be interesting to determine whether the single adult males in unimale bonnet troops continue to display the phenomenon.

Since subadult and subordinate adult males may often copulate at higher frequencies than do the more dominant individuals including the alpha male, both in the wild (Simonds 1992) and in captivity (Shively *et al.* 1982), it has been suggested that reproductive success for bonnet males may depend on individual mating strategies rather than dominance rank (Simonds 1992). Although definitely plausible, the use of molecular fingerprinting techniques would alone be able to confirm such a hypothesis. Also, since, as mentioned earlier, bonnet macaque males do not invariably transfer out of their natal troops, the levels of inbreeding within groups and to what extent inbreeding avoidance mechanisms operate in these situations remain open questions.

A rather different situation, however, appears to prevail in captive troops. Here, very young males mate primarily with young or subordinate females, and with increasing maturity come greater access to older and then to dominant females, both throughout the mating season, as well as at the time of conception (Glick 1980; Samuels *et al.* 1984). Moreover, high-ranking adult males are far more successful than subordinates in gaining access to conceiving females and to dominant females; this is perhaps facilitated by the stronger affiliative relations that females establish with dominant males over that with subordinate males (Glick 1980; Samuels *et al.* 1984).

Ali (1981) suggests, from circumstantial evidence, that low rates of male transfer, extensive inbreeding within the group, a complete lack of sexual consortships, and most striking of all, regular female emigration may be characteristic features of the southern subspecies of the bonnet macaque. Since there are obviously marked differences from what is known about the northern subspecies, more detailed comparative studies of the two subspecies are required and should reveal the evolutionary origins and life history implications of these intriguing, but unique, social strategies.

9.6 Adult-juvenile-infant relationships

Mother-infant relationships

The mother-infant relationship in bonnet macaques continues for about six to eight months of age until the infant is gradually weaned, but is most intense for the first few weeks of life (Simonds 1965; Rahaman and Parthasarathy 1969a, 1971b; Nathan *et al.* 1972; Singh *et al.* 1980; Ali 1981). The mother is extremely protective of her offspring during this period and allomothering by other females is never allowed, even if the other female is much more dominant (Rahaman and Parthasarathy 1969a, 1971b; Simonds 1974; Sinha *unpubl.*). The infant is carried everywhere in the ventro-ventral position, with the mother periodically checking its position, especially after vertical climbs. It is only after about two months that the infant is periodically left on its own while its mother forages a few metres away (Simonds 1965). Suckling is the only way in which a bonnet mother provides nourishment to her offspring; there is absolutely no sharing of solid food between them (Simonds 1965; Sinha *pers. obs.*).

Allogrooming of the offspring by the mother occurs continuously, but other adult and juvenile females are allowed to groom the infant only after several weeks of age (Simonds 1974; Singh *et al.* 1980; Ali 1981; Sinha *pers. obs.*). Most adult females allow their infants to huddle to them (occasionally with a nipple in mouth even if she is non-lactating) until the next infant is born. The process of weaning is slow, and frequently accompanied by mild non-contact and contact aggression towards the infant (Simonds 1965, 1974; Singh *et al.* 1980; Sinha *unpubl. ethogram*). Weaning is complete with the arrival of a new infant; this is usually followed by very restricted interaction – primarily grooming, and sitting and following in close proximity – between the older infant and its mother (Sinha *pers. obs.*). The limited interaction that occurs between the two siblings is also largely of an affiliative nature, leading to the suggestion that sibling rivalry is virtually absent in bonnet macaques (Singh and Sachdeva 1977). The mother, however, continues to be protective of both her offspring, fending off aggression from other adults and juveniles, even well after the older infant has become an independent juvenile.

In a captive social group, variation in proximity between infants and their mothers was found to depend only on family composition, and not on group membership, survival of the last infant, infant sex or on maternal rank, parity, experience, or age (Silk 1991). Thus, infants that had several immature sisters in the group were initially more independent of their mothers than were infants with fewer or no sisters, but gradually became more dependent as they reached six months of age (Silk 1991). This seemed to be related to the fact that members of families with several immature females were targets of more aggression than were members of other families.

Adult female-infant relationships

Infant handling by females other than the mother is usually gentle and non-intrusive among bonnet macaques, although occasionally dominant females may pull roughly at an infant of a subordinate female (Sinha *pers. obs.*). Adult and juvenile females often allogroom infants of other females, and occasionally protect them from aggression by adult males or other juveniles.

In captivity, adult and subadult females handle both male and female infants at comparable frequencies; rates of handling decrease sharply as the infants mature (Silk 1999a). Infants are handled more by related females than by unrelated females and more by higher-ranking females than by lower-ranking ones. Silk (1999a) suggests that a strong attraction to infants may have been favoured by selection because females that are highly responsive to infants make good mothers.

A strikingly different aspect of adult female-infant relationships in bonnet macaques is embodied in the frequent kidnapping attempts initiated by dominant females toward the infants of lower-ranking females, observed in captivity (Silk 1980). In contrast to other macaques, both parous (including lactating) and nulliparous bonnet females participate in kidnapping interactions at comparable rates, although the frequency and pattern of these interactions differ within and between lineages. The mothers consistently resist these kidnapping acts, and most attempts are, therefore, unsuccessful. Since the kidnapping females do not appear to rise in status or gain maternal experience, and since the mothers of kidnapped infants do not benefit at all, kidnapping may represent a form of competition among females that is detrimental to both infants and their mothers (Silk 1980). It is noteworthy that kidnapping has never been reported in the wild, a reflection once again perhaps on the evolution of novel social strategies under stressful conditions that may prevail in captivity.

Adult male-infant relationships

Adult males occasionally tend to interact affiliatively with small infants, less than a year old. Young adult males usually direct over twice as much of huddling and maintaining close proximity to infants as do prime adult and dominant males (Brandt *et al.* 1970). For mature adult males, however, affiliative interactions are largely restricted only to male infants and only to certain adult male - male infant pairs (Sinha *unpubl.*). Certain adult males may, therefore, carry a particular male infant in the typical ventro-ventral position, often rather unsuccessfully, and may hug it or huddle to it for short periods of time. On rare occasions, an adult male may intervene on behalf of an infant that is being harassed by an adult female or any other troop member (Simonds 1992). There does not appear to be any other form of regular alloparental care by male bonnet macaques (Simonds 1992). Although Simonds (1992) considers this true paternal care, it is not clear whether the interacting adult males have indeed fathered those particular infants. There does, however, seem to be a positive correlation between the time spent by adult males with particular adult females and their subsequent interaction with the male infants of these females – whether these males have indeed sired the infants remains to be investigated (Sinha *unpubl.*).

Adult female-juvenile relationships

Kinship, rank and sex have complex and variable influences on the relationships of adult females and immature bonnet macaques in captive social groups (Silk *et al.* 1981c). Kinship is an obviously important factor, for example, because females groom related immatures at higher rates than the offspring of unrelated females. Dominance rank also appears to influence grooming by immatures – daughters of lower-ranking females groom adult females more than do daughters of higher-ranking individuals.

In general, adult females primarily direct severe forms of aggression towards immature non-relatives (Silk *et al.* 1981c). Interestingly, however, females display aggression at similar rates towards the offspring of relatives and those of high-ranking females. The influence of sex on these interactions are also rather clear because immature females receive more aggression from unrelated females and are injured at higher rates than are immature males of the same maternal rank. Comparative investigations into the social dynamics of wild bonnet troops should reveal the selective value of these interactions under conditions of captivity.

9.7 Play behaviour

Play begins for bonnet macaques in the form of hopping when they are first able to walk about, normally at about a month of age (Simonds 1965). Chasing begins by about two months and wrestling by about six months of age (Simonds 1965). Violent rough-and-tumble play and wresting is, however, generally confined to the older juvenile males, subadult males and adult males (Simonds 1965; Sugiyama 1971).

Adult bonnet males play actively with infant and juvenile males, a feature not too commonly met with among the macaques (Simonds 1965; Sugiyama 1971; Sinha *pers. obs.*). Age seems to play an important role in these interactions; all young males invariably play at high frequencies, prime adult males almost never play, and only some old adult males indulge in it

(Simonds 1965; Sinha *pers. obs.*). Although play could serve as a social strategy, especially as it begins to overlap with aggressive behaviour against competing males of similar rank and age (Simonds 1965, 1974), it also seems to be largely shaped by personality traits. Some individual males, for example, tend to play throughout their lives, sometimes even when they are hold very high positions in the dominance hierarchy (A. Datta Roy *pers. comm.*; Sinha *pers. obs.*).

It is noteworthy that infant and juvenile females do not play as much as do their male counterparts (Sinha *pers. obs.*) Adult females also play only very rarely. A middle-ranking adult female was, however, observed to play quite often, but only with her juvenile offspring of both sexes; this could again be more a reflection of her personality (Sinha *pers. obs.*) than any particular social strategy.

9.8 Group fission

In cercopithecine primates, including macaques, group fission among adult females usually occurs along genealogical lines, with subordinate matrilines breaking away from those more dominant to them. Very little is known, however, about the influence of social relationships on individual decisions made during fission. The social dynamics of a bonnet macaque troop prior to fission revealed that the patterns of allogrooming and affiliative interactions between females of different matrilines could correctly predict the subsequent divide within the group (Subramanian and Sinha 1999). It was also evident that different mechanisms guide decision-making processes when individual bonnet females make social choices of this kind, many of which could obviously have far-reaching effects on their life histories.

10. Communication and Cognition

The development and maintenance of complex social relationships between individuals of different ages, sexes, dominance ranks and kinship groups, as is typical of bonnet macaques, have been expected to select for enhanced communicative and cognitive abilities in individuals living in such groups. Cognitively sophisticated decision-making processes and communicative skills could provide an individual with an increasing diversity of potentially advantageous strategies during competition for food and other resources, aggressive interactions, or mate choice and sexual contests.

Communication

As is typical for cercopithecine primates, bonnet macaques use a repertoire of olfactory, gestural, postural, tactile, and vocal signals to communicate with each other in different social contexts (Simonds 1965, 1977; Rahaman and Parthasarathy 1968; Krishnan 1972; Roonwal and Mohnot 1977; Ali 1981; Hohmann 1989; Sinha *unpubl. ethogram*). In particular situations, composite signals involving a combination of those from different categories may be utilised (Rahaman and Parthasarathy 1968). During sexual interactions, olfactory cues resulting from cyclical changes in the cervical mucosa are invariably used by males to evaluate the condition of oestrus females (Rahaman and Parthasarathy 1971a; Roonwal and Mohnot 1977). Facial gestures, body postures and tactile behaviour are the major components of the repertoire used in affiliative, dominance and agonistic interactions, either singly or in combination (Simonds 1977); a total of approximately 45 such communicative acts have been documented (Sinha *unpubl. ethogram*). It is interesting that while several of these signals are common to many cercopithecines, some of them are unique to bonnet macaques (Rahaman and Parthasarathy 1968). Individual variability in the use of facial expressions and other visual signals within and across groups have, however, not been documented in this species.

An analysis of the vocal repertoire of the southern bonnet subspecies – *M. r. diluta* – revealed at least 25 basic patterns (Hohmann 1989). The repertoire consists of well-separated sound classes as well as acoustic categories connected by structural intergradation. Besides structural variations within and between different elements of the repertoire, the vocal system is characterised by regular combinations of particular basic patterns, some of which are used in very different social contexts. Sex-specific asymmetries in these vocal signals also appear to be less pronounced than are the age-dependent characteristics (Hohmann 1989). Again, as with visual communication, there is some consistency in the composition and structural design of the vocal repertoire across different macaque species; there are, however, several structural and behavioural characteristics unique to the species (Krishnan 1972; Hohmann 1989).

Bonnet macaques also give loud alarm calls in response to different ground predators including tigers, leopards, dholes, jackals, domestic dogs and humans (Krishnan 1972; Makwana 1980; Hohmann 1989; Coss and Ramakrishnan 2000; Sinha *pers. obs.*). In addition to the visual detection of a potential predator, warning calls of distant conspecifics or other animals (including the common langur, Nilgiri langur, chital, sambar and giant squirrels) release alarm calls as well (Hohmann 1989; Ramakrishnan and Coss 2000). Raptors and large snakes, however, do not usually evoke any alarm response (Hohmann 1989).

Cognition

Studies on social cognition in bonnet macaques have so far documented knowledge of dominance ranks and social relationships (Sinha 1998b; Silk 1999b) and tactical deception (Sinha 1999; Sinha and Datta Roy 2001b) in this species. Patterns of agonistic behaviour and allogrooming choices provide evidence, for example, that wild bonnet females seem to be aware of the social popularity (as measured by the grooming received from all troop members) and relative dominance ranks of other individuals (Sinha 1998b). Such knowledge, used during decision-making, appears to be egotistical in that other individuals are evaluated relative to oneself, integrative in that information about all social interactants are used simultaneously, and hierarchical in the ability to preferentially utilise certain categories of knowledge for the storage of related information from other domains. Although it is clear that individual bonnet macaques observe and acquire social information about each other, it is still not understood how they evaluate the dominance ranks of others.

In a captive socially housed group, adult bonnet males consistently chose allies who outranked themselves and their opponents, and made such choices apparently on the basis of their knowledge of about third-party rank relationships (Silk 1999b).

Wild bonnet macaques also appear to employ tactical deception in a variety of social situations including contests over food, agonistic interactions and competition for allogrooming and mating partners (Sinha and Datta Roy 2001b). Several individuals exhibit simple manipulative behaviour, usually belonging to a single category of deceptive acts (Byrne and Whiten 1990). Other individuals, however, are versatile and employ deceptive strategies of different categories in different situations; these could include males who change their repertoire of deceptive acts following emigration into another troop. The display of some of these complex manipulative behaviours could perhaps be ascribed to opportunistic acquisition of deceptive strategies by rapid trial-and-error and other kinds of social learning. The striking individual variation in the preferential use of certain categories of deception in particular contexts and the fact that individuals did not invariably use these strategies in near-identical situations, however, suggests that bonnet macaques may be capable of intentional tactical deception, reminiscent of human-like deception in some ways (Sinha 1999).

Another aspect of primate intelligence concerns the ability that monkeys may have possibly evolved in response to the mechanical and technical challenges of their environment: the manufacture and use of tools. From an evolutionary point of view, tool-using abilities are believed to have originated as adaptations for omnivorous extractive foraging on embedded foods and many macaque species, which are generalist foragers on fruits and foliage, have been considered poor tool users. Bonnet macaques, however, do have the potential to elaborate tools under different, more specific, contexts (Sinha 1997). An old female, for example, was often observed to insert a short twig, dry stick, stiff leaf or grass blade, or a leaf-midrib into her vagina and scratch vigorously, possibly in response to some persistent irritation. What was more remarkable, however, was that on several occasions, she actively manufactured or modified her tools. The complex nature of this tool manufacture suggests that fairly sophisticated cognitive abilities, involving mental representation, may underlie active object manipulation of this kind.

11. Acknowledgements

I owe a deep sense of gratitude to my students and colleagues, particularly Anirban Datta Roy, Anupama Deshpande, Sunita Ram, K.A. Subramanian and Suri Venkatachalam, who have shared my love for bonnet macaques and from whom I have learnt much. I thank the University of Agricultural Sciences, Bangalore, for allowing me to observe bonnet macaques on their campus and the Forest Departments of Karnataka and Tamil Nadu for permission to conduct my research in the Bandipur National Park and Mudumalai Wildlife Sanctuary, respectively. A research grant from the Wenner-Gren Foundation for Anthropological Research, New York, U.S.A., which led to the initiation of the project on the demography of bonnet populations in Bandipur and Mudumalai, is gratefully acknowledged. I would also like to thank A.J.T. Johnsingh, who originally commissioned this review, for inspiring me and for his patience with me. My work has always been sustained by the constant enthusiasm, support and encouragement of Niranjan V. Joshi and T.R. Shankar Raman – they have contributed much more to my thinking and actions than they will ever know. Finally, I owe this paper and all my research efforts to Kakoli Mukhopadhyay, who, I know, will not like being acknowledged but without whom none of this would have ever been possible.

12. References

Agoramoorthy, G., Smallegange, I., Spruit, I. and Hsu, M.J. 2000. Swimming behaviour among bonnet macaques in Tamil Nadu. *Folia Primatologica* 71: 152-153.

Ali, R. 1981. The Ecology and Social Behaviour of the Agastyamalai Bonnet Macaque. Ph.D. thesis, Bristol University, Bristol, U.K.

Ali, R. 1984. Sexual behaviour in the southern bonnet macaque, *Macaca radiata diluta*. *International Journal of Primatology* 5: 319.

Ali, R. 1988. Feeding ecology of the bonnet macaque of the Mundanthurai Sanctuary, Tamilnadu. *Journal of the Bombay Natural History Society* 83: 98-110.

Anderson, J.R. 1998. Home range (core area) squatting in bonnet macaques *Macaca radiata*. *Mammalia* 62: 595-599.

Blanford, W.T. 1888-91. The fauna of British India including Burma and Ceylon: Mammalia. Taylor and Francis, London.

Brandt, E.M., Irons, R. and Mitchell, G. 1970. Paternalistic behavior in four species of macaques. In: Riss III, W. (ed.) *Brain, Behaviour and Evolution*. Karger, Basel. Pp. 415-420.

Byrne, R.W. and Whiten, A. 1990. Tactical deception in primates: The 1990 data-base. *Primate Report* 27: 1-101.

Coss, R. G. and Ramakrishnan, U. 2000. Perceptual aspects of leopard recognition by wild bonnet macaques (*Macaca radiata*). *Behaviour* 137: 315-336.

Defler, T.R. 1978. Allogrooming in two species of macaque (*Macaca nemestrina* and *Macaca radiata*). *Primates* 19: 153-167.

Delson, E. 1980. Fossil macaques, phyletic relationships and a scenario of deployment. In: Lindburg, D.G. (ed.) *The Macaques: Studies in Ecology, Behavior and Evolution*. Van Nostrand Reinhold Company, New York. Pp. 10-30.

D'Souza, L. and Singh, M. 1992. Density and demography in roadside bonnet monkeys *Macaca radiata* around Mysore. *Journal of Ecobiology* 4: 87-93.

Fooden, J. 1981. Taxonomy and evolution of the sinica group of macaques: 2. Species and subspecies accounts of the Indian bonnet macaque, *Macaca radiata*. *Fieldiana: Zoology*, N.S. 9: 1-52.

Fooden, J. 1986. Taxonomy and evolution of the sinica group of macaques: 5. Overview of natural history. *Fieldiana: Zoology*, N.S. 29: 1-22.

Fooden, J. 1989. Classification, distribution and ecology of Indian macaques. In: Seth, P.K. and Seth, S. (ed.) *Perspectives in Primate Biology Vol 2*. Today and Tomorrow's Printers and Publishers, New Delhi. Pp. 33-46.

Fooden, J., Mahabal, A. and Saha, S.S. 1981. Redefinition of rhesus macaque – bonnet macaque boundary in peninsular India. *Journal of the Bombay Natural History Society* 78: 463-474.

Glick, B.B. 1980. Ontogenetic and psychobiological aspects of the mating activities of male *Macaca radiata*. In: Lindburg, D.G. (ed.) *The Macaques: Studies in Ecology, Behavior and Evolution*. Van Nostrand Reinhold, New York. Pp. 345-370.

Hartman, C.G. 1938. Some observations on the bonnet macaque. *Journal of Mammalogy* 19: 468-474.

Hinton, M.A.C. and Wroughton, R.C. 1921. On the nomenclature of the South Indian long-tailed macaque. *Journal of the Bombay Natural History Society* 27: 813-815.

Hohmann, G. 1989. Vocal communication of wild bonnet macaques *Macaca radiata*. *Primates* 30: 325-345.

Kaufman I.C. and Rosenblum, L.A. 1966. A behavioral taxonomy for *Macaca nemestrina* and *Macaca radiata*: Based on longitudinal observation of family groups in the laboratory. *Primates* 7: 206-258.

Koyama, N. 1973. Dominance, grooming, and clasped-sleeping relationships among bonnet monkeys in India. *Primates* 14: 225-244.

Koyama, N. and Shekar, P.B. 1981. Geographic distribution of the rhesus and bonnet macaques in west-central India. *Journal of the Bombay Natural History Society* 78: 240-255.

Krishnamani, R. 1994. Diet composition of the bonnet macaque *Macaca radiata* in a tropical dry evergreen forest of southern India. *Tropical Biodiversity* 2: 285-302.

Krishnan, M. 1955. Ancient depictions of Hanuman. In: Guha, R. (ed.). *Nature's Spokesman: M. Krishnan and Indian Wildlife*. Oxford University Press, New Delhi. Pp. 32-34.

Krishnan, M. 1972. An ecological survey of the larger mammals of peninsular India. Part I. *Journal of the Bombay Natural History Society* 68: 503-555.

Kumar, A. and Kurup, G.U. 1985. Sexual behavior of the lion-tailed macaque, Macaca silenus. In: Heltne, P.G. (ed.) *The Lion-tailed Macaques: Status and Conservation. Monographs in Primatology, Vol 7*. Alan R. Liss, New York. Pp. 109-130.

Kurup, G.U. 1981. Report on the census surveys of rural and urban populations of non-human primates of south India. Man and Biosphere Programme: Project No 124. Zoological Survey of India, Calicut.

Kurup, G.U. 1988. The grooming patterns in bonnet macaques. *Annals of the New York Academy of Sciences* 525: 414-416.

Kuruvilla, G.P. 1980. Ecology of the bonnet macaques (*Macaca radiata*) with special reference to feeding habits. *Journal of the Bombay Natural History Society* 75: 976-988.

Makwana, S.C. 1980. Observations on population and behaviour of the bonnet monkey. *Comparative Physiology and Ecology* 5: 9-12.

McCann, C. 1933. Notes on some Indian macaques. *Journal of the Bombay Natural History Society* 36: 796-810.

Miller, G.S., Jr. 1933. The groups and names of macaques. In: Hartman, C.G. and Straus, W.L., Jr. (eds.) *The Anatomy of the Rhesus Monkey (Macaca mulatta)*. Hafner, New York. Pp. 1-9.

Nadler, R.D. and Rosenblum, L.A. 1969. Sexual behavior of male bonnet monkeys in the laboratory. *Brain and Behavioral Evolution* 2: 482-497.

Narain, S.D. 1965. Eco-ethological studies on *Macaca radiata* at Madumalai Wildlife Sanctuary, south India. *Tigerpaper* 12: 29-32.

Nathan, T.S., Kaufman, I.C. and Rosenblum, L.A. 1972. Perinatal observations of mother infant behavior in the bonnet macaque. *Annals of Psychiatry and Related Disciplines* 10: 245-266.

Nolte, A. 1955. Field observations on the daily routine and social behaviour of common Indian monkeys with special reference to the bonnet monkey *Macaca radiata* Geoffroy. *Journal of the Bombay Natural History Society* 53: 177-184.

Oi, T. (1996). Sexual behaviour and mating system of the wild pig-tailed macaque in West Sumatra. In: Fa, J.E. and Lindburg, D.G. (eds.) *Evolution and Ecology of Macaque Societies*. Cambridge University Press, Cambridge. Pp. 342-368.

Parthasarathy, M.D. 1972. Some comparative aspects of the socioecology and behavior of the Hanuman langur (*Presbytis entellus*) and the bonnet macaque (*Macaca radiata*). *Abstracts of the Fourth International Congress of Primatology*, Portland, U.S.A., August 1972. Pp. 56.

Parthasarathy, M.D. 1977. Ecology and ethology of Hanuman langur *Presbytis entellus* and the bonnet macaque *Macaca radiata*. In: Prasad, M.R.N. and Anand Kumar, T.C. (eds.) *Use of Non-Human Primates in Biomedical Research*. Indian National Science Academy, New Delhi. Pp. 46-51.

Pirta, R.S., Prakash, P. and Singh, M. 1981. A population study of two species of non-human primates: *Macaca mulatta* and *Macaca radiata*. *Journal of the Bombay Natural History Society* 77: 429-434.

Plimpton, E.H., Swartz, K.B. and Rosenblum, L.A. 1981. The effects of foraging demand on social interactions in a laboratory group of bonnet macaques. *International Journal of Primatology* 2: 175-185.

Pocock, R.I. 1931. The long-tailed macaque monkeys (*Macaca radiata* and *M. sinica*) of southern India and Ceylon. *Journal of the Bombay Natural History Society* 35: 276-288.

Pocock, R.I. 1939. Mammalia. I. Primates and Carnivora in Fauna of British India, including Ceylon and Burma. Taylor and Francis, London.

Prater, S.H. 1980. The Book of Indian Animals, 4th ed. Bombay Natural History Society, Mumbai.

Rahaman, H. 1975. Feeding of bonnet macaque on coffee, orange, cardamom and rice. *Indian Journal of Agricultural Sciences* 45: 44-46.

Rahaman, H. and Parthasarathy, M.D. 1967. A population survey of the bonnet monkey, *Macaca radiata* (Geoffroy), in Bangalore, south India. *Journal of the Bombay Natural History Society* 64: 251-255.

Rahaman, H. and Parthasarathy, M.D. 1968. The expressive movements of the bonnet macaque. *Primates* 9: 259-272.

Rahaman, H. and Parthasarathy, M.D. 1969a. Studies on the social behaviour of bonnet monkeys. *Primates* 10: 149-162.

Rahaman, H. and Parthasarathy, M.D. 1969b. The home range, roosting places and day ranges of the bonnet macaque *Macaca radiata*. *Journal of Zoology, London* 157: 267-276.

Rahaman, H. and Parthasarathy, M.D. 1971a. The role of the olfactory signals in the mating behaviour of bonnet monkeys (*Macaca radiata*). *Communications in Behavioral Biology* 6: 97-104.

Rahaman, H. and Parthasarathy, M.D. 1971b. Infant dependence on its mother among the bonnet macaque. *Communications in Behavioral Biology* 5: 315-320.

Rahaman, H. and Parthasarathy, M.D. 1979. Behavioural variants of bonnet macaques (*Macaca radiata*) inhabiting cultivated gardens. *Journal of the Bombay Natural History Society* 75: 406-425.

Rajagopal, A.S. 1965. Some observations on the social behaviour of the bonnet monkeys *Macaca radiata* of south India. *Journal of the Bengal Natural History Society* 33: 228-238.

Ram, S and Sinha, A. 1999. Behavioural strategies adopted by wild bonnet macaques during natural foraging and provisioning. *NIAS Report R 1-99*

Ram, S., Venkatachalam, S. and Sinha, A. 2001. Changing behavioural strategies of wild female bonnet macaques during natural foraging and on provisioning. *Submitted*

Ramakrishnan, U., and Coss, R. G. 2000. Recognition of heterospecific alarm vocalizations by bonnet macaques (*Macaca radiata*). *Journal of Comparative Psychology* 114: 3-12.

Rao, A.J., Ramesh, V., Ramachandra, S.G., Krishnamurthy, H.N., Ravindranath, N. and Moudgal, N.R. 1998. Growth and reproductive parameters of bonnet monkey (*Macaca radiata*). *Primates* 39: 97-107.

Roonwal, M.L. and Mohnot, S.M. 1977. Primates of South Asia: Ecology, Socio-biology and Behavior. Harvard University Press, Cambridge, Mass.

Rosenblum, L.A. and Kaufman, I.C. 1967. Laboratory observations of early mother-infant relations in pigtail and bonnet macaques. In: Altmann, S.A. (ed.). *Social Communication among Primates*. University of Chicago Press, Chicago. Pp. 33-41.

Rosenblum, L.A. and Nadler, R.D. 1971. The ontogeny of sexual behavior in male bonnet macaques. In: Ford, D.H. (ed.) *Influence of Hormones on the Nervous System*. S. Karger, Basel. Pp. 388-400.

Saha, S.S. 1984. The present southern limit of the rhesus macaque (Macaca mulatta) in peninsular India, specially in the Godavari and the Krishna river basins. In: Roonwal, M.L., Mohnot, S.M. and Rathore, N.S. (eds.) *Current Primate Researches*. Zoology Department, Jodhpur University, Jodhpur. Pp. 153-165.

Samuels, A., Silk, J.B. and Rodman, P.S. 1984. Changes in the dominance rank and reproductive behaviour of male bonnet macaques (*Macaca radiata*). *Animal Behaviour* 32: 994-1003.

Schlotterhausen, L. 1992. Interactions between People and Bonnet Monkeys *Macaca radiata* at Alagarkoil, a South Indian Temple. M.A. thesis, New York University, New York, U.S.A.

Schlotterhausen, L. 1999. Town Monkeys, Country Monkeys: A Socioecological Comparison of a Human Commensal and Wild Group of Bonnet Macaques (*Macaca radiata*). Ph.D. thesis, New York University, New York, U.S.A.

Shively, C., Clarke, S., King, N., Schapiro, S. and Mitchell, G. 1982. Patterns of sexual behavior in male macaques. *American Journal of Primatology* 2: 373-384.

Silk, J.B. 1980. Kidnapping and female competition among captive bonnet macaques. *Primates* 21: 100-110.

Silk, J.B. 1981. Altruism among female *Macaca radiata*: Explanation and analysis of patterns of grooming and coalition formation. *Behaviour* 79: 162-188.

Silk, J.B. 1988a. Social mechanisms of population regulation in a captive group of bonnet macaques (*Macaca radiata*). *American Journal of Primatology* 14: 111-124.

Silk, J.B. 1988b. Maternal investment in captive bonnet macaques (*Macaca radiata*). *American Naturalist* 132: 1-19.

Silk, J.B. 1989. Reproductive synchrony in captive macaques. *American Journal of Primatology* 19: 137-146.

Silk, J.B. 1990. Sources of variation in interbirth intervals among captive bonnet macaques (*Macaca radiata*). *American Journal of Physical Anthropology* 82: 213-230.

Silk, J.B. 1991. Mother-infant relationships in bonnet macaques: Sources of variation in proximity. *International Journal of Primatology* 12: 21-38.

Silk, J.B. 1992. The patterning of intervention among male bonnet macaques: Reciprocity, revenge and loyalty. *Current Anthropology* 33: 318-325.

Silk, J.B. 1993. Does participation in coalitions influence dominance relationships among male bonnet macaques? *Behaviour* 126: 171-189.

Silk, J.B. 1994. Social relationships of male bonnet macaques: Male bonding in a matrilineal society. *Behaviour* 130: 271-291.

Silk, J.B. 1999a. Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Animal Behaviour* 57: 1021-1032.

Silk, J.B. 1999b. Male bonnet macaques use information about third-party rank relationships to recruit allies. *Animal Behaviour* 58: 45-51.

Silk, J.B. and Samuels, A. 1984. Triadic interactions among *Macaca radiata*: Passports and buffers. *American Journal of Primatology* 6: 373-376.

Silk, J.B., Clark-Wheatley, C.B., Rodman, P.S. and Samuels, A. 1981a. Differential reproductive success and facultative adjustment of sex ratios among captive female bonnet macaques (*Macaca radiata*). *Animal Behaviour* 29: 1106-1120.

Silk, J.B., Samuels, A. and Rodman, P.S. 1981b. Hierarchical organization of female *Macaca radiata* in captivity. *Primates* 22: 84-95.

Silk, J.B., Samuels, A. and Rodman, P.S. 1981c. The influence of kinship, rank, and sex on affiliation and aggression between adult female and immature bonnet macaques (*Macaca radiata*). *Behaviour* 78: 111-137.

Simonds, P.E. 1965. The bonnet macaque in south India. In: DeVore, I. (ed.) *Primate Behavior: Field Studies of Monkeys and Apes*. Holt, Winehart and Winston, New York. Pp. 175-196.

Simonds, P.E. 1973. Outcast males and social structure among bonnet macaques (*Macaca radiata*). *American Journal of Physical Anthropology* 38: 599-604.

Simonds, P.E. 1974. Sex differences in bonnet macaque networks and social structure. *Archives of Sexual Behavior* 3: 151-166.

Simonds, P.E. 1977. Aggression and social bonds in an urban troop of bonnet macaques. *American Journal of Physical Anthropology* 47: 160-166.

Simonds, P.E. 1992. Primate behavioral dynamics. In: Seth, P.K. and Seth, S. (ed.). *Perspectives in Primate Biology Vol 4*. Today and Tomorrow's Printers and Publishers, New Delhi. Pp. 95-109.

Singh, M. and Pirta, R.S. 1978. Movement out of home range and disturbed behaviour patterns in a group of bonnet macaques: *Macaca radiata*. *American Journal of Physical Anthropology* 49: 265-269.

Singh, M. and Sachdeva, R. 1977. Behaviour of juvenile bonnet monkey before and after his mother gives birth to a new baby. *Primates* 18: 605-610.

Singh, M. and Vinathe, S. 1990. Inter-population differences in the time-budgets of bonnet monkeys *Macaca radiata*. *Primates* 31: 589-596.

Singh, M., Akram, N. and Pirta, R.S. 1984. Evolution of demographic patterns in the bonnet monkey *Macaca radiata*. In: Roonwal, M.L., S.M. Mohnot and N.S. Rathore (eds.). *Current Primate Researches*. Zoology Department, Jodhpur University, Jodhpur. Pp. 7-16.

Singh, M., Prakash, P. and Pirta, R.S. 1980. Changing patterns of behaviour during the early stages of bonnet monkey *Macaca radiata*. *Proceedings of the Indian Academy of Sciences Animal Sciences* 89: 101-108.

Singh, M., Singh, M., Kumara, H.N., Kumar, M.A. and D'Souza, L. 1997. Inter- and intra-specific associations of non-human primates in Anaimalai hills, south India. *Mammalia* 61: 17-28.

Sinha, A. 1996. A new twist in an old macaque tale: Allogrooming relationships among wild female bonnet macaques. Abstract at the *16th Congress of the International Primatological Society*, *Madison, Wisconsin, USA*, August 1996.

Sinha, A. 1997. Complex tool manufacture by a wild bonnet macaque, *Macaca radiata*. *Folia Primatologica* 68: 23-25.

Sinha, A. 1998a. Affiliative relationships and coalition formation among wild male bonnet macaques. Abstract at the *17th Congress of the International Primatological Society*, *Antananarivo, Madagascar*, August 1998.

Sinha, A. 1998b. Knowledge acquired and decisions made: Triadic interactions during allogrooming in wild bonnet macaques, *Macaca radiata*. *Philosophical Transactions of the Royal Society, London: Biological Sciences* 353: 619-631.

Sinha, A. 1999. Tactical deception in wild bonnet macaques: Evidence of intentionality. *Advances in Ethology* 34: 103. Abstract at the *26th International Ethological Conference, Bangalore, India*, August 1999.

Sinha, A. and Datta Roy, A. 2001a. The bonnet macaques of Bandipur: Social evolution in a wild primate species; submitted.

Sinha, A. and Datta Roy, A. 2001b. True lies: Tactical deception in wild bonnet macaques, *Macaca radiata*. *NIAS Report, National Institute of Advanced Studies, Bangalore*; in preparation.

Small, M.F. 1982. Comparative social behaviour of adult female rhesus macaques and bonnet macaques. *Zeitschrift für Tierpsychologie* 59: 1-6.

Subramanian, K.A. and Sinha, A. 1999. Social relationships influence decision-making during group fission in wild bonnet macaques. *Advances in Ethology* 34: 142. Abstract at the *26th International Ethological Conference, Bangalore, India*, August 1999.

Sugiyama, Y. 1971. Characteristics of the social life of bonnet macaques *Macaca radiata*. *Primates* 12: 247-266.