

Infant development and weaning in *Macaca silenus* in the natural habitats of the Western Ghats, India

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This article reports the development of behaviour in 31 lion-tailed macaque infants from birth to the age of 15 months. The study was conducted during January 2002–June 2005. The study animals included a large group of lion-tailed macaques inhabiting a rainforest fragment in the Western Ghats, India. Two critical stages were observed during the development of the infants: one at the age of five and a half months, and another at the age of nine months. When the infants were five and a half months old, there was a sudden increase in the occurrence of nipple contact, a sharp decline in the per cent of infants making nipple contact after this age, a peak in the occurrence of retrieve by the mother, a peak in the occurrence of play by the infant, and a peak in the occurrence of environmental exploration by the infant, and stabilization of exploration after this age. Up to the age of nine months, the occurrence of an infant approaching the mother and mother punishing the infant continued to increase, and these two behaviours abruptly ended at the age of nine months. Mother grooming the infant occurred with a peak at the infant's age of nine months. It appears that in lion-tailed macaques, the mother actively initiated weaning. It began at the infant's age of five and a half months and was completed by the time the infant was nine months old. The mother, however, increased the frequency of grooming the infant, and thus continued to care for the infant in ways that cost her less in terms of parental investment. A longer duration of nipple contact by some male infants, more retrieval and grooming of male infants, and more proximity of male infants to mothers indicated higher maternal parental investment on male infants.

Keywords. Infant development, lion-tailed macaque, nipple contact, play, weaning.

THE lion-tailed macaque (*Macaca silenus*) is one of the most endangered of the macaque species (EN C2a(i) in the IUCN Red List of Threatened Species)¹. This species is confined to a narrow stretch of rainforests in the Western Ghats hill ranges of southern India. Its numbers are

now estimated to be about 3500 individuals, with 49 sub-populations². As the species has been of special conservation concern, several studies have been reported on its distribution^{3–5}, demography^{6,7}, and ecology and behaviour⁸ during the past two decades or so. The behavioural studies have dealt with some general patterns such as social organization⁸, reproductive behaviour^{9–11}, feeding ecology^{6,12}, time-activity budgets^{13,14}, inter-troop encounters¹⁵, male migration¹⁶, behavioural responses to habitat degradation¹⁷, etc. Long-term studies on aspects of behaviour such as infant development, mother–infant interactions and infant socialization in natural habitats are still lacking in this species. There is only one study¹⁸ reported so far on infant development. It included only two infants and a period of development up to eight weeks of age of infants. Another study reported age gradations in vocalizations¹⁹.

Most primates live in varied habitats and in complex social groups. The young primates undergo a long process of 'socialization' through which they learn not only about the appropriate patterns of social behaviour but also about the minute aspects of their immediate environment²⁰. The patterns of infant development can be influenced by the phylogenetic position of a species and by the habitat characteristics²¹. In general, the early stages of the infant are characterized by close contact with and high degree of dependence on the mother. The infant then gradually develops towards more independence and its behaviours become increasingly environment-oriented. The latter include interactions with other groups members, specifically peers, as well as exploration and use of features of the physical environment. Sometime during this period, the mothers actively promote independence in the infant. The weaning sometime may result in parent–offspring conflict²².

In several primate species, parental investment has been observed to be sex-biased^{23–25}. These studies primarily deal with sex ratios at birth, differential mortality of the two sexes and inter-birth intervals. However, parental investment in mammals does not end with the birth of the offspring, as the mother has to continue to feed milk to the offspring. Sex-biased investment, therefore, could also occur during the period of offspring dependence²⁵. In

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this article, we investigate whether weaning and other mother-related and environment-oriented behaviours in male and female lion-tailed macaque infants differ.

Certain aspects of the socialization process such as acquiring foraging skills assume more significance in species that inhabit resource-limited habitats such as rainforests that are utilized by other sympatric primates and several other mammalian and bird species. The lion-tailed macaque may be a typical example of such a primate species. It is, therefore, necessary to record the development of an infant in as much detail as possible. Such information will, on one hand, add to our knowledge of the behaviour of this endangered species, and on the other hand, it will enrich the literature on behavioural development in primate infants in wild habitats. In this article, we describe the behaviour of lion-tailed macaque infants from birth to the age of 15 months. Although the process of socialization refers to a large number of behaviours, all such behavioural acts are difficult to include in an analysis, since many of them occur with rather low frequencies. We have, therefore, included only key aspects of behaviour that can indicate a transition in the infant from more mother-directed behaviours to those that are directed more toward the environment and conspecifics other than the mother.

Subjects

The study was carried out between January 2002 and June 2005 on a group of lion-tailed macaques inhabiting a rainforest fragment inside a tea/coffee garden called Puthuthotam Estates in the Anaimalai Hills, Western Ghats, Tamil Nadu, South India. This site is located at 10°20'N and 76°58'E. The average altitude of this habitat is about 1050 m. The area receives an average annual rainfall of about 5000 mm. For a detailed description of this habitat and its surrounding region see Singh *et al.*^{17,26} and Krishna *et al.*²⁷. The 322 ha area of the estate under tea and coffee plantations included 102 ha of rainforest. This fragment harboured two groups of lion-tailed macaques named PT1 and PT2 with overlapping home ranges, and our study was conducted on PT2. At the beginning of the study, the group consisted of four adult males, 17 adult females, 13 subadults and 22 immatures. By June 2005, the group size increased to 84 individuals with five adult males, 20 adult females, ten subadults and 49 immatures. PT1 had a group size of 16 consisting of two adult males, five adult females and nine immatures. We observed development in 22–33 infants at different age levels in PT2 (Table 1).

Methods

We made observations on the behaviour of infants using focal animal one-zero sampling method. This method was

specifically chosen since it is strongly recommended for recording intermittent behaviour patterns which start and stop repeatedly and rapidly, e.g. play, approach, nipple rejection, etc. where continuous recording or instantaneous sampling are not practicable²⁸. This method correlates strongly with per cent of net observation time²⁹ and has a high inter-observer reliability³⁰ of 0.98. An observation session lasted for a period of 10 min. This duration was divided into 30 intervals of 20 s each. Each behaviour of the infant that occurred during an interval was recorded, and no behaviour was recorded twice in an interval. For the purpose of analysis, occurrence of a behaviour per 20 s interval was calculated by dividing the occurrence of the behaviour in a certain number of 20 s intervals by the total number of 20 s intervals devoted to the observation of an animal. Data on mother–infant distance were collected through scan sampling³¹. Every 30 min, all visible infants were scanned and the distance between an infant and its mother was recorded in six distance classes, including 0 (body contact), 1–4 (within respective metres from the mother); and 5 (more than 5 m from the mother). In order to analyse behavioural development, we added data on each behaviour of an infant for a period of 15 days up to the age of 15 months (Table 1). The observations were made uninterrupted throughout the

Table 1. Number of infants observed at different age levels

Fifteen-day age periods	Male	Female	Total
1	19	14	33
2	19	14	33
3	19	14	33
4	19	14	33
5	19	14	33
6	19	14	33
7	19	14	33
8	19	14	33
9	19	14	33
10	19	14	33
11	16	11	27
12	16	11	27
13	16	11	27
14	15	11	26
15	15	11	26
16	15	11	26
17	14	11	25
18	14	11	25
19	14	11	25
20	12	11	23
21	12	11	23
22	11	11	22
23	11	11	22
24	11	11	22
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26	11	11	22
27	11	11	22
28	11	11	22
29	11	11	22
30	11	11	22

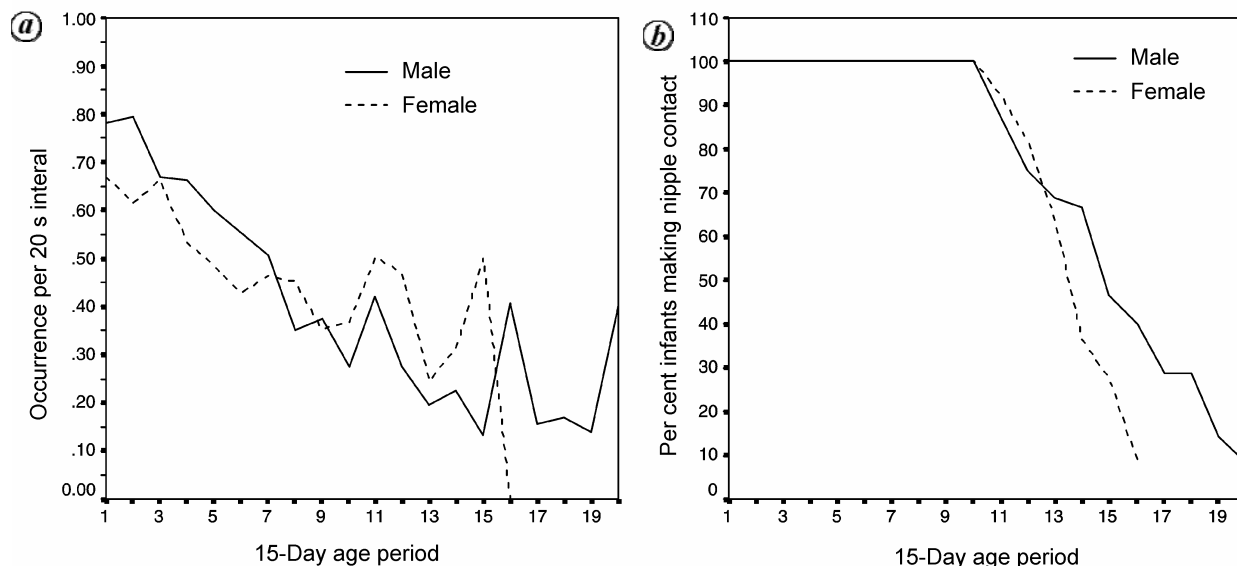


Figure 1. *a*, Occurrence per 20 s interval of nipple contact by male and female infants at different age periods of 15 days. *b*, Per cent male and female infants making nipple contact at different age periods of 15 days.

study period, and hence 15,083 sessions of 10 min each amounting to 2514 h of one-zero sampling and 14,390 scans were, by and large equally distributed among observed animals and different age levels.

Although data were collected on a large number of behavioural acts, in this article we have included only a few important ones to illustrate behavioural development. A brief description of the behaviours included in the analysis is given below.

Mother-related behaviours

Approach: Infant walks to the mother.

Distance from mother: Mother–infant distance recorded in six distance classes.

Mother grooms: Mother searching and manipulating the fur of the infant.

Nipple contact: Sucking of mother’s nipple by the infant.

Punish: Mother pulls away or even sometimes bites the infant and presses the infant down when the latter attempts to initiate nipple contact.

Retrieve: When the mother starts to move from a sitting position, she collects the infant with an arm to the ‘ventrally carried’ position.

Environment-oriented behaviours

Eat: Infants eating solid food, e.g. fruits, from the environment.

Environmental exploration: The infant explores the environment by visual inspection and/or touching objects.

Environmental manipulation: The manipulation of physical objects in the environment by the infant such as breaking twigs, rubbing objects, turning stones, etc.

Self-play: Solitary play by the infant.

Social play: Contact or non-contact play with others.

Results

In this section, the process of behavioural development in the lion-tailed macaques is illustrated by describing selected patterns of mother–infant interactions and environment-directed behaviours by analysing occurrence of each behaviour in consecutive age periods of 15 days, up to the age of 15 months, thus covering the period of infancy.

Mother–infant interactions

Nipple contact: Figure 1*a* presents the data on the occurrence of nipple contact per 20 s interval in the age periods of 15 days. During the first month of the infant, nipple contact was observed in over 70% of intervals. Up to the age of five months of the infant, occurrence of nipple contact steeply decreased. A sudden spurt in occurrence of nipple contact was observed at the age of about five and a half months in both male and female infants. Occurrence of nipple contact was observed up to the age of 10 months. The overall mean occurrence of 0.404 and 0.441 of nipple contact per 20 s interval in male and female infants respectively, during the entire duration of nipple contact, did not differ (Mann–Whitney $U = 112$; NS). However, further analysis revealed that the occur-

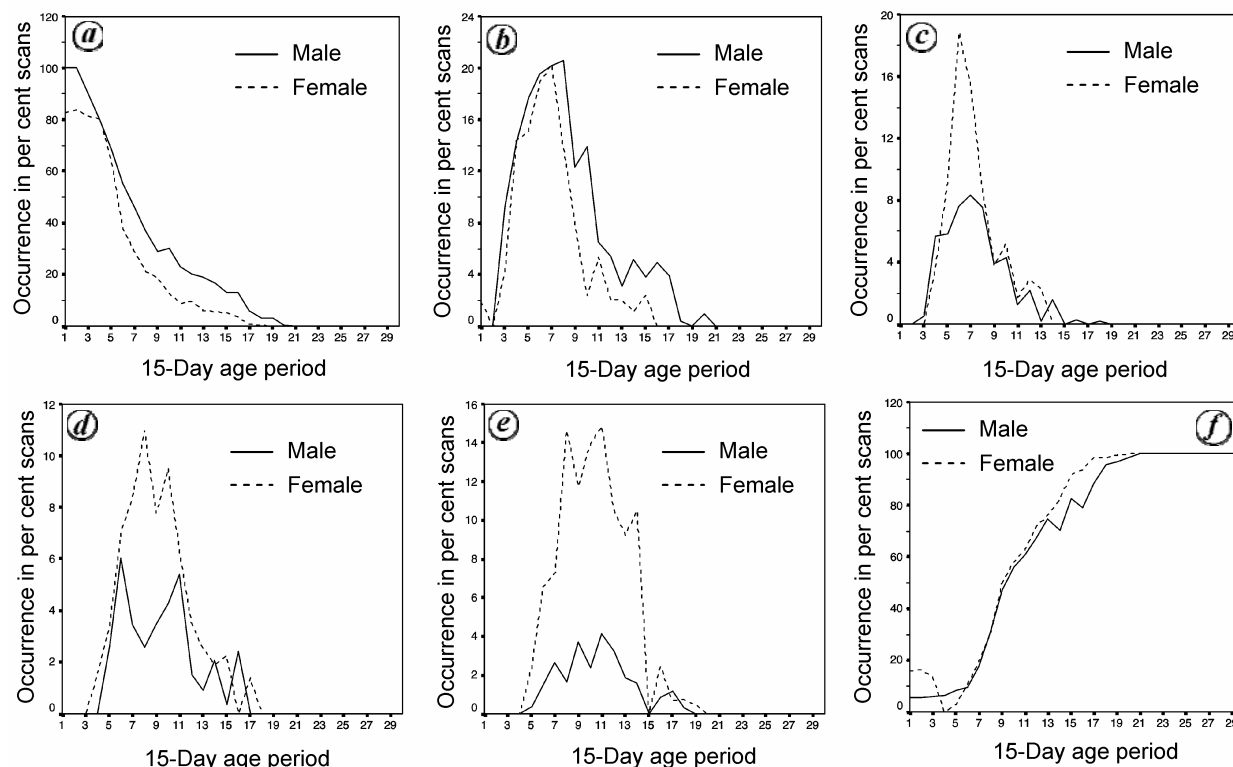


Figure 2. Distance class 0 (body contact with the mother) (a), 1 m (b), 2 m (c), 3 m (d), 4 m (e), 5 m and more (f), occurring respectively, in per cent scans in male and female infants at different age periods of 15 days.

rence of nipple contact ended at the age of seven and a half months in female infants, and beyond this age, it was only the male infants that showed this behaviour up to the age of ten months. All male and female infants made nipple contact up to the age of five months (Figure 1 b). Beyond the age of six and a half months, nipple contact was observed in a larger per cent of males than females, though with a decreasing per cent in both sexes.

Mother–infant distance: Figure 2 presents data on mother–infant distance with reference to distance classes and age periods observed in per cent scans. The infant remained close to the mother up to the age of about three months. Body contact with the mother was observed in 80–100% of the scans in female and male infants respectively, up to their age of 15 days (Figure 2 a). One metre distance from the mother was observed largely when the infants were about three months old (Figure 2 b). At the age of about three and a half months, the infants were more often seen within the distance class of 2 m (Figure 2 c). At the age of three and a half to five months and five to seven months, the infants were mostly in distance classes of 3 and 4 m respectively (Figure 2 d and e). However, at distance classes of 2, 3 and 4 m from the mother, more female than male infants were observed. By the age of about ten and a half months, all infants were

mainly seen at a distance of 5 m or more from the mother (Figure 2 f).

Retrieve: Young infants that were at a distance from the mother were retrieved by her when she moved from a sitting position. Figure 3 a shows the data on retrieval of male and female infants by the mother at different age periods of infants. Overall, male infants with a mean occurrence of 0.034 per interval were retrieved more (Mann–Whitney $U = 73.50$; $P < 0.05$) than female infants with a mean occurrence of 0.019. Further, retrieval of female infants almost ended at the age of about six months, whereas it continued in the case of male infants up to the age of eight and a half months. Beyond this age, no infant was retrieved.

Approach: The occurrence of infants approaching the mother, when they were at a distance, started to increase steadily from the infant’s age of about two months (Figure 3 b). In female infants, the peak of approach was observed to occur in about 9% of the intervals at the age of seven and a half months, and then it suddenly became almost zero. The male infants, however, continued to approach their mothers, reaching a peak at the age of nine months, though occurring only in about 3% of the intervals. No difference was observed in the overall mean occurrence of approach between the two sexes.

Punish: After a certain age of the infant, attempts to initiate nipple contact with the mother were rejected by the mother. The occurrence of punishment behaviour by the mother started at the infant's age of about two months (Figure 3c), coinciding with approach (Figure 3b). Female infants received highest occurrence of punishment once at the age of five and a half months, and then again at the age of seven and a half months. Male infants reached the peak of receiving punishment at the age of eight and a half months. Approach and punishment, combined for infants of both sexes, were found to be highly related (Pearson product moment correlation: $r = 0.94$; $N = 21$; $P < 0.001$).

Mother grooms: Figure 3d presents data on the occurrence of mothers grooming their male and female infants

at various age levels of the infant. Overall, male infants received more grooming at the mean occurrence rate of 0.040 per 20 s interval against the female mean occurrence rate of 0.019 per 20 s interval (Mann-Whitney $U = 92$; $P < 0.01$). Further, grooming by the mother terminated at the female infant's age of seven months, whereas it continued till the age of nine months in the case of male infants.

Environment-directed behaviours

Environmental exploration: Both male and female infants started to explore the environment at the age of about one and a half months (Figure 4a). The occurrence of this behaviour sharply increased between the ages of

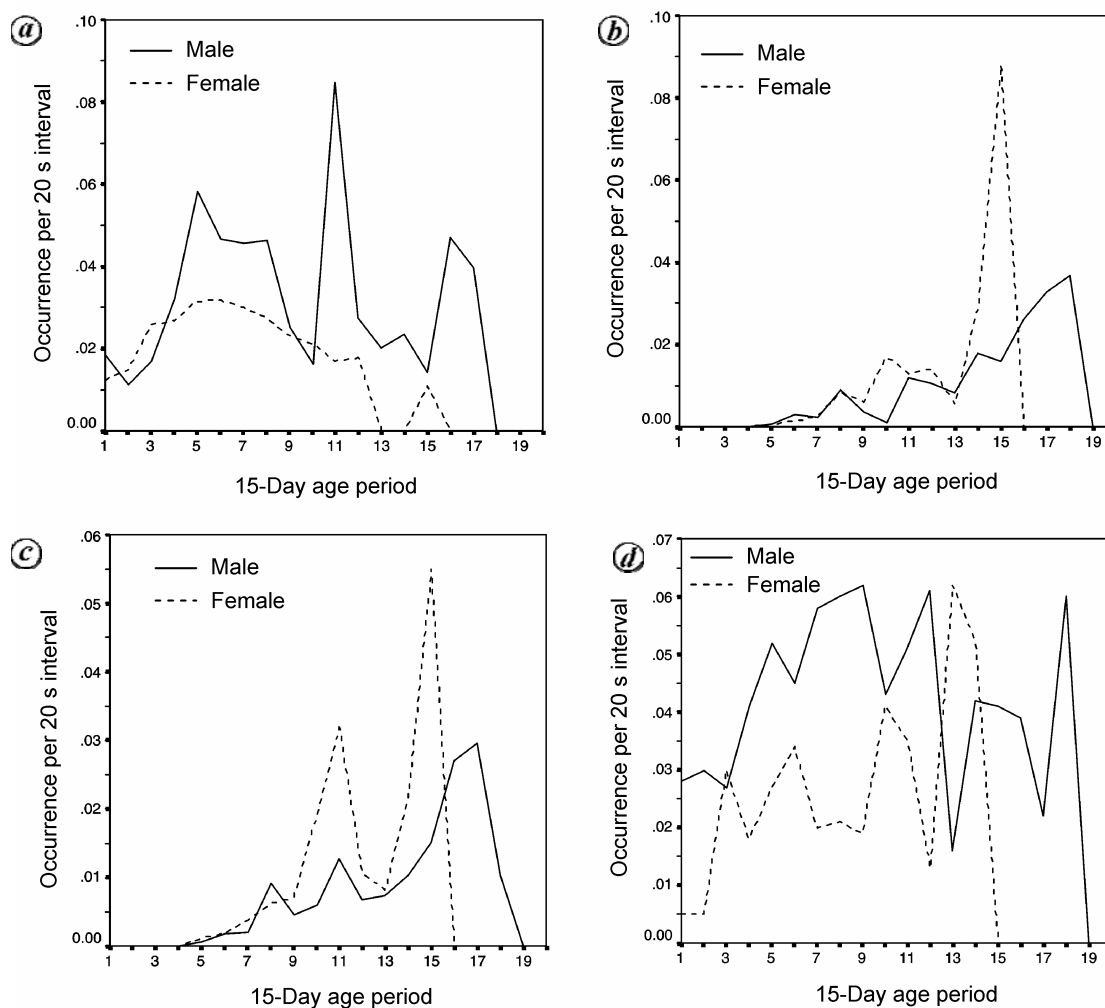


Figure 3. a, Occurrence per 20 s interval of retrieval by mother of male and female infants at different age periods of 15 days. b, Occurrence per 20 s interval of approaching mother by male and female infants at different age periods of 15 days. c, Occurrence per 20 s interval of punishment by mother to male and female infants at different age periods of 15 days. d, Occurrence per 20 s interval of mother grooming the male and female infants at different age periods of 15 days.

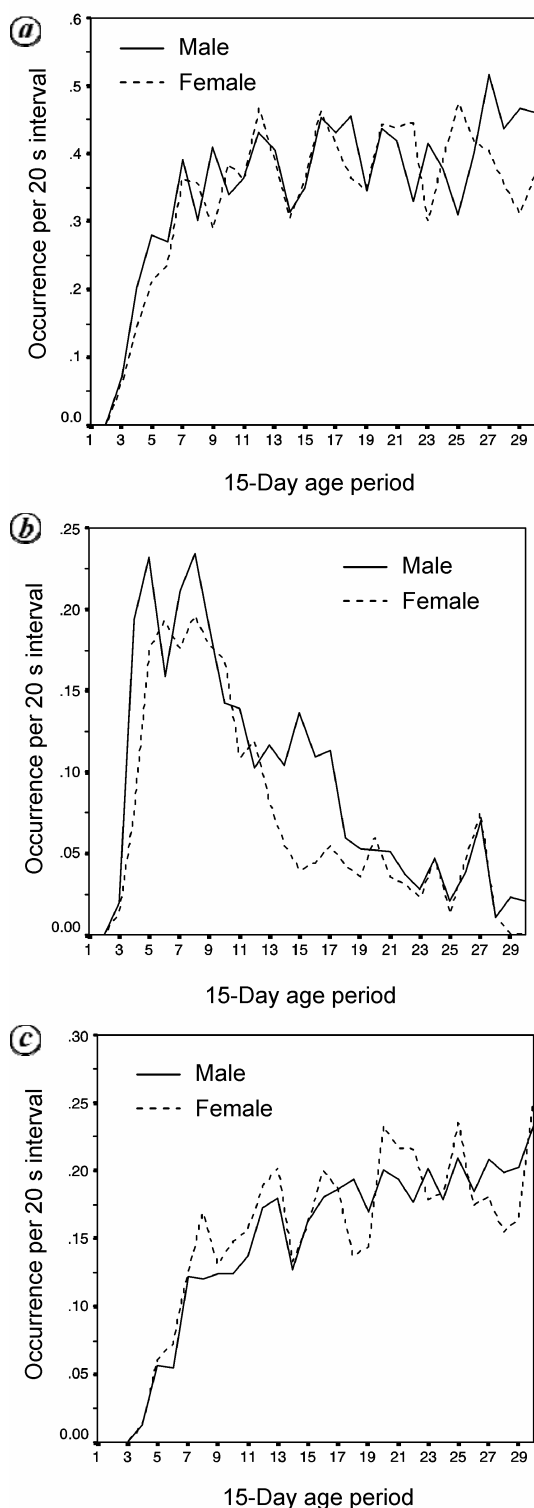


Figure 4. *a*, Occurrence per 20 s interval of environmental exploration by male and female infants at different age periods of 15 days. *b*, Occurrence per 20 s interval of manipulation of objects in the environment by male and female infants at different age periods of 15 days. *c*, Occurrence per 20 s interval of eating solid food by male and female infants at different age periods of 15 days.

one and a half months and three and a half months. By the time the infants were six months old, exploration occurred in more than 40% of the intervals. It then more or less remained constant. No difference was observed in the overall mean occurrence of exploration in the two sexes.

Environmental manipulation: Figure 4 *b* presents the data on manipulation of objects in the environment by infants at various age levels. The infants manipulated objects in about 20% of the intervals between the age of two and four months, and this behaviour sharply declined later. Although there was no overall difference between the two sexes, male infants between the age of seven and eight and a half months manipulated objects more than female infants.

Eat: Figure 4 *c* depicts the data on the occurrence of eating food from the environment at different age classes. No difference was observed in the occurrence rate of eating between male and female infants. Infants of both sexes started eating food at the age of about one and a half months. By the time the infants were six and a half months old, eating occurred in about 20% of the intervals. From then on, it increased only slightly.

Play: Infants of both sexes began solitary play at the age of about one and a half months (Figure 5 *a*). The occurrence of this behaviour markedly increased during the next few months and reached its peak, with occurrence in nearly 20% of the intervals, at the age of three and a half months. It then steadily decreased and became almost zero by the time the infants reached the age of 15 months. Social play began at the age of about two months (Figure 5 *b*). With a marked increase in the next few months, this behaviour reached its peak with an occurrence in about 15% of the intervals between the ages of five and a half and six months. There was then a steady decline in its occurrence, but it continued in about 3% of the intervals beyond the age of about one year. In the initial stages of development, the occurrence of self-play was more than that of social play. However, social play occurred more than self play after the age of four and a half months. No difference was observed either in the rate or in the pattern of occurrence at different age levels between male and female infants for both solitary and social plays.

Discussion

The early stages of development from birth to about one year of age in primates are characterized by marked changes in behaviour. Not only do the behaviours change in their frequency, some behaviours disappear at certain age levels and new behaviours are observed. In general, the very young infant is dependent on the mother for milk. Few months old infants start exploring the envi-

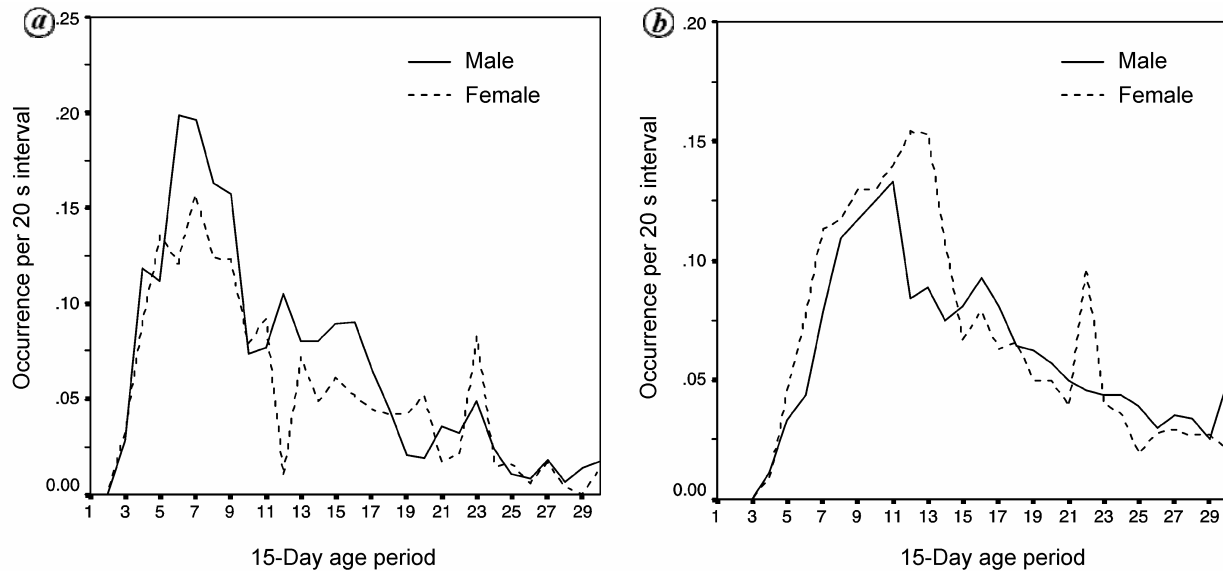


Figure 5. *a*, Occurrence per 20 s interval of self-play by male and female infants at different age periods of 15 days. *b*, Occurrence per 20 s interval of social play by male and female infants at different age periods of 15 days.

ronment and begin to feed on solid food. The mothers then begin to wean the young. Behaviours oriented towards environment and conspecifics other than the mother largely replace mother-oriented and self-oriented behaviours of the infant.

Two marked stages could be observed in terms of changes in the occurrence of behaviour in the lion-tailed macaque infants. The first stage was the infant's age of five and a half months, and the second was the age of about nine months. Between five and six months of the age of the infant, there was a slight increase in the occurrence of nipple contact, which was otherwise declining. On the other hand, retrieve also showed peaks at the same age. There were also small peaks in the occurrence of the infant approaching the mother and mother punishing the infant. These occurrences indicate that triggering of weaning in the lion-tailed macaques starts at the age of about five and a half months. Punishment also indicates that weaning in lion-tailed macaques is an actively initiated process by the mother, implicating parent-offspring conflict²². From six to nine months of age, the approaches by the infant and attempts at making nipple contact with the mother kept steeply increasing. At the same time, punishment by the mother also linearly increased. Both of these behaviours abruptly ended at the infant's age of about nine months. Occurrence of nipple contact ended in the female infants at the age of about seven months. However, in the case of some male infants, nipple contact continued till the infant's age of ten months. Between the ages of three and six months, more female infants were observed to be away from the mother at distances between 2 and 4 m than male infants. The mothers retrieved

male infants more than female infants. Male infants also received more than twice the grooming received by the female infants from their mothers. It, therefore, appears that in lion-tailed macaques, male and female infants are treated differently by the mother, thus indicating a sex-biased parental investment in which male infants receive more investment than female infants. This observation differs from the findings in a number of other nonhuman primate species where the parental investment has been found to be more female-biased^{25,32}. However, the results of the present study support the general tendency in cercopithecines where differential treatment by the mother based on the sex of the offspring begins only after the first few months of age of the infant³³.

Another critical behavioural manifestation at the infant's age of five and a half months was the peak in the occurrence of social play, environmental exploration and eating solid food. In a way, the lion-tailed macaque infants at this age showed signs of adult behaviour patterns. Eating occurred in about 25% of the intervals that is almost the same as in adult lion-tailed macaques³⁴. The time spent by infants in environmental exploration and social play was replaced by passivity in adults. After this age, occurrence of social play gradually declined but environmental exploration remained more or less constant. In macaque species that are largely commensal and not so much resource-limited such as the bonnet macaque, the occurrence of social play was observed in more than 50% of the intervals even at the infant's age of 12 to 15 months³⁵. Social play in infants and juveniles largely occurs when the group rests. Such resting periods are more in frequency and longer in duration in species where the

food search does not require longer periods. The lion-tailed macaques inhabit a resource-limited and competitive rainforest environment. Fruits of *Cullenia exarillata* dominate the diet of the lion-tailed macaques in the Anaimalai Hills³⁶. The fruits of this plant are also largely consumed by six other arboreal mammals and seven species of birds³⁷. In addition, the lion-tailed macaques also forage on fruits of several other plant species that are widely distributed in their habitat. As a result, nearly 62 (ref. 36) to 79% (ref. 14) of the time of a day is spent on food search and feeding by the lion-tailed macaques. While the adults range and forage, the infants and juveniles also move along with them; as a result, they have little time for play. The lion-tailed macaques spend only about 8% of their time in social activities^{14,34}. The occurrence of environmental exploration reaches a peak at the infant's age of about five and a half months and then it remains constant, indicating that infants also spend nearly 45% of their time in foraging.

At the infant's age of nine months, approach by the infant, punishment by the mother and grooming by the mother reached a peak. It, therefore, appears that an active weaning of the infant by the mother begins at the former's age of about five and a half months, and weaning is completed by the age of nine months. However, a high occurrence of the mother grooming the infant at this age indicates that the mother continues to care for the infant in ways that cost her less in terms of continuation of parental investment and future reproductive success³⁸.

The overall pattern of infant development in the lion-tailed macaques, therefore, can be summed up as a change from mother-related behaviour during the early stages to environment-oriented behaviour during the later stages of infancy. In its basic traits, the development pattern of lion-tailed macaques seems to correspond with that of other macaques³⁹. Weaning starts at the age of about five months. It is completed in female infants by the age of about seven and a half months. In the case of male infants, weaning is completed by the age of about nine months. After the age of about ten and a half months, the infants become more or less independent of their mothers. Despite differences in the rates of occurrence in several behaviours, the timings of development patterns in terms of peaks and changes were similar in male and female infants, indicating species-specific characteristics. The fact that these patterns were discerned by the results points to the reliability of the methods used.

The pattern of infant development described above raises a question about the long inter-birth intervals in lion-tailed macaques. If the infant is completely weaned by the age of about nine months, the females obviously do not lactate anymore. Why then do the females not become pregnant soon? The inter-birth interval in lion-tailed macaques is about 30 months if the infant survives, and it reduces to about 14 months if the infant dies⁴⁰. Further, though there is a peak in infant births during Febru-

ary and March⁴¹, the lion-tailed macaques do give birth to infants almost throughout the year. Seasonal effects, therefore, should not affect the next pregnancy. Long birth interval has also been observed in several other macaque species⁴². The weaning patterns, however, in most such species are not known. A correspondence between weaning and birth patterns has been observed in Drakensburg Mountain baboons^{43,44}. In the harsh environment of the Drakensburg Mountains, the infants are completely weaned only at the age of about 18 months. This could result in a long inter-birth interval in females.

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