Behavioural studies: A necessity for wildlife management

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A major concern of behavioural biology has been the study of evolutionary causative processes in animal behaviour, typically focusing on individuals or social groups. Conservation biology, on the other hand, deals with devising tools for the management of wildlife habitats and populations, and typically focuses on ecosystems. We argue that behavioural studies of individual animals in the appropriate social contexts are necessary for, and integral to, the development of effective management plans for any species. We use the results from our studies on lion-tailed macaques from wild habitats in the Western Ghats, and from captive populations in Europe, to demonstrate how information on behaviour and life-history can be incorporated into improved strategies for wildlife management. We explicitly conclude that one of the major goals of wildlife management should be to create conditions that facilitate the expression of the full range of behavioural patterns in the species being managed, so as to increase the likelihood of population stabilization through the optimization of life-history parameters.

Keywords: Behavioural biology, conservation biology, life-history, lion-tailed macaque, Western Ghats, wildlife management.

BEHAVIOURAL biology and conservation biology are two important branches of animal science. Conventionally, behavioural biology, which is primarily a basic science, has included: mechanisms (the internal and external stimuli eliciting behaviour), the evolutionary causes of behaviour (the selective pressures that favoured genetically transmitted patterns), the selective advantage of behaviour (the adaptive significance) and the ontogenetic development of behavioural traits[1]. The study of animal behaviour focuses on individuals, or social groups of individuals. Conservation biology deals with the study of diversity within and across species, analysis of changes in and threats to the habitats and populations of wild animals, and devises methods to manage and conserve biodiversity. Conservation biology is an applied science. The approach in conservation biology has been predominantly system-oriented, e.g. ecosystems and landscapes. Both behavioural and conservation biology have made considerable progress during recent decades. However, the two disciplines have remained unnecessarily distinct from each other. It is only recently that attempts have been made to integrate these two sciences[2]. The explicit aim of conservation biology is to provide management tools to maintain viable populations. Populations, however, consist of individuals and the dynamics of populations that affect issues like long-term likelihood of persistence are greatly affected by the life-histories and behaviour of individuals. Indeed, life-history patterns largely determine the fate of populations. One of the routes to manage populations, therefore, is through the understanding of the behaviour of individuals and their life-history traits. Behavioural biology, thus, provides basic data that could be used by a conservationist to develop appropriate management strategies for populations.

Perspective

The perspective of a wildlife manager is: does the species of concern occur in a given habitat? If yes, what is the population status? Is this population self-sustainable? If it is not, then management requires an active intervention in the habitats or population dynamics of a species with the intention of maximizing returns in terms of viable population levels from minimum resources. Management is also required for commensal populations of non-domesticated species that often come into conflict with humans. Moreover, an important but often ignored component of wildlife management is to maintain self-sustaining captive populations of species that are endangered in their natural habitats. The tools required by a wildlife manager include at least a rough estimation of the carrying capacity of the environment for a particular species, whether the carrying capacity is a stable equilibrium, the present population status of the species, distribution patterns and demography, life-history traits, feeding ecology and behaviour, sympatricity with congeneric or competing species, social structure and patterns of sociality, prey–predator relations, and the extent to which individuals of the species can adapt to man-made environmental changes through quick behavioural modifications and learning. We, therefore, believe that an understanding of the behaviour of animals is essential for the development of tools that are required for the management of a species. We will use the lion-tailed macaque (*Macaca silenus*) as an example

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since (i) it is an endangered species, and hence, there is a serious conservation concern, and (ii) there is considerable amount of data available on this species, both from its natural habitats (*in situ*) and from captive populations (*ex situ*), and our own research groups have been actively engaged in the study of this species.

We will organize this article by beginning with a description of various aspects of the behavioural biology of lion-tailed macaques. We will then discuss the relevance of the data for the conservation of the species. We will include data on distribution patterns, behavioural ecology, life history traits, social organization, and behavioural responses to environmental changes from natural populations and will include available corresponding data from captive populations.

The lion-tailed macaque: Ecology, distribution and conservation issue

The lion-tailed macaque is endemic to the Western Ghats in southern India. Its range passes through three states: Karnataka, Tamil Nadu and Kerala. It is a typical rainforest habitat specialist[3] and occurs in a narrow belt of rainforests. Now numbering less than 4000 individuals, distributed into 49 subpopulations in the wild[4], the species is considered to be 'endangered'[5]. During the past 100 years, the rainforests in the Western Ghats have become fragmented due to the establishment of plantations of tea, coffee and cinchona, construction of water reservoirs for irrigation and power generation, and human settlements to support such activities. As a result, the remaining population of lion-tailed macaques has become fragmented. Depending upon the size, these fragments harbour one to a few groups of macaques each[6], with little possibility of migration between fragments. Even in several large patches of rainforests, such as in the Coorg region of Karnataka, the once viable populations have been reduced to small numbers and have become isolated demes due to local pressures such as hunting[7]. On the one hand, the species is range-limited, it is a low colonizer and a habitat specialist, and on the other hand, its populations are fragmented. These isolated demes are subject to the problems of small populations such as inbreeding, genetic drift, etc. The challenge concerning the conservation of lion-tailed macaques, therefore, is the management of small and isolated populations.

For the purpose of this analysis, we will mostly use the field data from lion-tailed macaque groups in the Anaimalai Hills where we have been studying this species for the past several years. For the captive populations, the data used are from a European population for which records are available for more than 50 years[8].

Distribution and niche separation in Anaimalai Hills

The distribution of primate species in Anaimalai Hills has been documented in detail in several earlier publications[3,6,9]. The dry and the lower altitude regions are characterized by scrub and deciduous forests and are inhabited by bonnet macaques (*Macaca radiata*) and Hanuman langurs (*Semnopithecus entellus*). Bonnet macaques are primarily frugivorous and Hanuman langurs are primarily folivorous. Bonnets inhabit the lower canopy and ground whereas langurs remain in the upper canopy. There is, therefore, both dietary and vertical separation between these two sympatric species[10]. The wet and the higher altitude regions containing tropical evergreen rainforests are inhabited by lion-tailed macaques and Nilgiri langurs (*Trachypithecus johnii*). Lion-tailed macaques are frugivorous/insectivorous whereas Nilgiri langurs are primarily folivorous. Further, lion-tailed macaques move and feed in the upper canopy, and the Nilgiri langurs use the middle and lower canopies. Dietary and vertical separation is, thus, also apparent between these two sympatric species[11].

This indicates how feeding/foraging strategies facilitate evolution of niche separation, both for food and space, in sympatric species. Such information is vital for the management of forests where 'selective felling' of trees has often been carried out. The inadvertent removal of, or interference with, certain canopy levels may result in the loss of niche of one species, thereby making their coexistence in sympatry difficult. The forestry management therefore requires the information concerning the foraging behaviour of species' with particular reference to the use of strata.

A detailed study by Sushma[12] on niche overlap among four arboreal sympatric species including bonnet macaques, lion-tailed macaques, Nilgiri langurs and Malabar giant squirrels (*Ratufa indica*) indicated that maximum niche overlap occurred between lion-tailed macaques and bonnet macaques. This indicates that these two species utilize same resources to a large extent, and their long term co-existence is considered unlikely. Sushma[12] reported that the bonnet macaques were actually only seasonal visitors to the rainforest from the nearby deciduous forests. We have observed several instances where the bonnet macaques inhabiting human habitats were trapped and released in rainforest areas inhabited by lion-tailed macaques. Such practices of wildlife management are probably based on observing the occasional occurrence of two species in a habitat. In-depth behavioural studies have revealed that such co-existences are not possible on year-round basis. The management practice of releasing bonnet macaques in lion-tailed macaque habitats, at least in the Anaimalai Hills region, therefore should be abandoned.

Demography

Groups in animals could be 'casual'; they form or dissolve too quickly to have any major impact on the behaviour of individuals. The groups can also be 'demographic' and persist for periods long enough to affect reproductive processes and social behaviour of group members. The modal size of a group and the age–sex ratios are evolutionary outcomes of the interplay of several factors such as predator avoidance, energy harvest, energy utilized, mate access, kinship benefits, etc. Although there could be habitat-related intraspecific variations in group size, the modal size in a species shows remarkable consistency over long periods of time.

The lion-tailed macaques tend to live in medium-sized groups consisting of 15–17 individuals[13]. A group will usually have one adult male, but there could be more males at times. We gathered data over several years on the demography of lion-tailed macaque groups, both in contiguous forests and in forest fragments[6]. Groups in contiguous forests had very small variance in their size, and hence, they could be considered to be of modal size. On the other hand, groups in forest fragments were of either very small or very large size. As a result, the variance in group size in forest fragments was considerably higher than in contiguous forests. Since social behaviour is significantly influenced by demographic parameters, such variance in group size may affect behaviour and reproduction. In lion-tailed macaques, interference by females during mating, especially when the mating female is at the peak of her hormonal cycle, is a frequent phenomenon. The mating pair quite often moves away from the group for long periods of time during the day. Such separation may not be possible in large groups inhabiting small forest fragments. A large number of females may lead to repeated disruptions of mating resulting in the possibility of non-fertilization, more so in a species like the lion-tailed macaque where a male requires repeated and multiple mounts in a sequence for ejaculation to occur. On the other hand, in groups inhabiting forest fragments, inter-group male migration is almost absent. If there is a reproductive defect in the adult male, it may result in total failure of the group to reproduce. We have observed a group in a forest fragment at Varutaparai where there has not been a single birth for eight years. A carefully planned study should be conducted on the effect of group size on reproduction in fragments. In case the reproductive processes are found to be adversely affected, the group size and composition should be actively managed such that they are close to the modal size and composition to allow appropriate social interactions including reproductive behaviour.

Certain species of primates that are commensal and often come into conflict with humans for resources also require management strategies for ensuring their long-term survival. A metapopulation of bonnet macaques around the south Indian city of Mysore has been monitored for population dynamics for the past 20 years[14]. The number of groups and group size in scrub forests has remained stable, but has been reduced in regions with dry agricultural cultivation. It has been proposed that commensal animals such as bonnet macaques have a better chance of long-term survival in areas with scrub forests, a few places of Hindu worship and some tourism. These animals forage for natural food in these scrub forests surrounded by intense human activity such as agriculture, and they have also learned to receive handouts from visitors in places of worship. The population trends in other commensal areas indicate instability such that no management strategy is required since these populations have no future, and suggested changes would not be cost effective.

Male dispersal

Macaque societies in general are regarded as 'female-bonded'. Females remain in their natal groups, while males usually migrate between groups. Such male migration is quite common in the lion-tailed macaques. In our repeated counts of individuals in several groups, we found the number of females to be constant but the number of adult males was often found to vary. At the same time, we also observed solitary males in the forest. This indicated that males keep joining and leaving groups. In our long-term study area at Puthuthotam[15], we often encountered an adult male named BC as a solitary male. In 1997, this male joined our study group. The resident male RM was chased out by the new male but was allowed to reenter the group after a few days. To our surprise, the adult females of the group preferred the new male to the resident male in all social interactions such as proximity, grooming, approach, mating, etc. The females did not appear to be avoiding the new male. There was one adult female cycling at that time and she repeatedly mated but only with the migratory male, conceived and delivered an infant. After the infant's delivery, the new male left the group and again became solitary. Behavioural observations of this type may have strong implications for the management of lion-tailed macaque groups inhabiting isolated forest fragments and also those in captivity. Fragments could be connected with narrow corridors to facilitate male migration. On the other hand, if fragments are difficult to connect being distant from each other, adult males could be exchanged among groups to produce the effects that result from gene flow in contiguous populations. Since adult females can be expected to accept new males, there is little danger of conflicts during such male exchanges. Under captive conditions, management has to develop strategies such that the relevant features of male migration are realized.

Life history traits

The age at first birth in lion-tailed macaque females is estimated to be about 80 months in the wild[12] and about 48 months in captivity[8,16]. The birth rate, i.e. infants/female/year in natural habitats ranges from 0.28 to 0.42 (mean = 0.35) and the average survivorship of the infant unto one year is 0.87 (refs 13, 17–20). The mean inter-birth interval is estimated to be 34.3 months. With a reproductive span of about 15 years, a lion-tailed macaque female may contribute about five infants in her lifetime. This is a low reproductive output as compared to most other macaque species[13]. Although the lion-tailed macaque produces infants nearly throughout the year, a marked birth peak occurs in January–April[21]. Sharma *et al*.[21] argued that this birth-peak leads to initiation of weaning at the time of resource abundance during monsoon months (July–September). The infants, however, are effectively weaned only during the second year during the period of resource abundance. This probably is the reason for a long inter-birth interval in the lion-tailed macaques. This argument is further strengthened by the observation that under captive conditions, where the food supply is ensured throughout the year, lion-tailed macaque births are nearly equal in all months and inter-birth intervals are reduced[8,16]. In the natural habitat, there is a possibility of some subpopulation getting reduced to very low numbers in a forest fragment, or even in a large fragment, due to factors such as hunting[7]. An immediate management concern in such a situation would be to maintain and increase their numbers. This might be achieved by ensuring constant food supply throughout the year. This may reduce the inter-birth interval and increase the birth rate. However, such a management strategy may be applicable only in the short run and for small populations. The practice can be stopped once the numbers reach a modal size.

Feeding/foraging

The lion-tailed macaques are primarily frugivorous. Kumar[13] described their main diet as plant parts such as fruit flesh, seeds and nectar that are rich in carbohydrates but poor in protein. In compensation for this, the lion-tailed macaques depend a lot on faunal items[13,22]. Kumara *et al.*[22] reported that the faunal components included mostly invertebrates but also frogs and frog nests, lizards, small birds, their nestlings, etc. The fact that the species feeds on a large variety of plants, and that the animals they feed on are distributed in space, means that they spend a considerable part of their day searching and foraging for food. This has a special significance for their management in captivity.

Behavioural responses to habitat modification

Life-history patterns and behaviour of animals are adaptations to their environments. The environments in most places, especially in developing countries, are changing rapidly. The foremost requirement for management is to study the behavioural responses of a species to rapid changes in their environment. The lion-tailed macaques are characterized by certain typical behaviour patterns such as arboreal living, selectively feeding on a large variety of fruit trees[23], large inter-individual spaces while foraging, and time budgets with high proportion of time devoted to exploration and feeding[24]. For several years, we have been observing a group of lion-tailed macaques inhabiting a small and privately owned forest fragment, which is largely underplanted with coffee[19]. The area also contains several pioneer and exotic trees that are not native to the Western Ghats. In the 1990s, this patch of forest suffered two massive selective loggings. As a result, the forest canopy has become discontinuous and the proportion of native trees was drastically reduced. At the outset, it appeared that such drastic changes in the habitat would probably lead to local extinction of a species like the lion-tailed macaque. Interestingly, the birth rate in this habitat has not been affected and the group size has been continually increasing. It appears that the adaptation to this rapid change in the environment was made by these macaques through behavioural modifications. Their food now includes fruits, seeds, shoots, pith, flower, cone, mesocarp, etc. of many non-native and pioneer plants such as *Coffea*, *Maesopsis*, *Spathodia*, *Macaranga*, *Psidium*, *Lantana*, *Grevillea*, *Eucalyptus*, *Erythrina* and *Persea*. The seeds of exotic plants were found in 100% of the faecal samples collected. While the feeding frequency on native plants was 36.7%, it was 39.9% on non-native/exotic plants. Immature individuals are often seen playing on the ground and on buildings, indicating that the otherwise totally arboreal species has the capability of adapting to a largely terrestrial living. However, the distribution of food is now clumped and it forces animals to spend more time at particular places, making them more vulnerable to predators. Dependence on fruits also consumed by humans increases human–animal conflict. Non-native and exotic plants may not ensure a predictable food supply on an annual basis. The study concluded that a species like the lion-tailed macaque, which is range limited and a habitat specialist, has at least some ability, e.g. for feeding and foraging, to counteract rapid environmental changes through behaviour modifications, at least in the short run. The study showed that this species has a wide range of dietary adaptations.

An important implication of the findings of the above-mentioned study on behavioural modifications is in the area of managing forest fragments inhabited by the lion-tailed macaques. Several non-native plants mentioned above are commercial plants valuable to the tea/coffee planters as shade trees as well as for consumption of fruits. They are also used by the macaques. Most of these species are also fast growing. Planting of such trees in and around the forest fragments, and also linking nearby fragments by establishing narrow corridors made of such plants, could be useful both for planters and the lion-tailed macaques. However, such a strategy should be used only as a quick and short term plan. For the long term management, greater emphasis should be on planting species that are native to the rainforests of the region as only such species can ensure predictable food supply.

Captive populations: A model for fragmented populations

The lion-tailed macaque has been maintained in European and American zoos since the end of 19th century. Till about 1950, most of these animals were primarily wild caught and imported from India. Since the 1950s, lion-tailed macaques have been bred in captivity. However, it was only in the 1980s that international breeding programmes were established with an intention to develop captive populations to maintain species viability. Since then, the former isolated colonies have been treated as units of a metapopulation. The management plans were carried out with reference to the concepts of small population biology[25,26]. Although there have been attempts to exchange animals among the groups, the degree of isolation of small groups remains such that the metapopulation could be regarded as an extreme case of a fragmented population. We, therefore, will discuss the development of these populations with reference to their productivity, and consider whether they could serve as a model to predict what might happen in the fragmented populations in the wild.

For the purpose of this analysis, we will use the data on the European population for five decades (1950–2000). This population has been managed without the use of birth control. Moreover, the results have been published[27,28], and are available in EEP (European Breeding Programmes for Endangered Species) annual reports and stud books[8]. The present European population of about 220 individuals represents about one third of the total captive population in the world. Although there were several ups and downs throughout the decades, the population appears to have stabilized now.

Reproductive output

Of the 103 (56 females and 47 males) potential founders, only 47 (22 females and 17 males) successfully reproduced. An almost consistent pattern throughout the decades has been that almost half of the adult females failed to reproduce. The existing population therefore has a genetic representation of a much lesser number of females than their numbers in the population. Further, due to the limited exchange of males among groups, the resulting long male tenure, and the breeding groups being one male units, the genetic representation of males is also biased towards a few males. As a result, the effective breeding size of the population has decreased, and consequences such as reduced genetic variability due to random genetic drift cannot be ruled out.

The population has grown very slowly during this period due to the number of surviving infants being only slightly higher than the number of individuals dying on an annual basis. There has been a mean birth rate of 0.28 infants per female per year. The mean infant mortality was 0.27%. Most of the infant mortality occurred during the first few days of life. A most dramatic feature of infant mortality has been its irregularity and unpredictability on a year to year basis, with some years recording as low as 10% and other years as high as 70% mortality rates. The inter-birth interval in females has been about two years. Considering the above patterns of population growth, it would require 20 years for the present population to double. Even then, the number of adult females and offspring born per year would not increase significantly.

Probable reasons for low reproductive output

The population productivity has been slow despite the fact that these animals are not limited by food, or predators and benefit from veterinary care. The possible reasons therefore have to be traced elsewhere such as behaviour and social organization. Captivity, especially if the captive conditions are sub-optimal, is known to cause several behavioural abnormalities in the animals. A detailed discussion on the issue of such abnormal behaviour in captive non-human primates, especially in the lion-tailed macaques, is reported in this issue[29]. We will compare how the lion-tailed macaques live in their natural habitats, and what they lack in captivity. Although a direct impact of behavioural limitations in these living conditions on reproductive output remains to be determined, several speculations in this regard can safely be made.

As compared to the groups of lion-tailed macaques in large and undisturbed forests, groups in captivity are usually much smaller. Further, the representation of age-sex classes does not correspond to that in the wild groups. This situation puts limitations on the occurrence of full range of social behaviours thus impeding optimal social relationships. As an example, in a typical group of lion-tailed macaques, juveniles and infants often play with sub-adult males whereas in captive groups males are often removed even before they reach the sub-adult stage.

The wild groups of lion-tailed macaques travel long distances every day for foraging. Their home ranges are larger than many other macaques. Further, the inter-individual spacing is also very large and a group at times may be spread over half a square kilometer or so. Under captivity, the inter-individual distance are smaller. Wild groups of lion-tailed macaques frequently encounter each other. These encounters vary in their intensity, which may range from simple avoidance to overt aggression[30]. However, such encounters may have an effect on social activities within a group. During an encounter, the group members show more cohesiveness, reduced inter-individual spacing, social grooming, etc.[31]. The inter-group encounters increase the complexity of the social field that may require the development of special social skills to deal with such a situation. Such an opportunity usually is not available in captive groups.

In the wild habitats of lion-tailed macaques, many adult males are found to be solitary. Further, the number of adult males in a group varies over time, indicating that the migrating males quite often join different groups. When a male attempts to enter a group, there is an overt aggression between the outsider and the resident males. The females have been observed to make loud 'proceptive calls' if outside males are in the vicinity, probably inviting these outgroup males[32]. The females in a captive group are forced to live with a single male over long periods of time. Harvey and Lindburg[33] reported that a long tenure of a male not only resulted in decreased sexual skin swellings in the females but also a decreased frequency of proceptive calling.

Because of the year-round superabundance of food, limited space availability and protection against predators, the captive situation puts limitations on the normal time-activity budgets of a species. Exploration of the environment, especially by younger individuals, is one of the most engaging activities in lion-tailed macaques in their wild habitats. 'Passivity' in wild habitats accounts only for about 17% of their activities[34]. The altered time activity budgets in captivity result in increased passivity among individuals.

The populations in captivity share many features with those inhabiting isolated forest fragments. In both places, the demographic structure has deviated from the groups in large forest complexes. Adult male tenures are long. The migration of males among groups is limited. The groups hardly ever engage in inter-group encounters. Most of the behavioural consequences observed in captivity are probably the same as in forest fragments. The low reproductive output in captivity therefore makes us predict that the populations in forest fragments have a limited probability of growth. In addition, such populations are also subjected to fluctuating food supply and exposure to predators. Kumar *et al.* [35] observed that it is not the size but the quality of a forest fragment that is important for wildlife. However, our conclusions further state that in addition to enhancement of quality, the fragments need to be managed such that a full range of species' behaviours is made possible.

In order to stress the desirability of behavioural studies for management, we would like to emphasize again the observation that almost half of the adult females failed to reproduce in captivity. As of now, no specific explanation has been found for this. For a more effective biological management of a species like the lion-tailed macaques with its peculiar life-history patterns, it is necessary that more females produce, perhaps with lower birth rates, rather than less females produce with high birth rates[27]. To investigate why many females do not reproduce at all, we may have to look at three levels: behaviour at the individual level, behaviour at the social level, and reproductive physiology. At the individual level, it is possible that some females have traits such as avoidance of or aversive reactions to the male. Such behaviours often develop as a consequence of inappropriate socialization under conditions where the full range of age-sex classes was not represented for proper behavioural development to take place. At the social level, the reasons could be that the female does not have much access to the adult male, or that mating is frequently disturbed by other individuals resulting in non-fertilization. At the physiological levels, a regular checking of cycling females through noninvasive techniques is necessary. Similar problems may also be present in forest fragments where demography is not always optimal.

Two specific points emerge from the above discussion: (i) The study of behaviour of animals of a species is necessary before a management plan is prepared for a species, be it in natural habitats or in captivity, and (ii) The goal of management should be such that an environment is created for the animals to express their full range of adaptive behaviours. Behavioural optimization is likely to result in optimization of life-history patterns that, in turn, may stabilize population dynamics.

According to McLean[36], a conservation biologist views adaptation to a particular environment as a result of selection, and hence, processes such as rehabilitation, translocation, etc. may not be viewed as possible. On the other hand, a behavioural biologist views much of adaptation as adjustment or adaptive phenotypic plasticity. Many populations may be able to adapt to modified habitats such as a forest fragment if adjustments came within the current tolerance limits. Our lion-tailed macaque populations have provided a proof of this. It may be specifically mentioned that the information on changing food habits and adaptation to new food items, male migration patterns and female responses to such migrations, implications of behavioural data for management, etc. came through highly systematic and long-term studies on behaviour carried out by trained observers. The conservation biologists and the wildlife managers usually have neither the required training nor time for such long-term behavioural studies. Behavioural biology and conservation biology, therefore, need to be integrated.

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