Chapter 8

Concluding remarks
The distribution of species is governed by various factors, the more important of which include the location and time of their origin, historical radiation patterns, their ecological flexibility and the interspecies competition faced by them. The bonnet macaque and the rhesus macaque, two of the most common of the eight macaques of India, share a common distribution boundary in central India, which, in the last few decades, appears to have changed significantly under human influence. There also seems to have been concomitant demographic changes in these regions with the appearance of a unique kind of mixed-species troops in which individuals of one species are stably integrated into the troops of the other species. The focus of this thesis was to examine the possible factors that have led to the formation of such troops and to conduct a study on their distribution and social behaviour, especially in comparison with pure troops of rhesus and bonnet macaques.

This thesis thus consists of two sections, the first section describing the biogeographic distribution and demography of the two common macaque species and their mixed-species troops in peninsular India. The second section of the thesis attempts to understand the formation of these unusual troops from the interactions of these two primates and examines their behavioural dynamics. In the final concluding pages of this thesis, I present a brief review and draw some conclusions arising from this work.

8.1 Changing distributions

The distribution patterns of rhesus and bonnet macaques had never before been clearly delineated in the central regions of peninsular India prior to this work; a single common distribution boundary alone had been proposed. Based on extensive surveys, this study has re-defined the geographical distribution of these two species, especially where they abound against one another. One of the most striking features of the recent changes in the distribution of these species is the formation of an overlap zone in eastern peninsular India, wherein the rhesus macaque has extended its range southward into areas typically inhabited by the bonnet macaque, facilitated by the translocation of individuals from regions of human-primate conflict and human-induced land use changes. This study also reports the occurrence of a number of mixed-species troops of these two species in the overlap
zone of their respective distribution ranges. Such an overlap appears to have
developed in the recent past either due to the range extension of the rhesus
macaque brought about by anthropogenic land-use changes or due to the
translocation of problem rhesus macaque individuals into the distribution range of
the bonnet macaque. Although the current study is localised to peninsular India, a
pan-Indian or even a pan-Asian study would throw valuable light of the present
distribution of the rhesus macaque, a species second only to humans in its
distribution and ecological adaptability, as well as its interactions with other
macaques sympatric to it.

8.1.1 Whither bonnet macaques?

Many species that were once extensively distributed or had large populations
worldwide have undergone drastic declines or even extinctions, as for example,
passerine pigeons, vultures or common sparrows. The need for conservation of
many of these species has to be prioritised as funds available for conservation are
extremely limited and the directives of world-bodies like the IUCN are followed in
directing such universally recognised conservation priorities. The neglect of species
lower in conservation priorities, belonging to the lower categories of the IUCN list,
for example, is, however, not judicious as these low-concern species can become
rare or extinct even by a single calamity. The case of the endemic bonnet macaque
is one such example. With recent studies reporting drastic declines in bonnet
macaque populations in different regions (Singh and Rao 2004; Kumara et al 2009;
Kumara et al 2010; Singh et al. 2011), this once-common species now requires
urgent conservation action even though it is considered a problematic pest species
in many areas where it occurs together with people.

8.1.2 Monkeys of a feather?

The formation of stable mixed-species troops, particularly among primates, is an
interesting phenomenon. In areas where both species are present, a dispersing
individual may find more troops of the other species and integrate into such groups
in the absence of conspecifics. Such integrations have been observed to be rather
stable and have given rise to widespread speculation that hybrid individuals may
result from these associations. The formation of such hybrids due to gene flow across closely related species may be quite common in macaques though recognition of hybrid individuals based on shared morphological traits may not always be possible. Hybridisation is likely to be a strong force in speciation and many new species are believed to have emerged from the union of species. Amongst macaques, the stump-tailed macaque *Macaca arctoides* (Tosi et al. 2003) and the Arunachal macaque *M. munzala* (Chakraborty et al. 2007) clearly illustrate the potential of speciation arising from past hybridisation events. Genetic studies are thus essential to establish the occurrence of hybridisation and to understand the nature of the subsequent processes leading to the formation of new species.

### 8.2 Differing demographies

Rhesus macaques and bonnet macaques appear to prefer different habitats, with the former occurring mainly in anthropogenic areas where they form relatively larger troops. Bonnet macaques, in contrast, are principally distributed in forested habitats where they, in turn, live in larger troops as opposed to the much smaller groups observed in urban and rural areas. A striking, albeit disturbing, observation made by our study is that of the lower birth rate that prevails in relatively larger troops of bonnet macaques in contrast to the situation in rhesus macaques where the birth rate increases with increasing group size. These rapidly growing troops of rhesus macaques in urban and rural areas thus come in direct competition with the resident human populations, leading to elevated conflict, accentuated by the aggressive temperament of both species. This, unfortunately, has serious implications for other primate species, which occasionally face increasing human intolerance and retaliation, even though they may not be as aggressive as rhesus macaques.

Our study has also documented an absence of significant differences in the demography of each species in the habitats in which they were studied, possibly due to a common adaptation to the presence of competing species such as humans. Such demographic analyses over the entire distribution range of a species may provide evidence for the ecological flexibility of the species, especially in response
to various environmental pressures including those arising from anthropogenic activities.

8.3 Patterns of behaviour

The nature of social relationships that prevail in mixed-species groups of social primates have rarely before been studied in any detail. This thus led us to conduct a quantitative study on the patterns of social behaviour that characterise mixed-species troops of bonnet and rhesus macaques, especially in comparison to that displayed by these species alone.

8.3.1 Female bonnet macaques

Adult female bonnet macaques were observed to form stable, linear, transitive dominance hierarchies with a relative lack of nepotism, in which affiliative behaviours including allogrooming were preferentially directed down the hierarchy. In spite of such general trends, however, certain adult females exhibited idiosyncratic choices in their grooming partners, which cut across categories of age, kinship and dominance ranks. This, I am of the opinion, could potentially be attributed to inherited differences in the personality and temperament of these females, individual attributes the importance of which are only now being recognised. Comparative studies on the consistency of such behavioural traits in space and time over a large number of troops and individuals in the future could establish the importance of these individual attributes in the appearance of group-level behavioural patterns.

8.3.2 Female rhesus macaques

Rhesus macaque females, in contrast to bonnet macaques, distributed affiliative behaviours up the dominance hierarchy, a more characteristic feature of female-bonded cercopithecine species. This is a more nepotistic species and certain allogrooming patterns displayed by the females allowed us to identify matriline and kin-related subgroups within the troop. More rigorous studies on a larger number of troops could provide a more detailed understanding of the social
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behaviour of this species, especially with regard to the formation of subgroups, often in response to the ecology of the group’s home range.

8.3.3 An uneasy alliance?

A close study of the behaviour of the female bonnet macaques and the sole female rhesus macaque in each of two mixed-species troops has clearly revealed the importance of the level of integration of the foreign species in the group while reiterating the importance of ecology in driving the evolution of social behavioural patterns in these two species. The difference in affiliative behaviour displayed by these two troops – one in a forested habitat and the other in an area with human habitations – could, for example, be attributed to differences in their ecological habitats. The differential nature of interactions of the females of the major species with the lowest-ranked conspecific female and with the female of the foreign species in the two troops, on the other hand, was possibly due to differences in the level of integration of the latter female in these two groups. More detailed studies on a greater number of troops in different environments could enable us to distinguish between ecological and behavioural factors in determining the nature of behavioural interactions between the two species in such mixed-species troops.

Our comparison of the behavioural patterns of the adult females of the mixed-species troops with those of the pure-species troop suggests that local ecological factors could be more important that phylogenetic inertia in determining the patterns of behaviour displayed by the two species that reside in mixed troops. It is noteworthy that I was also able to observe significant behavioural changes in the repertoire of one of the species, with the bonnet macaque females in both mixed-species troops frequently emitting food calls, a typical feature of rhesus macaques. There were, however, differences in the structure of this call, with the troop in the anthropogenic habitat using the typical rhesus call while the calls used by the females in the forested area had a distinct structure. There were also qualitative differences in the gestures used by the females in the mixed-species troops but they appeared to be recognised by members of both species possibly because of the close phylogenetic relationships between rhesus and bonnet macaques. More studies are, however, required to unravel the processes by which individuals of one
species, integrated into the troop of another, are able to learn new communicatory signals and incorporate them into their own behavioural repertoire.

8.4 The way ahead!

This thesis addresses several questions concerning the distribution, demography and behaviour of cercopithecine mixed-species troops but also paves the way for further questions and newer avenues of research needed to understand the dynamics of such troops. A more rigorous study on these aspects of mixed-species troop biology would enable a better comprehension of the processes involved in their formation. More important, however, are the concerns raised in this work regarding the status of rhesus and bonnet macaques in the regions of overlapping distributions and the problems they face from unplanned translocations and conflict with people. Thus, even as we begin to understand many aspects of their biology, hitherto unstudied, we must explore how the many threatened populations of such commensal species continue to survive amidst overwhelming odds and ensure that we are able to evolve strategies to protect them from local extinction.