LIFE HISTORY PARAMETERS OF THE LION-TAILED MACAQUE, MACACA SILENUS: A COMPARISON OF WILD AND CAPTIVE POPULATIONS.

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ABSTRACT

Reproductive parameters of a wild population of lion-tailed macaque in the Indira Gandhi Wildlife Sanctuary are summarised and compared with those of the captive population in American zoos. Survival rate of immatures is greater in the wild, but birth rate is lower, interbirth interval is longer and age at first birth is higher. Both wild and captive populations seem to have lower birth rates, longer interbirth interval and higher age at first birth than not only captive but even wild populations of other macaques. Sexual cycles are of similar length in the wild and captivity. The frequency of mounting in the wild increases from the start of the sexual swelling reaching a peak four days prior to deflation. In captivity it shows no fluctuations in the follicular phase, but dropped abruptly in the luteal phase. The aseasonality in births in the wild is largely similar to that in captivity with births occurring in 9 months of the year with a peak in June. However, in the wild there is a high degree of synchrony in sexual cycles. The areas where captive management could benefit from observations in the wild are discussed.

INTRODUCTION

The lion-tailed macaque, one of the most endangered primates, is confined to patches of rain forest along the Western Ghat mountain ranges in South India (Green & Minkowski 1977; Kurup 1978; Ali 1985; Karanth 1985; Kumar *et. al.*, 1995). The wild population is now estimated to about 4,000 animals (Kumar *et. al.*, 1995). Extensive studies have been completed both in the wild and in captivity which makes it possible to compare some important life history parameters between the wild and captive populations. The studies on the wild populations spanned a period of about six years from 1978 to 1984, when demographic parameters were monitored and intensive ecological and behavioural studies were carried out on a population in the Indira Gandhi (previously Anamalai) Wildlife Sanctuary, Tamil Nadu State (Kumar 1987, 1995a & b; Kurup & Kumar 1993, Kumar & Kurup 1995). The studies on the captive colonies involved a detailed analysis of the demographic information available from North American zoos for the last two decades (Lindburg et. al., 1988), supplemented with intensive studies on the reproductive behaviour and physiology (Lasley *et. al.*, 1985; Lindburg & Lasley 1985; Lindburg *et. al.*, 1985). The objective of this paper is to summarise some important life history parameters from the wild population and then to discuss them in relation to those from the captive studies. The parameters to be discussed are immature and adult survival rates, birth rate and interbirth interval. Female sexual cycles, to which birth rate and interbirth interval are linked, are also discussed briefly.

LIFE HISTORY PARAMETERS IN THE WILD

Data Source

The data on the wild population of the lion-tailed macaque presented below come from a field study in the Indira Gandhi Wildlife Sanctuary from March 1978 to April 1984. This period was divided into three phases:

(a) July 1978 to March 1980: when intensive ecological and behavioural studies were carried out on one group and demographic data were monitored from five selected groups;

(b) April 1980 to March 1982: when only one visit was made to the study area (in March 1981) to monitor demographic data from the selected groups; and

(c) April 1982 to April 1984: when intensive ecological studies were carried out on the same group as in 1978-80, demographic data were monitored from the selected groups, and a population survey was carried out.

The study site and data collection procedures are described in detail elsewhere (Kumar 1987) and are not repeated here. All the births and mortality (disappearance of an individual) in the main study group were noted within one week of its occurrence in 1978-80 and 1982-84. During these two periods the monitored groups were censused at least at 30-40 days intervals. Data for 1980-81 and 1981-82 were derived from only one census each at the end of the year; in March 1981 and April 1982. Data on reproductive behaviour come from intensive ecological studies on the main study group in 1978-80 and 1982- 84. Further details are given at the beginning of each section.

Survival rate

Survival rate was estimated as the proportion of animals which survived an observed year (1 April to 31 March) out of the total number of animals under observation during that year. Data for this were taken from the groups which were monitored at least for one year (Table 1). As in most field studies mortality was assumed upon the disappearance of an individual. Since only few individuals were identifiable mortality between two censuses was estimated on the basis of the relative differences between the age/sex classes (see Kumar 1987 & Kumar & Kurup 1988 for details). Only three age/sex classes are considered; immatures (below 6 years of age), adult females and subadult and adult males. Since intergroup migrations in macaques are largely confined to the subadult and adult males their disappearance from a group is considered as mortality/emigration.

Table 1 : Survival rate for all age/sex classes and immatures in five groups.

Group name	Years monit.	Total animal years	Deaths	Immature animal years	Deaths	Immature survival
VSI	5	89.09	3	53.09	1	0.98
VSII	6	90.75	6	44.75	5	0.94
AS	3	86.25	3	41.25	1	0.98
ASII	2	30.75	1	14.25	1	0.97
BS	1	22.58	0	10.86	0	....
Total	17	319.42	13	164.42	8	0.95

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A total of 17 group-years of data, consisting of 319.5 animal years, were collected between 1978 and 1984, during which 13 animals disappeared. At least three cases of male emigration/death were recorded, during the 37 animal years, giving a death/emigration rate of about 0.08/male/year or a survival of 0.92/male/year. Two of these were fully adult males, and the other a subadult male. It should be noted that all these death/emigrations were identified in the groups with which I was most familiar. It was very likely that emigrations followed by immigration in other groups could have gone unidentified.

A total of 118 animal years of data were collected on adult females during which four disappearances were recorded. This gave a survival rate of 0.97/female/year. Two adult females which disappeared were the oldest females in their groups. A total of 164.4 animal years of data were collected on immatures, out of which eight immatures disappeared. This gave a mean survival rate of 0.95/individual/year for the immatures.

Birth Rate

A total of 154 animal years (the sum of the number of adult females present in each group at the start of each observed year) were monitored during 1978-84 from eight groups (Table 2). A total of 43 infants were born into the above eight groups giving an average birth rate of 0.28/female/year. There was no significant difference between the years in birth rate (x^2=1.9, df=4, p>0.05).

Age at First Birth

The most reliable observation on age at first birth comes from one individual in the main study group. When observations started on the main study group in August 1978 it was estimated to be about 12-15 months old and most probably born in May-June 1977. It gave birth for the first time in June 1983 at about 6 years of age. Estimates from 4 other individuals in the main study group are also available, though less accurate. Ages of these were deduced from the first appearance of nipples and sexual swellings and calibrating them to the age at which these happened in the previous female. Three were estimated to have given birth for the first time between 6 and 7 years of age, and one only between 7 and 8 years of age. These five cases indicated a mean age at first birth of about 6.6 years (s.e=0.2, n=5).

Female Sexual Cycle

Three identifiable females gave birth twice during the 6-year period, with interbirth intervals of 30, 28 and 31 months or a mean interval of about 29.7 months (2.47 years). Two other females, on the other hand, did not give birth even about 51 months after their last parturition. The former died at the end of the 51st month, while the latter was alive in March 1984, but showing no signs of sexual cycles. The duration of the post-partum amenorrhea could not be reliably estimated in the field. The period when cyclical fluctuations in oestrogen and progesterone occur is characterised in the lion-tailed macaque by the cyclical appearance and disappearance of sexual swellings (see Fooden 1975 for the morphology of the swelling; Lindburg *et. al.*, 1985 and Lasley *et. al.*, 1985 for the physiology). From the first swelling marking the end of the post-partum amenorrhea the cyclical appearance and disappearance of swelling continue either until the female conceive or until the next summer amenorrhea (see below). In the former case swelling reappears only after the next post-partum amenorrhea and in the latter after the summer amenorrhea.

The interval between the onset of two consecutive swellings (of females which were neither pregnant nor in post-partum or summer amenorrhea) varied from 17 to 47 days with a mean of 30.0 days and a median of 27 days (n=5). The duration of the swelling phase ranged from 8 to 19 days with a mean of 14.1 days (n=7), and the non- swelling phase ranged from 6 to 25 days, with a mean of 16.4 days (n=7).

Mounting Frequency and Sexual Cycle

The mean frequency of mounting per hour on successive days of the sexual cycle was estimated from six incompletely observed sexual cycles. The sexual cycles were aligned by the day when the swelling disappeared. The frequency of copulatory calls which are given by the female in 80.3% of the mountings when she had sexual swelling was used as an index of mounting frequency. The estimated frequency do not represent absolute frequency and is used only for comparison between days.

The frequency of mounting started to increase 3-4 days before the appearance of the swelling, but in all cases decreased almost to zero on the last day of swelling (Figure 1). In five of the six cases the peak mounting frequency was seen on the fourth day prior to deflation. The interval between the onset of swelling and peak sexual activity varied from 10 to 15 days, with a mean of 12.7 days. This interval appeared to be more variable (coefficient of variation c.v.=22.8%) than the interval between peak sexual activity and deflation (c.v.=15.1%).

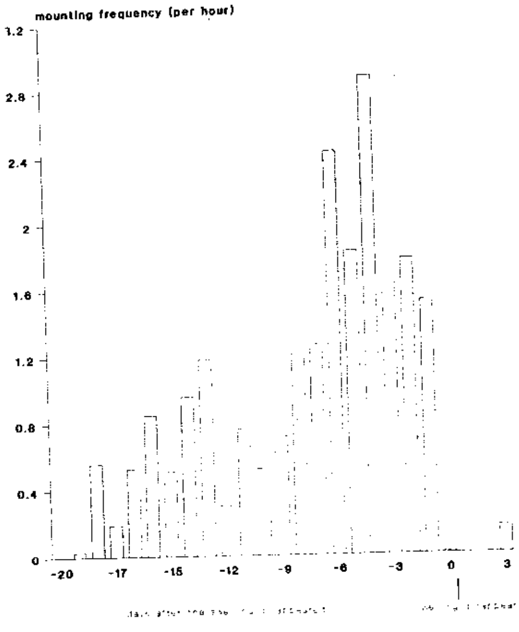

Figure 1 : Mounting frequency (per hour) by the adult male of the study group on successive days of the sexual cycle when there was only one adult female with sexual swelling: mean for six cycles. The sexual cycles are sligned by the day on which swelling disappeared (Day 0; see Table 1.)

Reproductive Seasonality

The incidence of sexual swelling in each month was systematically recorded only from the main study group. Between March 1979 and February 1980, at least one female with swelling was present in the group in every month from the last week of May 1979 until the end of the study in February 1980 (Figure 2). Between December 1982 and March 1984, swellings were seen every month from September 1983 until February 1984. Combining the two study periods the only months in which no females showed swelling were, therefore, the summer months of March and April. Although systematic data was not collected from other groups, swelling was also not seen in them in March, April and May of 1979 and 1983. It appears, therefore, that there is a summer amenorrhea in the lion-tailed macaque.

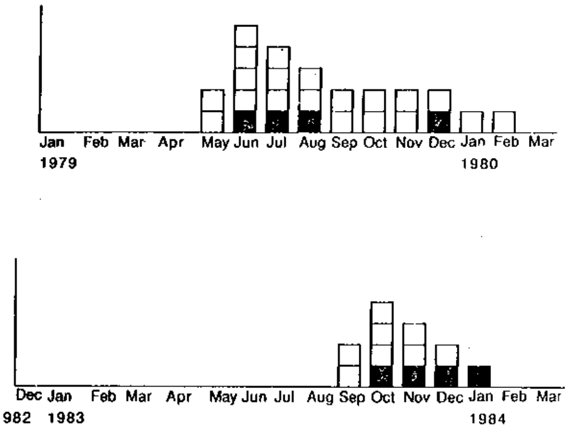

Figure 2: The incidence of sexual cycles and conceptions in the main study groups in 1979-80 and 1982-84. Each square shows one swelling cycle in a female in that month. The shaded squares represent sexual swellings in which conceptions occurred.

Maximum synchrony of sexual cycles of adult females in the group occurred one cycle (i.e about 30 days) after the first female started cycling in the season (Figure 2). In 1979-80, two females showed swellings in the last week of May, and in June all the five females of the group had swellings. All the four adult females which showed swellings between December 1982 and February 1984 did so in October 1983, one swelling cycle after the first swelling in September.

In both the study periods , conceptions (Conception dates were estimated using a gestation period of 172 days.) in the main study group did not indicate a peak corresponding to that of sexual swellings at the beginning of the season (Figure 2). Of the five females which showed swellings in June 1979 only one conceived in that month to give birth in December 1979. In the subsequent months the females which had not conceived continued to cycle but with only one female conceiving each month and then stopping the sexual cycle. In 1983 all the four females which showed sexual swelling during that mating season did so in synchrony in October, but only one stopped cycling after that month. The remaining three females showed swelling in November, but with only one conception. Of the remaining two females one conceived in December 1983 and the other in January 1984.

A total of 26 births were recorded within the first week of birth in eight groups during 1978-84, and the probable month of birth could be estimated in 14 more births (Figure 3). The distribution of the 26 births suggest that births tend to occur in all the months of the year except August, September and October. Inclusion of the 14 births on which data were less reliable did not change the overall pattern. The absence of births in August-October corresponds to the period of summer amenorrhea in March-May suggested earlier.

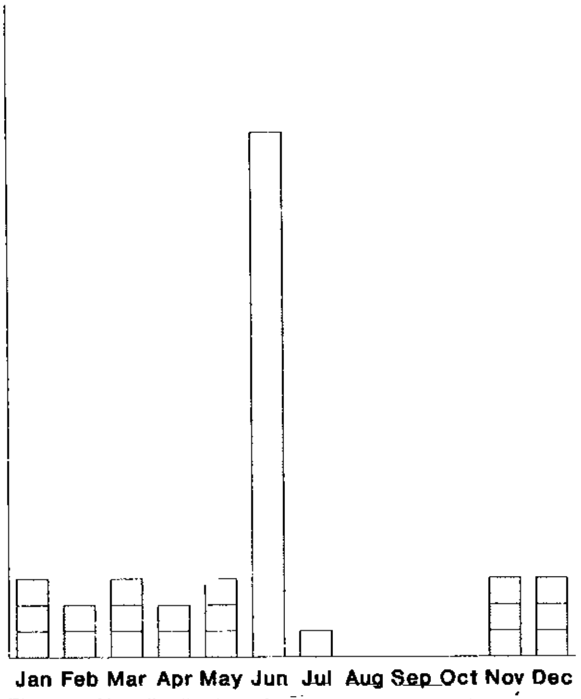

Figure 3: The distribution of 40 births in the Anamalai population of the lion-tailed macaque in 11979-80 and 1982-84. Each block represents one birth in that month.

COMPARISON WITH CAPTIVE POPULATION

The high age at first birth and low birth rate in the lion-tailed macaque in the wild in relation to other macaques are not explained by allometry and might represent adaptations to its stable habitat (Kumar 1987). Age at first birth, birth rate and interbirth interval in captivity seem to further support the above conclusion. In comparison to an age at first birth of 6.6 years in the wild, in captivity it is 4.9±1.2 years (Lindburg *et. al.*, 1988). Moreover, only 60% of the females in captivity had given birth by at 5.5 years of age. The age at first birth of the lion-tailed macaque in captivity, therefore, seem to be higher than not only captive but even wild populations of other macaques. The same is also true of the birth rate. It is 0.28/year/female in the wild and 0.35/year/female in captivity. The latter is lower than even the wild populations of the other macaques. The low birth rate is reflected in the long interbirth interval both in the wild (29.7 months) and in captivity (17 months). While the high age at first birth, low birth rate and long interbirth interval in the wild might be explicable as being resource induced this is unlikely to be so in well maintained captive colonies. The other possibility is poor conditioning to captivity which is not related to nutrition. Conditioning to captivity is, however, often measured in terms of the reproductive performance of the colony. On the basis of the close parallel between the data from the wild and captivity it is suggested that the high age at first birth, low birth rate and long interbirth interval in the lion-tailed macaque compared to other macaques might be adaptations to its stable habitat. Captive management should, therefore, address this possibility.

Birth rate varies significantly with age in captivity, the maximum being at 6-7 years of age and becoming negligible after

20 years of age (Lindburg *et. al.*, 1988). While there is no data on age specific birth rate in the wild two old females in the main study group did not give birth for a period of over 50 months. The most significant factor affecting birth rate in the wild, was found to be group size. Birth rate in eight groups declined as the group size increased (Pearson r=-0.89, n=8; Kumar 1995b). This decline appears to be largely the result of increasing intragroup feeding competition as the group size increases (Kumar 1987). The effect is, however, unlikely to occur in well maintained captive colonies.

The mean survival rate for the immatures in the wild was 0.95/year. The survival rate to age at first conception at about 6 years of age could be, therefore, estimated as 0.74. This is greater than that in captivity (0.68, Lindburg *et. al.*, 1988). Although there is no data on age specific survival rate of immatures in the wild, limited data suggest that the above difference might be largely accounted for by the difference in the survival of infants. Infant mortality appeared to be about 13% in the wild compared to 26.8% in captivity (Lindburg, *op. cit.*). While it would be hard to speculate on this relatively low infant survival in captivity, it is interesting that infants of primiparous females had a significantly low survival rate compared to the infants of multiparous females. It is noteworthy that in the wild, subadult females frequently allomother infants for longer than two hours (Kumar & Kurup 1981). The difference between immature survival in the wild and captivity, infant survival in particular, suggest that this might be an area where captive management could improve reproductive performance.

Swelling cycles are similar in length to menstrual cycles measured in captivity (Hadidian & Bernstein 1979). This also appears to be true for lion-tailed macaque, with the swelling cycle of about 30 days in the wild being equal to the combined durations of follicular phase (14 days) and luteal phase (16 days) reported from captivity (Lindburg *et. al.*, 1985).

In the field, mounting increased 4-5 days prior to the appearance of swelling (Swelling was probably inconspicuous during at least 1-2 of these days since inflation was slow compared to deflation), but otherwise was largely confined to the swelling phase. Within the swelling phase the mounting frequency tended to increase, reaching a peak about 4 days prior to deflation. In captivity, mounting frequency was almost constant throughout the follicular phase, but with a sharp drop in the luteal phase (Linburg *et. al.*, 1985).

The occurrence of sexual cycles and births in nine months of the year largely confirms the reproductive aseasonality observed in captivity (Lindburg *et. al.*, 1988). The absence of sexual swellings in March, April and May and of births in August, September and October suggest a summer amenorrhea in the wild. There is no evidence of this in captivity.

Although sexual cycles and births occurred in most months of the year, it should be noted that there was a high synchrony in sexual cycles in the main study group in 1979 and 1983. This synchrony occurred one cycle after the first cycle after the summer amenorrhea when all the females which showed sexual swellings in that year did so together. The absence of seasonality in births in the whole population in spite of a high synchrony in sexual cycles of females in individual groups was due to two factors. First, the timing of the synchrony in sexual cycles seemed to differ between groups as well as within the group between years. For example, peak synchrony in the main study group was in June in 1979 and in October in 1983. Secondly, even though there was peak synchrony in sexual cycles in a group, as was shown above, conceptions rarely showed a corresponding peak, but appeared to be more spread out. Females in the main study group took 1 to 7 sexual cycles to conceive with a mean of 3.4 cycles (s.e.=1.2, n=8).

The absence of seasonality in births, therefore, revolves around two questions; why does the timing of synchrony in sexual cycles vary between groups in population and between years in a group? Why conceptions do not correspond to the peak in synchrony of sexual cycles? The timing of reproductive seasonality has been discussed in detail elsewhere (Lancaster & Lee 1965; Lindburg 1987). Synchrony in sexual cycles is a precondition to synchrony in births, but not the only one, since conceptions also should occur. As was shown earlier, conceptions do not coincide with the peak synchrony in sexual cycles in the wild, with a female taking 1 to 7 sexual cycles to conceive. Although no data are available from captivity on the number of cycles to conception, nonconceptive cycles might be common. An important factor which might postpone conception in the lion-tails in the wild appear to be sexual competition between ovulating females (Kumar 1987; Kumar, in press). The factors which might induce such a competition are the high adult female/male ratio (mean=5, Kumar 1995), the high synchrony in sexual cycles, and multiple mount pattern in the male. Moreover, most of the groups are one male units. Female sexual competition is indicated by the high incidence of harassment of sexually interacting adult male and female by other females with swellings. These harassments appeared to curtail mounting from taking place, bring mounting to premature termination and often redirect the mounting to the harasser. The incidence of harassment increased with the number of females with swellings in the group. As much as 35% of the mounting by the male were curtailed when there were three females with swelling in the group. The resulting reduction in the probability of conception would be greater if the harassment occurred around the ovulation time of the harassed female. Another important factor might be an asymmetry in the occurrence of harassment, for example according to the dominance hierarchy. While postponement of conception resulting at least partly from sexual harassment within a year would cause births to be more dispersed within the year, postponement up to the summer amenorrhea would mean loss of a reproductive year for the female. If harassment is related to dominance hierarchy, the result would be reproductive suppression of some females which is linked to dominance. A definite answer to this would require long term studies on identifiable females in social groups where the dominance and sexual interactions and sexual status of females could be continuously monitored

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