9261

LONG-TERM STUDIES OF CAPTIVE LION-TAILED MACAQUES. LINDBURG, D.G. AND FORNEY, K.A.

Introduction

Lion-tailed macaques (*Macaca silenus*) derive from the rain forests of the Western Ghats in southwest India. Following on several years of census activity, the wild population is believed to number in excess of 2000 individuals, and one recent estimate places the number closer to 5000 (KARANTH, 1985). The species is considered by the IUCN and most other conservation entities to be endangered. The first in-depth study of a wild population was carried out during 1973-75 (GREEN and MINKOWSKI, 1977). Shortly thereafter several Indian primatologists, including Kurup, Ali, Johnson, and Karanth, collected census and ecological data. Most notable in terms of socio-ecological investigations are the five years of intensive study by KUMAR (1987), between 1978 and 1984.

In captivity the lion-tailed macaque has been nearly exclusively a resident of zoological gardens. Its rareness and attractive phenotype are factors that have contributed to its value as an exhibit animal. Recent estimates place the size of the captive population at 450-500 individuals (GLEDHILL, personal comm.). Scientific interest in the species has increased in recent years in connection with the development of conservation programs.

In this report we compare results from nearly a century of life in captivity to information that has recently become available from field investigations. Captive demographics are affected directly by such human practices as withholding of breeding opportunities or loss of individuals through exportation. In other, less obvious ways, the life history of lion-tails may be influenced by nutritional and environmental (e.g. climate) differences in the two locales and by health care impacts on such parameters as survivorship and longevity.

Although the incompleteness of records from the earlier decades of confinement and the relatively small sampling of individuals from both populations are limiting factors, there are compelling reasons for making such comparisons at this point in time. Over 90% of the lion-tails living in zoos today are captive born. Since it is difficult to imagine a circumstance under which additional wild-caught individuals would be brought into the captive sector, future generations must derive from the brood stock now in hand. Timeliness is also found in the fact that detailed management plans have been drawn up for the North American population and are in the formative stages for populations in Europe and Japan. It seems important to these plans to have in hand a knowledge of the potential impact of captivity on demographic and life history variables. Information of this kind will aid in assessing the state of the captive population and in guiding management decisions.

Methods

Only data drawn from the lion-tails born in North American zoos are used to estimate parameters for the captive population. Methods of data collection for this population are described in LINDBURG et al. (1989). For the life table, a broader data set is used, in that animals which were either shipped out of North America or who were brought in from zoos in other countries are included for the years they resided in North America. This table was generated using a program written by Jonathan Ballou of the National Zoological Park, Washington, DC. Information on wild populations is derived exclusively from KUMAR (1987). Where essential to the drawing of valid comparisons, our analysis has followed sampling procedures used in the field. For example, in calculating annual birth rates we have used data from a comparable 5 year period and have included only those infants surviving at the end of each 'census' year in order to approximate Kumar's annual census of wild troops.

History of the North American zoo population

Although earliest records are scant, lion-tails probably first appeared in captivity in European zoos well over a century ago (JONES, 1985). In North America the earliest verifiable record was the importation of a single individual by the Philadelphia Zoo in 1899 (GLEDHILL, 1987). From then until the onset of World War II, small numbers appeared in zoos in New York City, St. Louis, Chicago and San Diego. The heaviest period of import was during the 1950s and 1960s (Fig. 1A), when 54.7% of all wild caught animals were obtained. Imports declined rather suddenly after 1965, the last definite record being a trio imported in 1968.

Slightly smaller numbers of lion-tails of unknown origin appear in zoo records in roughly the same temporal pattern as shown by imports (Fig. 1B). It is reasonable to assume that the majority of these were also of wild provenance, particularly in the pre-war years.

The first captive births of record are three infants born at the Philadelphia Zoo between 1932-36. However, nearly three decades were to pass before births began to occur on a regular basis (Fig. 1C). Considering all sources, then, it can be seen (Table 1) that of nearly 600 lion-tails of record in North American zoos, 72% can be confirmed as captive born, with the vast majority of these occurring in the last two decades. On the basis of these data, the captive history of lion-tails can be divided into three periods:

1. 1899-1953 An initial period of over 50 years' duration in which the goal was to add lion-tails to exhibit collections exclusively through stock drawn from the wild.
2. 1954-1982 A transitional period, marked initially by frequent imports, but also a time when births would eventually exceed imports in annual additions to the captive stock.
3. 1983-present The final period, beginning with publication of a studbook, is indicative of an organized attempt among cooperating zoos to manage the captive gene pool in ways designed to preserve genetic diversity. This effort, like those for other endangered species, was in response to the precarious status of the wild population and to the realization that such steps would have to be taken to sustain the captive population (FOOSE and CONWAY, 1985).

Table 1: Origin of North American Lion-tailed macaques 1899-1986.

DECADE	SOURCE						
	Wild		Unknown		Captive born		Total
	#	%	#	%	#	%	#
- 1909	8	100.0					8
1910 - 1919			2	100.0			2
1920 - 1929	9	75.0	3	25.0			12
1930 - 1939	17	70.8	4	16.7	3	12.5	24
1940 - 1949	4	80.0	1	20.0			5
1950 - 1959	39	57.4	11	16.2	18	26.4	68
1960 - 1969	29	23.2	30	24.0	66	52.8	125
1970 - 1979			10	5.9	160	94.1	170
1980 - 1986					175	100.0	175
Total	106	18.0	61	10.4	422	71.6	589

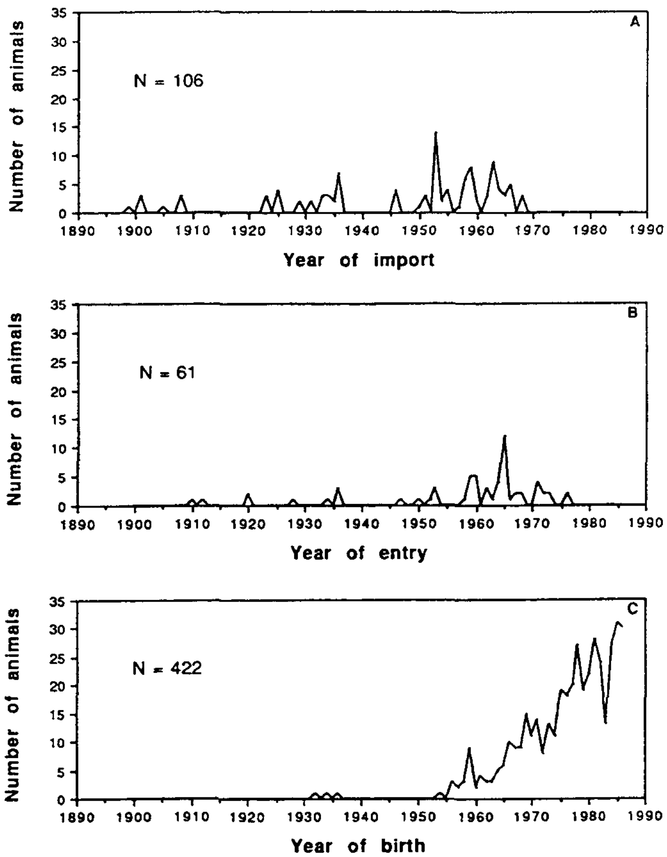

Fig. 1: Provenance of the captive North American population of lion-tailed macaques, 1899-1986. A = wild caught, B = unknown origin, C = captive born.

Population structure

The structure of the captive population at the end of 1986 is shown in Figure 2. The first 6 age classes are designated as immatures, following age criteria applied to the wild population, and comprise 52.3% of the total. In the wild, immatures averaged 47.3% of the population during 5 years of censusing.

Although the numbers for each sex in captivity are equal, this was achieved in part by shipment of 'surplus' males to zoos overseas, beginning in 1977. It has previously been reported that the captive sex ratio at birth strongly favored males (58.5%), and that males experienced a higher rate of mortality than females (LINDBURG et al., 1989). No data on natal sex ratios from wild lion-tails have as yet been reported. The most striking contrast between the wild and captive population is the proportion of adults (including subadults) of each sex. Whereas they occur in nearly equal numbers in the present-day captive population, comprising 22.9% and 24.8% respectively for males and females, males comprise only about 14% of the total in Kumar's study population. This compares with 39% adult and subadult females in the wild.

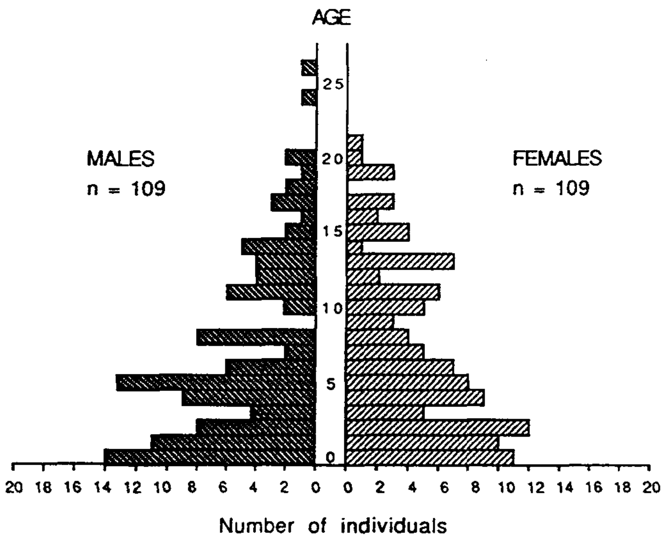

Fig. 2: Population pyramid for the captive population, 1986.

Birth rates

The birth rate is commonly defined as the number of offspring of either sex produced by breeding age females annually (ALTMANN and ALTMANN, 1970; DUNBAR, 1987). KUMAR's (1987) data on this point are based on an annual census of 3-6 troops, and results for 5 years indicate a mean rate of about 30% (Table 2). The interval between births in 3 observed cases averaged 29.7 months, but is probably an underestimate, given the number of infants seen during the study. The mean birth rate in the captive sector during an equivalent 5 year period was 29.5% (Table 2), whereas birth intervals for both lactating and non-lactating females combined (n=189) averaged 16 months.

Table 2: Comparison of Lion-tailed macaque birth rates in wild and captive populations

WILD		CAPTIVE	
1979 - 80	0.22	1982	0.31
1980 - 81	0.26	1983	0.17
1981 - 82	0.26	1984	0.32
1982 - 83	0.40	1985	0.34
1983- 84	0.34	1986	0.32
5-year mean	0.299		0.295

Age-specific fertility (Mx) for captive lion-tails is presented numerically in the life table (Table 3) and plotted in Figure 3. Above age 18 the fertility rates were highly erratic, which, for females, is due to extremely small sample sizes (0-2) per age class. Although current studbook records list one female who first reproduced at 23 months of age (age class 1 in the life table), this is undoubtedly a reporting error. Excluding this case, the earliest birth of record in the captive population was at 2.8 years, whereas mean age at first birth was 4.9 years (LINDBURG, et al., 1989).

Table 3: Lion-tailed macaque life table: Captive born North American population through 12/31/86

MALES				FEMALES			
AGE	Px	Lx	Mx	AGE	Px	Lx	Mx
0	0.739	1.000	0.000	0	0.819	1.000	0.000
1	0.933	0.739	0.000	1	0.966	0.819	0.005
2	0.956	0.689	0.000	2	0.944	0.791	0.005
3	0.961	0.659	0.016	3	0.978	0.747	0.086
4	0.957	0.633	0.128	4	0.964	0.730	0.186
5	0.962	0.606	0.239	5	0.958	0.704	0.343
6	0.985	0.583	0.252	6	0.984	0.675	0.290
7	0.967	0.574	0.337	7	0.964	0.664	0.385
8	0.961	0.555	0.253	8	0.979	0.640	0.263
9	0.956	0.534	0.384	9	0.976	0.626	0.291
10	0.977	0.510	0.330	10	0.974	0.611	0.371
11	1.000	0.499	0.314	11	1.000	0.595	0.465
12	0.969	0.499	0.321	12	0.965	0.595	0.300
13	0.962	0.483	0.383	13	1.000	0.575	0.447
14	0.949	0.465	0.229	14	0.947	0.575	0.392
15	1.000	0.441	0.408	15	1.000	0.544	0.459
16	1.000	0.441	0.415	16	1.000	0.544	0.323
17	0.753	0.441	0.526	17	1.000	0.544	0.391
18	1.000	0.332	0.532	18	0.875	0.544	0.580
19	1.000	0.332	1.235	19	0.810	0.476	0.127
20	1.000	0.332	0.672	20	1.000	0.386	0.417
21	1.000	0.332	1.653	21	1.000	0.386	0.615
22	1.000	0.332	1.929	22	1.000	0.386	1.115
23	1.000	0.332	1.102	23	0.968	0.386	0.000
24	1.000	0.332	0.964	24	1.000	0.373	0.000
25	1.000	0.332	2.204	25	1.000	0.373	0.000
26	1.000	0.332	1.136	26	1.000	0.373	0.000
27	1.000	0.332	0.000	27	1.000	0.373	0.000
28	0.000	0.332	0.000	28	0.000	0.373	0.000

Since adult ages could not be reliably estimated in the wild, no information on age-specific fertility for this population is available. However, KUMAR (1987) cautiously estimated the age at first reproduction for five young females followed over several years of observation as occurring at a mean age of 6.6 years.

For captive born males, average age at first reproduction has been reported as occurring at 6.6 years (LINDBURG, et al., 1989). Fertility rates beyond age 18 showed considerable fluctuation, as was noted earlier for females. Although the number of births per age class for these older males was slightly higher (2-10) than for females of equivalent age, the results are likely to be biased due to unequal breeding opportunities. Data on age at first reproduction for males in the wild state are as yet unavailable.

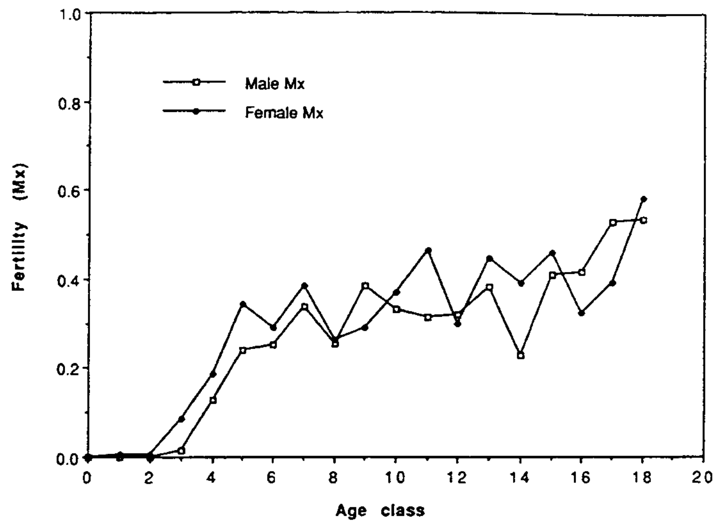

Fig. 3: Age-specific fertility of captive lion-tailed macaques.

Mortality

First year mortality of captive born lion-tails, based on our life table (Table 3) occurred at a rate of 26.1% for males and 19.1% for females. (See also Figure 4 for plotted estimates of age-specific survivorship for both sexes.) A life table by definition excludes unsexed individuals and therefore does not account for approximately 20 infants of unknown sex that were either stillborn or that died shortly after birth. Inclusion of these individuals brings the overall mortality rate during the first year of life to just over 28%, as reported by LINDBURG, et al. (1989).

To these results may be added the finding that captive mortality during the first year of life has declined from 48.6% of births during the early 1960s to 19.5% in the most recent three year period, 1984-86 (Figure 5). Also, captive living adults have shown a survival rate of 98.5% over the last five years of record (1982-86).

For wild troops KUMAR (1987) gave a mean survival rate of 96% for all age classes, drawn from a sample of 319 animal years. Though the exact numbers dying each year could not be distinguished from losses due to emigration, it seems quite certain that overall mortality rates in the wild were low. For example, in the immature age classes (up to 6 years of age) only 6 to 8 individuals disappeared from the 8 troops under surveillance during 6 years of census activity, despite the birth of 43 infants during this same period. The field data, unfortunately, do not permit a comparison of first year mortality rates to those in the captive sector.

Discussion

In the wild state lion-tailed macaques are described by KUMAR (1987) as having a late onset of reproduction, a low birth rate, and high survivorship during infant and adult stages. It is notable that Kumar's conclusions are in general agreement with those of GREEN and MINKOWSKI (1977), who initially characterized wild females as late to mature and as reproducing infrequently. In zoos, on the other hand, females begin reproducing earlier but lose offspring during infancy at a much higher rate than in the wild.

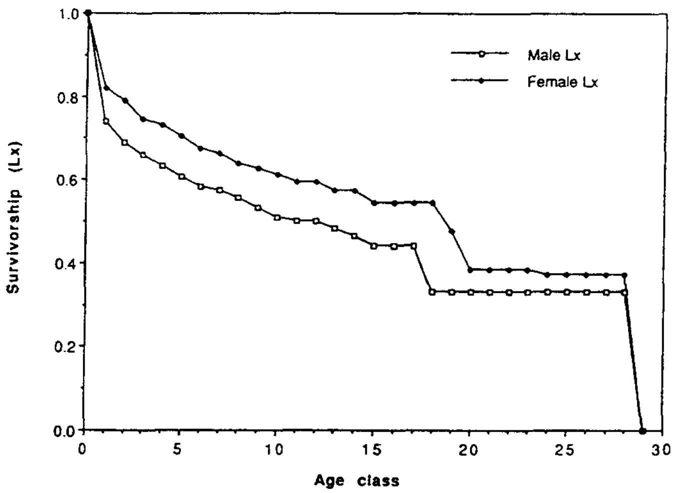

Fig. 4: Age-specific survivorship of captive lion-tailed macaques.

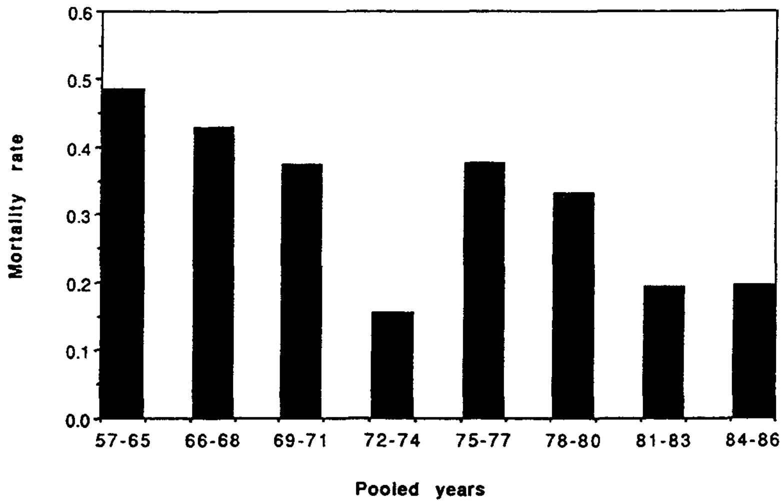

Fig. 5: First year mortality of captive-born lion-tails, 1957-1986.

An advancement in the age of first reproduction has been shown to occur in a number of wild primate populations that are provisioned (LYLES and DOBSON, 1988; LOY, 1988), suggesting a beneficial effect of nutrition on female maturation and reproduction. Since zoos are locales in which "the effects of resource limitation" are minimized (LYLES and DOBSON, 1988), it should not be surprising to find a similar result in our comparison of captive and wild lion-tail populations.

A shortened interval between births, perhaps by as much as 40 to 50%, may be a second effect of improved nutrition in the captive sector. As noted earlier, intervals in the wild are unusually long for macaques--provisionally placed at about 2.5 years but possibly averaging closer to 3.5 years--and are undoubtedly a major reason for its low birth rate. Some of the interval difference is attributable to the different mortality rates for infants in the two populations, but even so intervals of captive females are much shorter than for the wild population when only females whose infants survived to one year of age are considered (LINDBURG et al., 1989).

In other respects the beneficial effects of provisioning, seen to occur in wild primates, are not so evident in the captive lion-tail population. Whereas one of the primary effects of enhanced food resources is to lower mortality rates (LYLES and DOBSON, 1988), even the first year mortality rate of 19% seen in recent years in zoos runs appreciably ahead of mortality rates in the wild. The decline in mortality of the zoo-based population from approximately 50 to 19% (shown in Figure 5) corresponds in time to an era of increased attention to captive breeding, and thus to related improvements in housing and management. This decline offers presumptive evidence of the impact of factors other than nutrition on survivorship in zoos.

An increased birth rate is yet another major effect to emerge from studies of provisioned populations (LYLES and DOBSON, 1988; Loy, 1988). Too little information is available from the wild population to permit valid comparisons of this parameter, but it should be pointed out that over a third of sexually mature females in captivity have not borne offspring (LINDBURG et al., 1989). The birth rate used here (see Table 2) includes 12 females aged 15 or beyond that had never reproduced, and which therefore contributed only zero scores to the 5 year period used for comparison to the wild population. We suspect that neglect of social, environmental, and health requirements have been the more likely causes of reproductive failure in these females. Relatively high female infertility rates may therefore be a major reason for the low captive birth rate and one of the major concerns deserving attention in managing the captive population.

From the foregoing we conclude that the close agreement in birth rates between wild and captive populations is attributable to different factors and is thus in part coincidental. But a real species difference might also be indicated by the fact that a birth rate of 30% for both captive and wild lion-tails is low compared to reports for other macaques, e.g., 49% for *M. sylvanus* (FA, 1986), 80% for Cayo Santiago rhesus (RAWLINS and KESSLER, 1986), and nearly 77% for unprotected rhesus in India (SOUTHWICK et al., 1980). In discussing this point, KUMAR (1987) notes that the birth rate in the wild is lower than would be predicted by allometry and may represent an adaptation of the species to rain forest habitat.

One of the more critical issues for the captive population is the proportion comprised of adult males. It is invariably the case that in wild macaque populations, adult females outnumber males by 2 or 3 to 1 (MELNICK and PEARL, 1987). With proportions of 14% and 39% respectively for males and females, wild lion-tails are no exception to this general finding. As yet no information exists on sex ratios at birth in the wild population, but since these ratios generally approach parity in large macaque breeding colonies (e.g. RAWLINS and KESSLER, 1986; PAUL and KUESTER, 1988) and in wild primates generally (DUNBAR, 1987), we may assume that the adult proportions in the wild are largely attributable to a higher mortality rate for males.

In captivity, also, males experience a higher mortality than females, but much of this difference is in the first year of life. Presumably, since infant mortality is quite low in wild troops, males in that locale continue to undergo heavier mortality after infancy. By contrast, harem grouping in captivity reduces the incidence of conflict among juvenile and reproductive age males, and probably therefore increases the survivorship of these age classes. This situation is further exacerbated by the strongly male-biased sex ratio at birth. Although the higher incidence of male offspring is unexplained, its occurrence in artificially maintained primate populations has been shown by van SCHAIK and van NOORDWIJK (1983) to be common. These authors further suggest that social stress may lead females under these conditions to bias the sex of their offspring in favor of males. While resolution of this question must be left to future studies, it is clear that the male-biased natal sex ratio and relatively protected existence of males in the captive sector continue to produce a substantial population of singly housed males that are often referred to as the "surplus male" problem.

In summary, birth rates in both the captive and wild populations are low by comparison with other macaques and could be an indication of a species difference in reproductive capacity. However, the captive birth rate reflects the inclusion of a substantial number of infertile females, and represents an important focus for further research. Although females in the captive sector begin reproducing at an earlier age than their wild counterparts, the rate at which their infants perish suggests the need for more attention to disease, crowding effects, and socially induced trauma. From a captive management standpoint, one of the more burdensome aspects is the proportion of "surplus" adult males. The solution to this problem is complex, entailing the cost of maintaining unneeded individuals, the need to satisfy the genetic requirements of a small population, and the development of alternatives to housing this surplus in the limited space available in zoos.

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