Predominant primate socioecological theories explain observed variations in social systems (and its components) among primate species through different environmental scenarios that promote different grouping patterns, giving rise to specific social structures within which particular behavioural patterns also evolve. They also emphasise the relatively greater challenges faced by females due to changing natural and social environments as, in most primate species, females are responsible for the birth and survival of the offspring. Thus, while female reproductive success is dependent upon the availability of vital natural resources such as food, males depend more upon the availability of fertilisable females in space and time to maximize their reproductive success. Environmental changes especially in patterns of availability and distribution of food resources therefore, determine female grouping patterns around which specific male association patterns emerge.

This theoretical framework however, in explaining variations observed across different primate species, considers different social systems to represent the typical characteristics of individual primate species, and therefore a consequence of long-term evolution.

However, over the last few decades an increasing number of long-term field studies on different primate species have revealed stark variations within individual species and sometimes even within individual populations. Such observations suggest the potential for individual animals to display high levels of flexible, adaptive behaviours, i.e. behavioural flexibility.

Investigating intra-specific or intra-population variation also helps in dissecting out behaviours that are more phylogenetically rooted from those that are more responsive to the local environment, besides displaying the potential extent to which individual animals may display behavioural flexibility. It is therefore, necessary to examine how different environmental pressures can lead to within-population variation in social organisation, and further, how different social organisations may influence changes in the social structure and mating systems within individual populations and even species.
Behaviour is a dynamic phenotypic expression that can be extremely responsive to the external environment and therefore, relatively more labile than the usual hard-wired genetic traits such as morphological characteristics; behavioural traits can therefore also potentially alter the direction in which natural selection operates. This is possible because environmental changes can induce the expression of novel behaviours or behavioural patterns in a population, which may not only promote the immediate survival of individuals but also contribute to enhanced reproductive success. Moreover, behaviour can be transmitted through epigenetic means such as social learning, unlike adaptive physical modifications, and spread rapidly in the population by vertical, horizontal and diagonal transmission. Finally, when such behavioural alterations confer a selective advantage over a considerable period of time, any independent change in the genome that promotes the constitutive expression of the trait (without the requirement of individual or social learning) can be subject to natural selection.

Behavioural flexibility broadly defined here, as any reversible change in the individual behavioural phenotype (alternative behavioural phenotypes) in response to external variations, induced endogenously, exogenously or through a combination of both. Behavioural flexibility sensu lato has been observed widely across different primate taxa, at both individual- as well as group- or population-level, but has rarely been described comprehensively for a single primate species at multiple levels of the social system.

Further, given the paucity of our understanding of the contributions made by behavioural flexibility to variability in social structures under different ecological constraints, the current study attempted to investigate intra-population variation in social organisation and behavioural strategies in a cercopithecin species, the bonnet macaque, in southern India.

Of the two species of macaques endemic to peninsular India, the bonnet macaque Macaca radiata is ubiquitously distributed across a variety of ecological habitats. Its ubiquity and the consequent popularity as street performers (human-trained), has led to this species being widely referred to as the ‘common performing monkey’ of peninsular India. It is also one of the more well studied species from the Indian subcontinent, with descriptive accounts of the species dating
back to 1925, besides the subsequent numerous scientific investigations on the species’ biology, ecology and demography.

Bonnet macaques are typically known to reside in multimale-multifemale social systems and unimale social organisations in this species have only been occasionally reported in the literature. The incidence of a high proportion of such rarely observed grouping patterns or social organisations within a single population in the Bandipur National Park of Karnataka state in southern India thus, provides an ideal scenario to test whether observed differences in social organisation also translate into distinct patterns of social structure and mating patterns over relatively short periods of time. Such rapid changes in behavioural strategies in response to changes in the natural and social environments, if established, could provide evidence for the capacity of individual primates to adapt to varying socioecological conditions through phenotypic behavioural flexibility.

The observed social variation in the bonnet macaque population of the Bandipur National Park in southern India has been hypothesised by Sinha and coworkers, to have possibly evolved through both genetic evolution and phenotypic flexibility, largely in response to relatively recent but rapid changes in the foraging regimes faced by the individuals. The results of this study establish three main claims of the model. First, reduced forage availability in the dry season coupled with a patchy distribution of rich human-origin food provided by tourists visiting the sanctuary induce high competition levels, as manifest through increased aggression, especially among females. Second, the formation of smaller groups of females, brought about by troop fission in response to such heightened inter-female aggression, significantly reduces this intense competition. Third, the males in these two types of social organisations adopt rather different behavioural strategies in order to increase their respective success; such flexibility may promote the continued survival and stability of these social organisations.

The study also establishes that larger aggregations of females expectedly experience higher levels of aggression, even outside the context of food, the effects of which largely impact the lower ranking females within a group. Further, it has been hypothesised that under highly competitive regimes, females who bear the maximum costs (mostly lower ranking females) will
strive to cope by trading affiliative behaviours such as allogrooming for tolerance from more dominant individuals. This study, however, shows that although lower ranking females, especially in the larger multimale troops, face the larger brunt of aggression, they do not necessarily form such trading relationships. Instead, they appear to invest more in specific affiliative relationships based on reciprocal patterns of affiliation and allogrooming. Interestingly further, females who reciprocate affiliative and allogrooming behaviours seem to do so only during periods of high competition, the dry season, and when feeding and foraging on provisioned resources; another indication of how behavioural strategies may be altered across different periods of time, over variable situations. Additionally, this investigation also is possibly the first to show that, besides allogrooming, even subtle affiliative behaviours such as sitting together or huddling, may contribute substantially towards maintaining such reciprocal relationships.

Among males as well, the study revealed distinct behavioural strategies being utilized by adult males in the two different social organisations. Males in unimale troops employed behaviours such as ‘herding’ and mate guarding’ at significantly higher frequencies, than adult males in multimale troops, and especially during the mating period. Interestingly, adult males in multimale troops, showed no rank-dependent affiliative or allogrooming behavioural patterns, perhaps indicating that males, like females, may not utilise such behaviours to gain access to fertile females (by appeasing more dominant males), but may in fact be shaped through other factors such as kinship ties, thus maintaining coalitions. Females also did not preferably affiliate or allogroom more dominant males during the mating period, although more dominant males did achieve greater mating success, as inferred from successful copulations. The same females however, directed allogrooming and affiliation preferentially towards higher ranking males in the non-mating period, perhaps to buy more support that could potentially increase offspring survival. This latter observation also indicates flexibility in behaviour on the part of females.

Most important of all, the study provides empirical evidence for a more recent proposition that individual primates can potentially adopt different behavioural strategies under varying socioecological conditions, thus giving rise to different behavioural patterns at multiple levels within primate social system. The study also establishes the extent of such population-level or
group-level behavioural malleability by showing that varying behavioural tactics and strategies may be exhibited not with respect to relatively stable environmental changes alone but also over much shorter time frames, as, for instance, seasonal fluctuations of food resources.

The understanding of such wide scaled behavioural flexibility displayed across various levels of the social structure has serious implications for our understanding of how social systems and indeed, social animals themselves evolve over time. Its potential for a high degree of behavioural flexibility as a response to diverse environmental and social scenarios may also go on to explain how such ‘uncommon performances’ may have led the bonnet macaque to become the common performing monkey of peninsular India.