Reproductive biology of lion-tailed macaque (*Macaca silenus*): An important key to the conservation of an endangered species

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The lion-tailed macaque (*Macaca silenus*), endemic to rainforests of the Western Ghats in southern India, is an endangered species. Most of its population now lives in fragmented pockets of rainforests. Considerable research has been carried out on its reproductive biology both on wild and captive populations in North America and Europe. We review studies carried out on birth seasonality, life-history parameters, and reproductive physiology and behaviour. The captive populations differ considerably from wild populations on several parameters of reproductive biology. Because of a low population turnover in this species due to a delayed age at first birth and long inter-birth intervals, and further degradation of its natural habitats, rapid population replenishment or augmentation is unlikely. This article shows that the study of reproductive biology may provide an important key to the conservation of this species. It also indicates that several aspects of reproductive biology of lion-tailed macaque still remain to be addressed.

Keywords: Birth seasonality, conservation, lion-tailed macaque, reproductive life-history, reproductive physiology.

THE lion-tailed macaque (*Macaca silenus*) is an endangered species[1] inhabiting rainforests of the Western Ghats hill ranges of southern India. The present estimated number in the wild is less than 4000 individuals, which are distributed in 49 subpopulations at seven locations[2]. Most of these subpopulations are found in small and isolated forest fragments. The species is a serious conservation concern and several studies have been taken up on the species, both in its natural habitats and in captivity. Special breeding programmes have been initiated in North America and Europe to establish viable captive populations of this species. It appears that several features of its reproductive biology are such that the population turnover is small. The fact that most of the remaining population of this species lives in forest fragments, it is possible that several

features of its reproductive biology are affected due to unnatural demographic structures. In the past two decades or so, considerable research has been carried out on its reproductive biology. Here we review the research on birth patterns and seasonality, life-history parameters and reproductive physiology and behaviour, both from wild habitats and captivity. Considerable amount of this research is from our own groups.

Methods

Although there may be occasional references to other studies as and when relevant, our review of the reproductive biology of the lion-tailed macaques is based on five major studies: (a) a five-year study on the ecology and population dynamics in the wild[3], (b) a five-year study on the reproductive behaviour of lion-tailed macaque in its natural habitats[4], (c) a compilation of reproductive data on the captive lion-tailed macaques in Europe for over four decades[5,6], (d) analysis of data on reproduction in captive lion-tailed macaques in North America for over 50 years[7], and (e) ten-year data on a single off-exhibit colony maintained at Wild Animal Park, Escondido by the Zoological Society of San Diego[8].

Birth seasonality

The environmental and social factors determining birth seasonality or synchronization of births in primate females have been discussed in several studies. In primates, frugivory is more associated with birth seasonality than folivory, because fruit abundance occurs during a few months only[9]. In the lion-tailed macaque, which is primarily frugivorous[3], conflicting reports are available regarding birth seasonality. Here we review and discuss data on timing of birth in lion-tailed macaques.

In the wild habitats (eight groups), births (*n* = 127) were observed to occur throughout the year, except in the month of June[4] (Figure 1). However, most of the births occurred during January–April. This period, therefore, could be considered as the birth peak period. The peak period
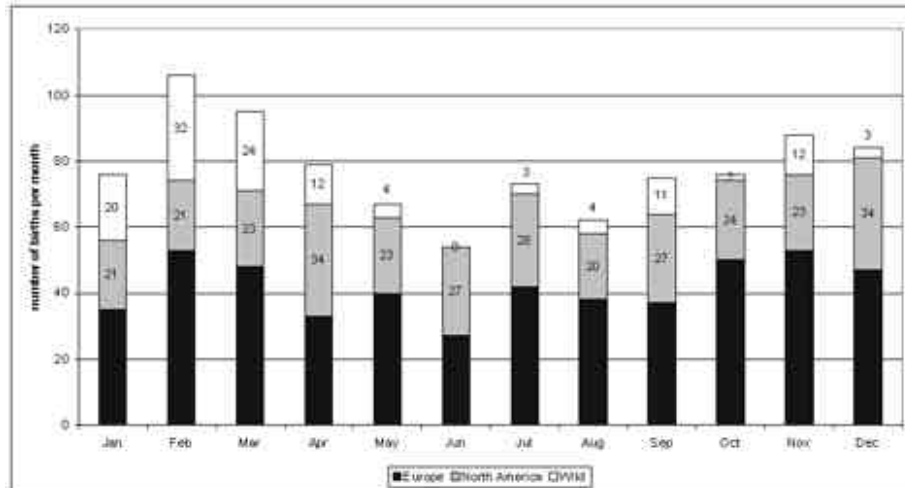
Figure 1. Number of births per month in European, North American and wild populations of *Macaca silenus*.
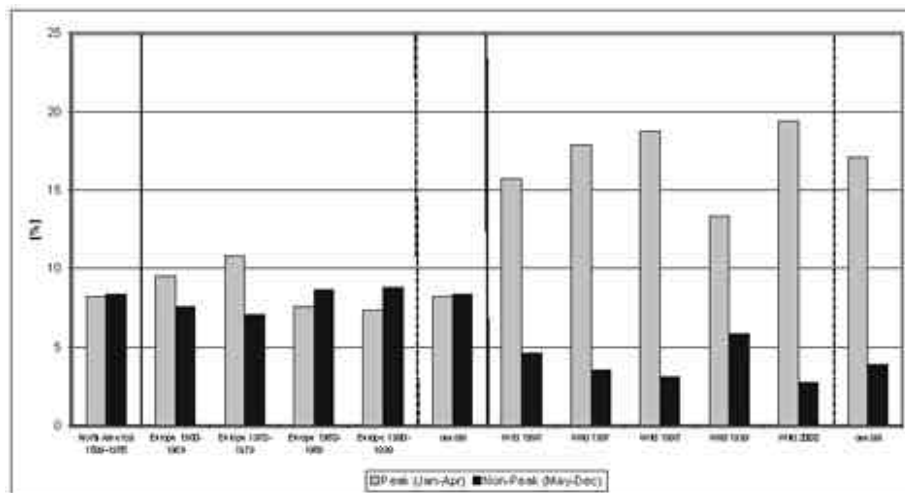

Figure 2. Percentage of births during January–April and May–December periods in different populations of *M. silenus*. In the case of North America, data are compiled for a period of 90 years and for the European population data are for decades.

accounted for 17.13% births per month, whereas the non-peak period accounted only for 3.94% births per month (Figure 1). Further, this pattern of birth was consistent over a period of five years (Figure 2). The species may not qualify to be called strictly seasonal, but it could be said to be partially seasonal, implicating the significant role of ecological factors.

In the European captive population[5,9], 8.27% births per month was observed during the January–April period as against 8.37% births per month for the rest of eight months (Figure 1) (*N* = 503; years = 40). The births, therefore, in this captive population were randomly distributed throughout the year with no indication of seasonality. Further, the same pattern of births was observed for each decade over four decades[5] (Figure 2).

In the North American captive population, births (*N* = 305; years = 90) were recorded which were almost equally distributed over the months, indicating no seasonality[7]. Further

analysis carried out for comparing this pattern of births with that in the wild showed that 8.20% births per month occurred during January–April and 8.40% births per month occurred during the rest eight months (Figure 1). The analysis, therefore, revealed that the pattern of births in this captive population and in the wild was different.

However, when the birth data from a single large breeding colony at San Diego[8] were analysed for a period of ten years, it was observed that 75% of births (21 out of 28) occurred in 'cohorts' with two to five infants born within a period of less than 90 days. Further, the cohort was observed to shift to different months over the years. On the one hand, these cohorts indicated birth synchrony while the shifting of cohorts to different months, on the other hand, indicated non-seasonality of births[8]. It may be mentioned that this group was one of the few captive groups with a size almost equal to that of mean group size in the wild (about 20 individuals). The long-term data from the San Diego groups

reveal that there is something more than the ecological factors to at least breeding synchrony, if not breeding seasonality. Clarke *et al.*[8] discussed several possible advantages of synchrony proposed by earlier researchers, including facilitating mate choice[10,11], diffusing male reproductive competition[12,13], increasing male parental investment[14] or reducing chances of male infanticide[15], but none of these explanations were found applicable to their population. However, the only possible advantage appears to be to have similar aged offspring together, which might facilitate infant socialization[16].

Life-history parameters

Lion-tailed macaque females in captivity produce their first offspring at the age of about 48 months (North American population[7]) or 65.2 months (European population[5]), and about 80 months in the wild[3]. Onset of reproduction, therefore, starts earlier in captivity due probably to favourable food availability. Birth rate (i.e. number of infants per adult female per year) is an indicator of the growth of a population. The birth rate[3,4,17,18] in different wild populations of lion-tailed macaques varies from 0.28 to 0.42 (Figure 3). On an average, an adult female produced 0.35 infants per year. It, therefore, requires 2.86 female-years to produce one offspring, or a female, on an average, has an inter-birth interval of about 34.3 months (Figure 4). The average survivorship rate[3,4] of an infant in the wild is about 0.87. The inter-birth interval reduces if the infant does not survive (Figure 4). Considering a reproductive span of 15 years, an average female may, therefore, contribute only 4 to 5 infants during her life time. It may be concluded that in lion-tailed macaques, a female produces only a few offspring but the offspring have a high survivorship rate.

Under captive conditions, the North American[7] and the European[5] populations of lion-tailed macaques have recorded a birth rate of 0.34 and 0.28 respectively, providing a mean birth rate of 0.31 in captivity (Figure 3). Infants in these populations survived at the rate of 0.73 (Figure 3). The respective inter-birth interval in North America and Europe was 35.3 and 42.9 months (Figure 4), providing an average of 39.1 months. Taking into consideration the above rates, it may be deduced that an average lion-tailed macaque female in captivity may contribute only 3.6 offspring in her life time. However, a large number of females in captivity included in this analysis did not reproduce at all. In the European population, the number of females that reproduced[5] amounted to only 50.2%. Among the females who were successful breeders and whose offspring survived, the inter-birth interval in North American and in European populations was 17.3 and 22.8 months respectively, providing an average inter-birth interval of only 20.1 months as against the same being 30.0 months in the wild[4] (Figure 4). On the other hand, inter-birth interval in the case of females whose offspring did not survive was more or less the same in the wild and in captivity (Figure 4).

Whatever may be the differences in reproductive output between wild and captive lion-tailed macaque females, the species as such may have a low reproductive potential compared to other macaques[3].

Reproductive physiology

Lion-tailed macaque females show conspicuous external swelling of sexual skin, especially in the sub-caudal region, which is probably correlated with hormonal patterns and bleeding. The research group at San Diego categorized the swelling into degrees ranging from 0 to 3 based on the size of swelling, and the tightness, colour and shine of the skin. The inflating phase (follicular phase) from 0 to degree 3 is a slow process, whereas the deflating phase (luteal phase) may occur suddenly from degree 3 to degree 0, or
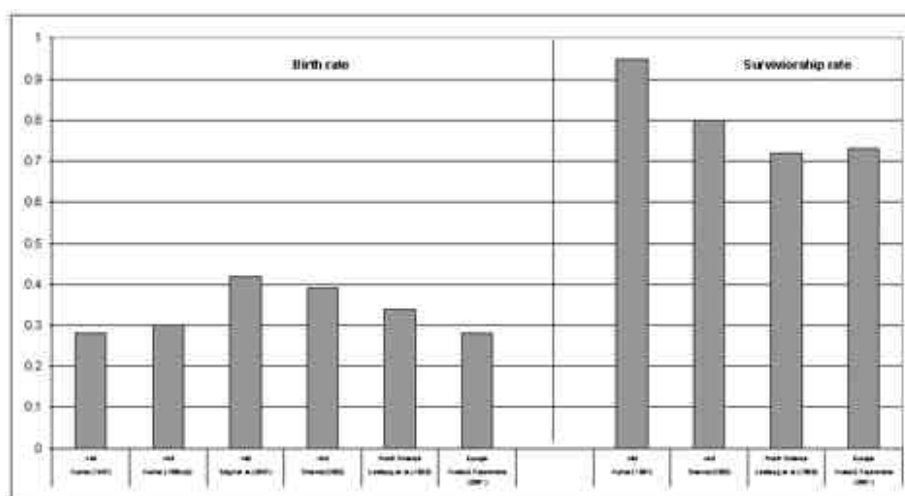

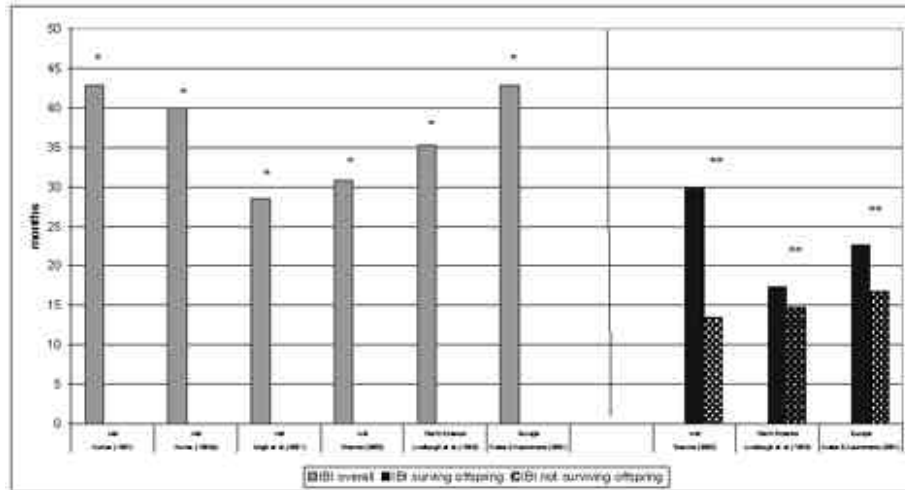**Figure 3.** Birth rate and survivorship rate of *M. silenus* in wild and captivity.

Figure 4. Mean inter-birth interval of *M. silenus* in wild and captivity.

it may occur through 2 and 1 degrees. Sharma[4] employed the same categories in his study on reproductive behaviour in the lion-tailed macaques in their natural habitats.

Sharma[4] recorded 78 complete cycles inferred from swelling patterns in six adult females in a group. The mean cycle length was found to be 40.55 days (median = 38.50; minimum–maximum = 15–87). Though the inter-individual difference for cycle length among females was non-significant, each female had a considerably high standard deviation indicating high intra-individual variations in cycle duration. The follicular and luteal phases had a length of 22.97 (median = 22.00; minimum–maximum = 4–67) and 17.58 (median = 16.00; minimum–maximum = 3–58) days respectively. Kumar[3] found a mean sexual cycle length of 30 days (minimum–maximum = 17–47). The means for follicular and luteal phases were 14.1 (minimum–maximum = 8–19) and 16.4 (minimum–maximum = 6–25) days respectively. The length and variability of cycle duration observed by Sharma[4], compared to other studies from the wild[3] and captivity (see below), are unusual for a macaque. In addition, Sharma did not observe any decline in birth rate. It, therefore, remains to be verified whether these differences are due to observer biases or habitat characteristics. It is important to mention here that in the study by Kumar, except one group inhabiting a forest fragment, the other groups inhabited a large and relatively undisturbed forest complex. The study by Sharma, on the other hand, was from a single group inhabiting a highly disturbed and a small forest fragment. The monkeys in this forest fragment feed on a large variety of non-native and exotic trees, including coffee seeds[18]. They also confront people and street dogs. It is a research question for future to determine whether the large length of the cycle and of the follicular phase, with a high intra-individual variation in days, in the commensal group observed by Sharma was atypical and a function of changes in living conditions.

Studies from captivity[19] revealed that the onset of first menstruation occurs at the mean age of 3.12 years (1140

days). First conception occurs at the mean age of 3.48 years (1270 days), with a gap of about 130 days between first menses and conception. Length of the menstrual cycle determined from urine-based hormonal analysis was found to be 32.0 (± 0.4) and 32.5 (± 6.2) days respectively. Analysis of hormones from faecal powder revealed a mean cycle length of 32.2 (± 3.0) days[20]. The mid-cycle estrogen peak was observed about 13 days after the onset of menstruation, and ovulation occurred about 24 to 28 days after estrogen peak[21–23]. Faecal analysis revealed the follicular and luteal phases to last 16.0 (± 3.2) and 16.2 (± 2.0) days respectively[20]. Heistermann *et al.*[20] also observed in their sample that these cycles were quite regular in females below the age of 20 years. However, females older than 20 years showed irregular cycle patterns, such as the follicular phase lasting from 25 to 70 days and luteal phase being less than seven days.

An interesting change in the pattern of cycling has been reported by Harvey and Lindburg[24]. In their off-exhibit colony at San Diego, all females except one were successfully breeding. Due to population control measures, the alpha male (and a few other males) had to be vasectomized. Following this, some dramatic changes occurred in female cycles. The average swelling duration of 18.5 (± 1.5) days in the pre-vasectomization period declined to 10.2 (± 1.1) days by the fourth year post-vasectomy. The most drastic change was observed for the third stage of swelling (hormonal peak?). The pre-vasectomy mean of 3.9 (± 1.0) days reduced to only 0.2 (± 0.9) in the fourth year post-vasectomy. The male copulation proportion of 0.70 of swelling days pre-vasectomy reduced to 0.18 post-vasectomy. Data presented by Harvey and Lindburg[24] raise several questions regarding cycles in lion-tailed macaque females. Did the cycling frequency reduce because the male was vasectomized? Or did this frequency reduce because of the long tenure of the male (more than ten years)? The research team from Zoological Society of San Diego is presently investigating these questions.
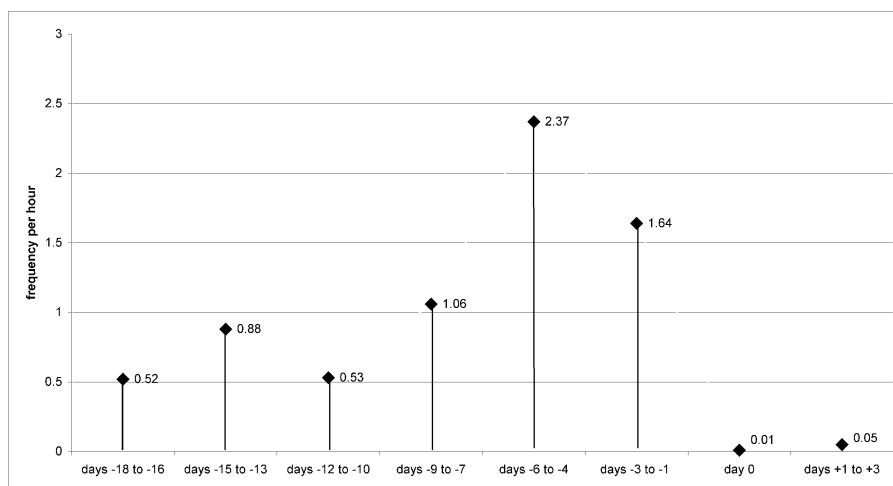
Figure 5. Mounting frequency per hour before and after disappearance of swelling in *M. silenus* (after Kumar[3]).
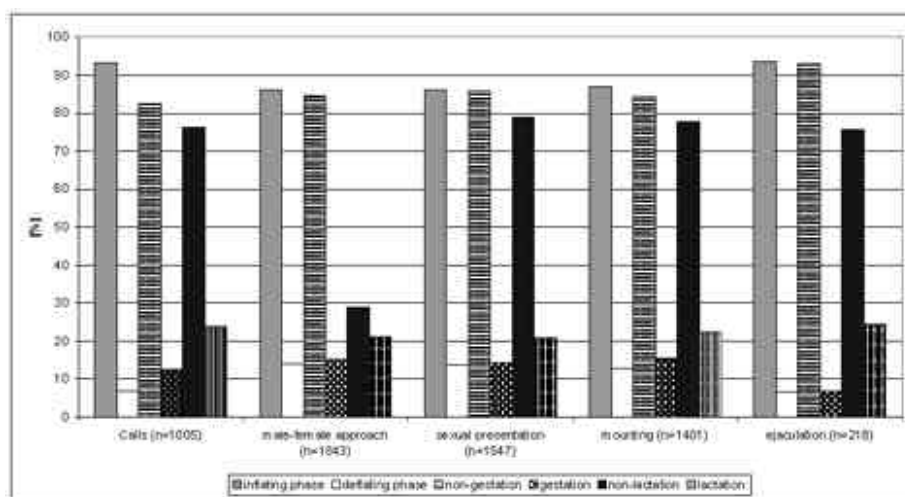

Figure 6. Calls, approaches, presentations, mounts and ejaculations during different stages of sexual and reproductive cycle in *M. silenus.*

Reproductive behaviour

In the following section, we discuss behaviours related to reproduction with reference to inflating (follicular) and deflating (luteal) phases of swelling in the females. Copulation starts 2.3 ($\pm$ 4.2) days after the first day of menstruation and ceases 1.1 ($\pm$ 0.3) days after detumescence, and the mean copulatory phase lasts 10.6 ($\pm$ 0.5) days[19]. Kumar[3] also reported that most of the mounts by the male occurred one to nine days before the day when swelling in the female disappeared (Figure 5). Figure 6 (adapted from Sharma[4]) presents the occurrence of some behaviours in per cent 20 s intervals during the two phases. One of the behaviours comprises two conspicuous calls made by the females. 'Staccato call' is uttered during mating and 'proceptive call' is made throughout the swelling period[25]. We have combined these two calls and data shown

in Figure 6 reveal that these calls are made with a much higher frequency during the inflating phase. Other behaviours related to reproduction, including approaches among males and females, sexual presentation by females, mounting and ejaculation by males occur with a significantly higher frequency during the inflating than the deflating phase (Figure 6). Females made staccato calls during 83.6% of mounts in the swelling phase as against calls during only 9.1% mounts in the non-swelling phase[3]. Proceptive calls, however, are made throughout the swelling period. During gestation and lactation phases, females made fewer calls (Figure 6), further indicating that the calls were made during the mating periods. Lindburg[25] reported that such calls were made with a higher frequency if outside males were visible than during the absence of outside males. He hypothesized that a function of these calls could be to attract non-group males for mating. This could result in better oppor-
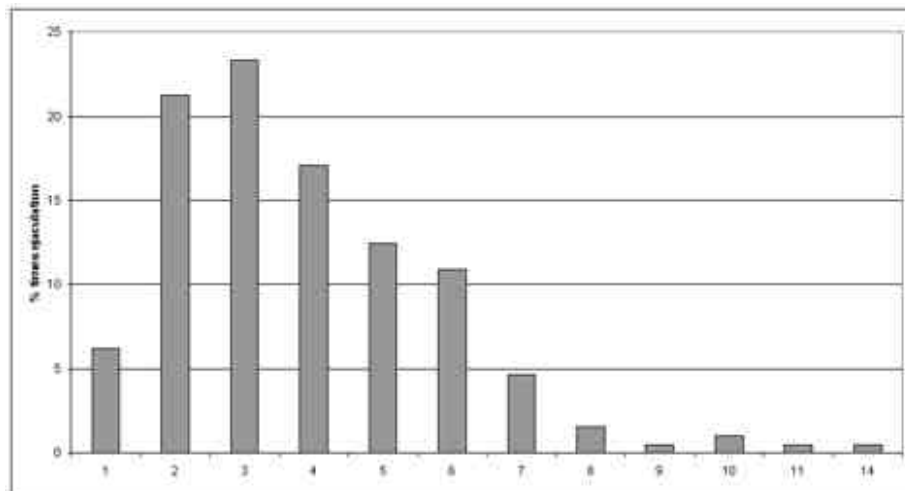
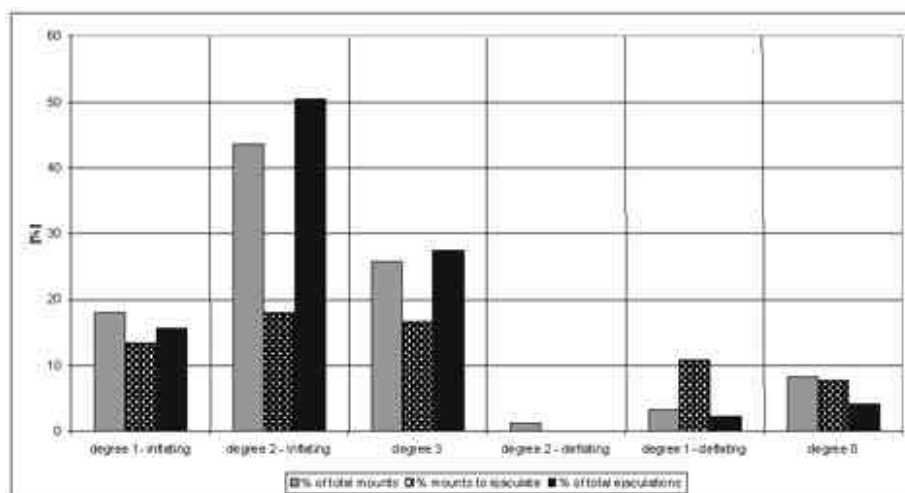**Figure 7.** Number of mounts to ejaculation in *M. silenus.*

Figure 8. Per cent mounts, per cent mounts to ejaculation and per cent of total ejaculation at different stages of swelling in *M. silenus*. *X*-axis indicates number of mounts.

tunities for mate choice and outbreeding. It, therefore, may have implications for managing males both in captivity and in forest fragments that are inhabited by single groups of lion-tailed macaques.

Mating in lion-tailed macaques follows a Multiple-Mount-to-Ejaculate (MME) pattern. Multiple mount refers to repeated mountings by the male with a short gap between the mounts, and each mount does not result in ejaculation. The lion-tailed macaque males averaged 9.1 ($\pm$ 1.2) mounts to ejaculation, and the average duration of a copulation bout was 33.3 ($\pm$ 5.2) minutes[23]. Figure 7 (adapted from Sharma[4]) shows the per cent ejaculations against number of mounts. Only about 6% ejaculations occurred after a single mount, and in most of these instances, the adult male had masturbated before mounting[4]. Ejaculation could occur after as many as 14 mounts.

The per cent mounts and ejaculations varies in relation to the swelling phase of the female (Figure 8, adapted from

Sharma[4]). Significantly higher mounts were observed during the inflating phase. The per cent mounts resulting in ejaculation were also higher during swelling, and no ejaculation was observed in mounts that followed immediately after deflation. A high per cent of the total ejaculations occurred during the swelling phase of females.

A typical behaviour observed in the lion-tailed macaques is the interference in or the harassment of the mating pair by others. Such interference could be by either age–sex class individually or by several individuals together. Sharma observed a total of 1221 and 180 matings during follicular and luteal phases, of which 72 (5.90%) and 16 (8.89%) were disturbed respectively. One would expect more matings to be disturbed during the follicular phase, which was not the case in the study by Sharma, as most of the times the consort pair moves away from the core of the group. However, most of such harassment occurs when a female being mated has a higher degree of swelling. Figure 9

(adapted from Sharma[4]) shows that the frequency with which other animals harass the mating pair differs with the degree of swelling of the female being mated. Maximum interference occurs when the female is in the second or the third degree of swelling. This is probably the phase of the cycle when conception might take place. Kumar[3] reported 74 instances of interference in 577 sexual interactions. The other females interfered in 11.9% of matings where mated female had swelling, while no interference was observed if the mated female had no swelling. Kumar also reported that the frequency of harassment was higher if several females showed swelling simultaneously. Interference could occur at pre-mounting or mounting stage. Interference decreased the mounting probability from 0.58 to 0.07, brought premature termination preventing ejaculation, and sometimes redirected mounting towards interfering female[3]. In lion-tailed macaques, where each mount does not result in ejaculation, prevention of mounting and ejaculations by harassment can hinder fertilization. An important research question is whether the demographic structure, especially the proportion of adult females and males in the group, has any relationship with the interference frequency. Such being the case, its repercussions in captive populations and in forest fragments where demography is usually not optimal, can be serious in reproductive suppression of certain females.

In a study group of Ananda Kumar et al.[26], a male named RM was the resident male and another male named BC migrated into the group. Females groomed, remained in the proximity of, and sexually presented to, the migratory male with a higher frequency than to the resident male of the group. During this period of male migration, there was only one female, BUL, who had swelling. She mated with a much higher frequency with the migratory male (66 times) than with the resident male (four times). The migratory male was also observed to ejaculate 11 times as against only once by the resident male during these matings. The migratory male left the group after BUL delivered an infant.
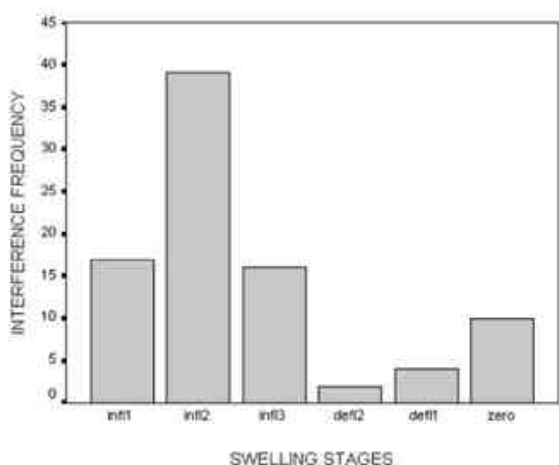

Figure 9. Interference frequency at different swelling stages of the female.

Conclusion

A review of the reproductive biology of the lion-tailed macaques brings out the following facts. In its natural habitats, the species is largely a seasonal breeder indicating that the seasonal abundance of food, due primarily to monsoons, is a limiting factor in their reproduction. Large populations of this species inhabit forest fragments where there is depletion of food resources, putting further constraints on reproduction. As an adaptation to a resource-limited environment, the species has evolved life-history traits such that the female has a low lifetime reproductive output. Harassment of a female being mated by other females, especially when she is at the peak of swelling, indicates severe reproductive competition among females. Due to such constraints, the lion-tailed macaques were probably always low in numbers in their natural rainforest habitats. Today, the populations reduced to low numbers have a little chance of recovery on their own. An active management approach, therefore, appears to be a necessity.

Since forest fragmentation is the main reason for most of the problems faced by this species, managing such habitats and the populations therein is the main challenge of lion-tailed macaque conservation. The goal of management is to optimize reproductive output in the fragmented habitats. Kumar et al.[27] clearly brought out that the rate of reproduction in forest fragments was lower than in more contiguous habitats of the lion-tailed macaques, and that the resource quality of a habitat was a more important factor than other features such as size of the fragment. Singh et al.[18] on the other hand, observed that in a forest fragment where monkeys adapted to feed on fruits of pioneer and exotic tree species, including coffee seeds, the birth and survivorship rates did not decline. Many forest fragments are privately owned and used for other purposes such as agriculture. The management should be oriented such that tree species that are farmer-friendly (e.g. providing good shade for coffee plants) and provide sufficient food resources for monkeys are raised, so that the reproductive output does not further decline.

Two important behaviours related to lion-tailed macaque reproduction include mating interference and its avoidance by a consort pair to move away from the core group, and male migration providing female choice for partners. Both are constrained in forest fragments due to disturbed demography and limited opportunities for dispersal. The management requires either linking the forest fragments or an active manipulation of demographic structures. Our long term observations have revealed that the lion-tailed macaque females do not appear to be overtly xenophobic towards a new male, and appear to prefer the new male for all social, including reproductive interactions. This observation has significance for the management of lion-tailed macaques, both in captivity and in small forest fragments, where dispersal of males is impossible or restricted. Males in such situations need to be replaced every few years as

a management practice. Such replacements may have the genetic consequences that are usually associated with male migrations in natural populations, with groups having overlapping home range.

The above review does bring out aspects of reproductive biology of the lion-tailed macaques that have immediate conservation implications. However, there are other reproductive traits in this species that may be theoretically interesting to understand its evolution, and these traits have not been paid much attention. The lion-tailed macaque females cycle throughout the year, as menstruation is seen in all months. Why then do they have such long inter-birth intervals in nature? When the young are weaned and the females cycle and mate, why does fertilization not occur? Is the effective weaning in lion-tailed macaques much delayed compared to other macaque species? Even 14 to 16 month-old young are seen in ventral and nipple contact with mothers, but do the mothers really produce milk even after more than a year of birth of an infant? Nutrition does affect reproductive processes in individuals. Hardly any work has been done to assess the quality of food available in the rainforest habitats of lion-tailed macaques. Could it be that the quality and quantity of food in habitats of this species is sub-optimal, thereby affecting its reproduction? These are some questions that remain to be addressed in future research on the reproductive biology of this endangered species, and the new information may further help plan effective conservation strategies.

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